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Dry grasslands and thorn-cushion communities of Armenia: a first syntaxonomic classification

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Abstract

Aim: To provide the first syntaxonomic, plot-based classification of the dry grasslands and thorn-cushion communities in Armenia. **Study area:** Armenia. **Methods:** We sampled 111 vegetation plots (10 m^2) and recorded environmental and structural parameters. We collected additional 487 relevés from surrounding countries for a broad-scale comparison. We used modified TWINSPAN to derive a syntaxonomic classification system, whose units were then compared among each other regarding species composition, structure, site conditions and distribution. **Results:** The classification of Armenian vegetation plots resulted in a 12-cluster solution. Unsupervised classification of the broad-scale dataset yielded five main groups, which were used for the high-level syntaxonomic assignments of the Armenian data. We assigned about half of the plots of the Armenian dataset to the *Festuco-Brometea*, while the remaining represented a potential new class, preliminarily called "*Ziziphora tenuior-Stipa arabica* grasslands". Most of the syntaxa below class level are new to science, therefore we provide formal descriptions of three orders (*Plantagini atratae-Bromopsietalia variegatae*, *Onobrychido transcaucasicae-Stipetalia pulcherrimae*, *Cousinio brachypterae-Stipetalia arabicae*), four alliances (*Acantholimono caryophyllacei-Stipion holosericeae*, *Artemision fragrantis*, *Onobrychido michauxii-Stipion capillatae*, *Onobrychido transcaucasicae-Stipion pulcherrimae*) and six associations. We found significant differences in the topographic, climatic and soil characteristics, and structural parameters, species life forms and distribution range types between the grassland types at different syntaxonomic levels. The mean species richness was 47.3 (vascular plants: 46.8, bryophytes: 0.4, lichens: 0.1). **Conclusions:** We found remarkable differences of the Armenian dry grasslands from the previously known units and described most of the higher syntaxa and all the associations as new to science. Our study provides arguments for a potential new class of *Ziziphora tenuior-Stipa arabica* grasslands separate both from the Euro-Siberian *Festuco-Brometea* and the Anatolian *Astragalo-Brometea*. Finally, we found plot scale richness of vascular plants clearly above the Palaearctic average of dry grasslands and that of non-vascular plants clearly below, which calls for further biodiversity analyses.

Taxonomic reference: Euro+Med (2023) for vascular plants, Hodgetts et al. (2020) for bryophytes, Nimis et al. (2018) for lichens except for *Xanthoparmelia camtschadalis* (Ach.) Hale.

Abbreviations: EDGG = Eurasian Dry Grassland Group; DCA = detrended correspondence analysis; ICPN = International Code of Phytosociological Nomenclature (Theurillat et al. 2021); TWINSPAN = two-way indicator species analysis.

Keywords

Armenia, classification, dry grassland, *Festuco-Brometea*, Irano-Turanian, mountain steppe, *Onobrychido transcaucasicae-Stipetalia pulcherrimae*, *Plantagini atratae-Bromopsietalia variegatae*, species richness, syntaxonomy, thorn-cushion community, *Cousinio brachypterae-Stipetalia arabicae*

Introduction

Armenia is a land-lock country located in the southern part of the Lesser Caucasus, belonging to two global biodiversity hotspots: the Caucasian and the Irano-Anatolian (Mittermeier et al. 2004). With 3,800 vascular plant species, including 144 country endemics, it has an outstandingly rich vascular plant flora for a territory of less than 30,000 km^2 (Biodiversity and Landscape Conservation Union 2014). The specificity of the vegetation of Armenia is caused by the fact that the country is located on the border between the Euro-Siberian (or Circumboreal) and Irano-Turanian biogeographical regions (Takhtajan 1986; Manafzadeh et al. 2017; Loidi et al. 2022), which are belonging to different subkingdoms: Boreal and Ancient Mediterranean (Takhtajan 1986).

Grasslands and shrublands in the Middle East and the Caucasus areas are of great interest as they host a high biodiversity of species and habitats (Ambarlı et al. 2020), and have been shown to be the area of origin of important elements of Western Asian and European dry grasslands (e.g. *Euphorbia seguieriana*, Frajman et al. 2019; *Euphorbia nicaeensis* group, Stojilkovič et al. 2022). Grasslands are linked to human activities, so can be heavily impacted by changes in land use that are leading to the loss and disturbance of these habitats, with the consequent loss of biodiversity (Török and Dengler 2018). In this area, unregulated (unsustainable) grazing, conversion to cropland, afforestation with non-native tree species, and mining and energy production projects are the major threats (Ambarlı et al. 2020). The knowledge of these habitats in Armenia is crucial for understanding their biodiversity and actual distribution, which will make it possible to establish the necessary management measures for conservation (Ambarlı et al. 2018).

Due to the abovementioned importance of the typology of habitats and vegetation, there is a growing international consensus on the need for coherent vegetation classification systems based on the analysis of vegetation-plot data (De Cáceres et al. 2015). There are different plot-based vegetation classification approaches (De Cáceres et al. 2018), the most important globally being the phytosociological approach (Dengler et al. 2008) and the EcoVeg approach (Faber-Langendoen et al. 2014). The latter, which is applied by the International Vegetation Classification (IVC, Faber-Langendoen et al. 2020) formally incorporates two levels above the class level, which is the highest formal level in the phytosociological approach. The *formation* is based on physiognomic-structural features of the vegetation and thus it is very useful to define biomes. Recently Willner and Faber-Langendoen (2021) made a first attempt to link the European classification system, based on the phytosociological approach (EVC, Mucina et al. 2016), with the International Vegetation Classification.

Up to date, there is no formalised plot-based classification system for Armenia, which was a Soviet Socialist Republic until 1991. As the Braun-Blanquet approach to vegetation classification (Braun-Blanquet 1964; Guarino et al. 2018) developed in Central and Western Europe, it did not play a role in the USSR for political reasons (Masing 1991). Hierarchical classifications based on syntaxa were virtually non-existent in Armenia, at least not for grasslands, as vegetation scientists followed the so-called dominance approach, which categorised vegetation according to dominant and ecologically significant species (Sukachev 1928). This approach does not usually produce complete species lists with abundance data for small sample areas of defined size, i.e. it does not produce relevés or vegetation plots. As a result, the first classification attempt of grassland habitats in Armenia identified three vegetation types (Grossgeim 1928): semi-deserts, mountain-xerophilous vegetation and mountain steppes. Afterwards, different classifications were developed for dry grasslands and steppe vegetation. First, Makagian (1941) defined four types of steppes and steppe-like vegetation (stony semi-deserts, steppes, meadow-steppes and highland xerophytes). Later, Ziroyan (1989) categorised natural dry grasslands in Armenia into five vegetation types related to zonal and altitudinal distribution (deserts, semi-deserts, highland xerophytes, mountain steppes and mountain meadow steppes). Finally, Fayvush (1992) recognised four steppe subtypes (true steppes, thorny-cushion steppes, shrubby steppes and meadow steppes) with 12 classes of formations. The lack of a unified framework of grassland typology impedes acquiring knowledge about their distribution and diversity, which is harmful to their conservation.

Although the phytosociological approach has not been applied to the survey of Armenian grasslands, those of neighbouring countries of the Southern Caucasus have been at least fragmentarily studied in Transcaucasia (Azerbaijan: Peper et al. 2010; Etzold et al. 2016; Jabbarov et al. 2020; Georgia: Pyšek and Šrůtek 1989; Nakhutsrishvili et al. 2022, etc.), Eastern Anatolia in Turkey (Çetik and Tatlı 1975; Tatlı 1991; Gümüs 1992; Gümüs et al. 2003; Hamzaoğlu 2006, etc.) and North Iran (Klein 1982, 1987; Klein and Lacoste 1994; Noroozi et al. 2010, 2014, 2017, etc.).

Many of the data used for these phytosociological surveys are stored in vegetation-plot databases. In the last decades small regional and/or personal databases have been compiled in large vegetation plots databases. The European Vegetation Archive (EVA, Chytrý et al. 2016) was the pioneer, followed by the global vegetation database (sPlot, Bruelheide et al. 2019) and by GrassPlot (Dengler et al. 2018). These databases are the basis for large-scale vegetation classification studies (Novák et al. 2023b; Peterka et al. 2023), but they also permit macroecological studies to great scales leading to a broad understanding of the distribution and diversity patterns (Graco-Roza et al. 2022; Sabatini et al. 2022; Večeřa et al. 2023). Especially for grasslands, the GrassPlot database hosts high-quality data from the Palaearctic realm, sampled on precisely delimited plots, including vascular plants and cryptogam data (Dengler et al. 2018; Biurrun et al. 2019). At the regional scale, the Transcaucasian Vegetation Database, a phytosociological database of the Southern Caucasus, was recently established (Novák et al. 2023a). However, it currently lacks vegetation plots of dry grassland and thorn-cushion communities in Armenia.

It is therefore both an opportunity and a challenge to record vegetation plots and apply the Braun-Blanquet classification approach to Armenia – as its vegetation, to our knowledge, has never been studied according to this approach. Therefore, the Eurasian Dry Grassland Group (EDGG; www.edgg.org) conducted an international research expedition (called "Field Workshop") in Armenia to collect standardised, high-quality vegetation-plot data from dry grasslands and thorn-cushion communities throughout the country. In principle the EDGG Field Workshops aim at collecting such data for regional studies on biodiversity patterns (Kuzemko et al. 2016; Dembicz et al. 2021b; Bergauer et al. 2022) and phytosociology (García-Mijangos et al. 2021; Magnes et al. 2021). Moreover, these data are provided to the GrassPlot database (Dengler et al. 2018) for biodiversity studies across all Palaearctic grasslands and other open habitats (Biurrun et al. 2021; Dembicz et al. 2021a; Zhang et al. 2021) as well as to the European Vegetation Archive (EVA; Chytrý et al. 2016) and the global vegetation-plot database sPlot (Bruelheide et al. 2019) to fill important data gaps in continental and global studies of biodiversity, global change and syntaxonomy.

In this paper, we used the plot data sampled during the Field Workshop to provide the first syntaxonomic classification scheme of the dry grasslands and thorn-cushion communities of the country, using numerical methods of unsupervised classification and determination of diagnostic species. Specifically, we asked:

(1) Which association-rank communities can be distinguished, and to which higher-rank syntaxa do they belong?
(2) How do the syntaxa in Armenia compare to those in the neighbouring countries of Western Asia?
(3) How are the syntaxa in Armenia differentiated from each other in terms of species composition, species richness, structure, site conditions and distribution?

Study area

Physiogeography, climate, soils, geology

Armenia is a South Caucasian republic, bordering Georgia, Azerbaijan, Turkey, and Iran. It is a landlocked country with a total area of 29,740 km^2, at about 145 km from the Black Sea and 175 km from the Caspian Sea. It lies between 38°50' and 41°18' northern latitude and between 43°27' and 46°37' eastern longitude, and measures 400 km along its main axis (north-west to south-east). Armenia is generally a mountainous country, having its lowest point at 375 m a.s.l. and culminating at 4,095 m a.s.l. in the Aragats, with an average elevation of 1,850 m a.s.l.

The location of Armenia at the intersection of two phytogeographical subkingdoms (Boreal and Ancient Mediterranean), together with the diversity in climatic conditions and the active geological processes, have resulted in the formation of diverse ecosystems and high biodiversity with a high level of endemism (Fayvush and Aleksanyan 2016). On the small territory of the country, there are about 3,800 species of vascular plants, 497 species of soil and water algae, 433 species of bryophytes, 4,577 species of non-lichenized fungi, 619 species of lichens, 567 species of vertebrates and about 17,000 species of invertebrates (Fayvush 2023).

A wide range of climatic zones are distinguished within Armenia, which experiences large climatic contrasts because of its intricate terrain and the big climatic gradients (Ministry of Nature Protection of the Republic of Armenia 2015). The basic climate types mainly follow the elevational gradient, from dry subtropical up to severe alpine. The average annual temperature ranges from -8°C in high-altitude mountainous regions (2,500 m a.s.l. and higher) to 12–14°C in low-traced valleys. The overall climate is best characterised as dry continental, in some areas with an annual rhythm like the Mediterranean climate regime. The average annual precipitation in Armenia is 592 mm. The most arid regions are the Ararat valley and the region of Meghri with annual precipitation of 200–250 mm. The highest annual precipitation of 800–1000 mm is observed in high-altitude mountain regions.

From the orographical and physico-geographical points of view, Armenia forms the northern edge of the system of folded-block mountains of the Armenian Highland. Unlike the Greater Caucasus, Armenia and the Lesser Caucasus are not a single, distinct watershed ridge. It is a system of coulisse-spaced ridges that merge with the mountain formations of the inner parts of the Armenian Highland and adjacent high areas (Aslanyan 1958, 1985). Four main geomorphological regions can be recognized within Armenia. (1) Mountain ridges and valleys in the north-east of the country which bear witness of extensive erosion. (2) Areas covered by lava of relatively recent (upper Pliocene) origin within Asia Minor are characterised by gentle slopes with little evidence of erosion but, in which larger rivers have carved out deep gorges and canyons. (3) A series of ridged mountains in the south of Armenia, which constitute the Lesser Caucasus system and show intense erosion. (4) The Ararat Valley represents the lowest part of the Ararat depression covered with alluvial and proluvial sediments (Aslanyan 1958; Gabrielyan 1962; Dumitrashko 1979).

In our study we tried to cover as much of the country's dry grassland diversity as possible within 11 days, with a focus on the northwestern and central parts (Figure 1). In total, we sampled in five of the 11 administrative provinces of the country (Aragatsotn, Ararat, Gegharkunik, Shirak, Vayots Dzor) and seven of the 12 floristic regions. We covered an elevational gradient from 1,338 to 2,350 m a.s.l.

National typologies of Armenian dry grasslands

So far, the syntaxonomy of grassland or thorn-cushion vegetation of Armenia hasn't been developed yet. The only existing vegetation typologies are based on the dominance approach. The first overview of the Armenian vegetation types was performed by Grossgeim (1928). He distinguished eight main types of vegetation: (1) aquatic and bog vegetation; (2) forest vegetation; (3) semi-deserts; (4) mountain-xerophilous vegetation (mountain semi-desert); (5) mountain steppes; (6) meadow-like vegetation; (7) solonetzs and solonchaks; (8) weeds. In the semi-desert type, he selected three subtypes: (a) alkaline-loamy semi-desert on the alluvium of the Aras River; (b) wormwood semi-desert on eruptive rocks; (c) sandy semi-desert.

Takhtajan (1941) explored the phytogeographic patterns of Armenia, including the division of the region into phytogeographic provinces and districts, the historical

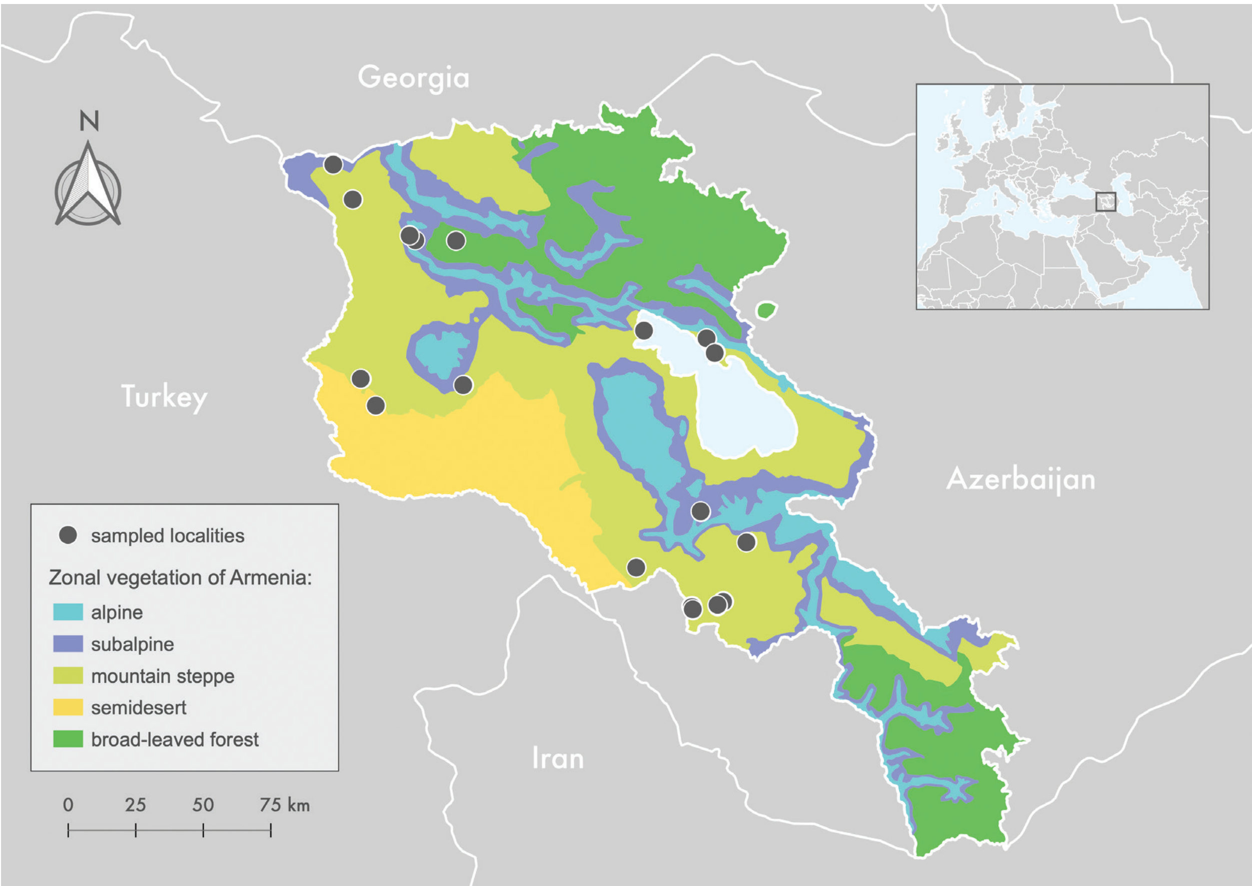

Figure 1. Map of Armenia indicating zonal vegetation types based on Grossgeim (1928). Black dots indicate the sampling localities. The light blue area refers to the Lake Sevan.

development of its vegetation, and the classification of vegetation into broad types. Among these types, subalpine vegetation, mountain-steppes, xerophilous vegetation of skeleton mountains, and wormwood semi-deserts could be considered as the scope of our study.

Makagian (1941) developed the vegetation typology of Armenia in more detail. The steppe and steppe-like vegetation included in his scheme was classified as:

- Stony semi-deserts (wormwood semi-desert, wormwood-ephemeral semi-desert, wormwood semi-desert with perennial grasses, etc.)
- Steppes (grass-forb and dry forb-grass steppe, feather-grass steppe, beardgrass steppe, fescue and fescue-junegrass steppe, mixed-grass steppe, forb and legume steppe)
- Meadow-steppes (grass meadow-steppe, forb and forb-grass meadow-steppe, legume meadow-steppe, dwarf-sedge meadow-steppe)
- Highland xerophytic vegetation (Minor-Asian thorn-cushion shrubs of *Astracantha*, *Acantholimon* etc., xeromorphic vegetation of screes and rocks)

Afterwards, the classification of natural grasslands of Armenia was done by Ziroyan (1989) on the principles of the dominant approach. The author distinguished five vegetation types of desert and steppe vegetation which have strong zonal character and mainly are characteristic to a particular altitudinal belt: **deserts** (two classes of formations, 16 formations) in the lowest elevations up to 1,000 m a.s.l.; **semi-deserts** (two classes of formations, 12 formations) at the elevations 1,000–1,300 m a.s.l.; **highland xerophytic vegetation** (one class of formations, 12 formations), 1,200–1,600 m a.s.l.; **mountain steppes** (two classes of formations, 12 formations), 1,600–2,000 m a.s.l.; **mountain meadow steppes** (two classes of formations, 12 formations), 2,000–2,400 (occasionally up to 2,800) m a.s.l.

Fayvush (1992) presents a detailed classification of the types of mountain steppes of Armenia based on the dominance approach. The author distinguishes four subtypes (true steppe, thorny-cushion steppe, shrubby steppe and meadow steppe) and 12 classes of formations within it.

Overview on the described syntaxa from the surrounding countries

In the Transcaucasus region, the first work with a description of syntaxa following the Braun-Blanquet approach was done by M. Guinochet in Azerbaijan and Georgia. Guinochet (1984) described two associations of steppe-like communities without an assignment to higher syntaxonomic units. The association *Ziziphoro serpyllaceae-Scutellarietum orientalis* Guinochet 1984 is characterized by the presence of many therophytes and is described from the lower elevations in Azerbaijan. Guinochet concludes that this vegetation type could be like the class *Thero-Brachypodietea* and emphasizes that a unique class and order should be described to include this association. The other association is described from higher elevations in the Pirqulu State Reserve (Azerbaijan), from the subalpine belt: *Onobrychieto cyri-Festucetum sulcatae* Guinochet 1984 nom. inval. (Article 2b ICPN, Theurillat et al. 2021). This association comprises mountain steppes and is similar, according to M. Guinochet, to the concept of the subalpine steppe of Gadzhiev (1962) from the national typology of Azerbaijan. Additionally, Guinochet (1984) described in Georgia another association from the alpine belt not belonging to the steppic vegetation and assigned to the class *Carici rupestris-Kobresietea bellardii*: *Alchemillo caucasicae-Festucetum supinae*, together with the new order *Campanulo-tridentatae-Caricetalia tristis* and the new alliance *Alchemillo-Festucion supinae*, all three being invalidly published due to insufficient original diagnosis (Article 2b ICPN, Theurillat et al. 2021). Lately, there was an attempt to classify the phryganoid vegetation of the Nakhchivan region of Azerbaijan (Jabbarov et al. 2020). The authors outlined several association-level units without a formal description ("*Thymeto-Acantholimonetum bracteatae*", "*Thymeto-Onobrychetum cornutae*"), and assigned them to the order *Astragalo-Brometalia* Quézel 1973 and the class *Astragalo-Brometea* Quézel 1973. Recently, a new study on the syntaxonomy of alpine and subalpine grasslands has been conducted in Georgia (Nakhutsrishvili et al. 2022). The authors proposed a new class *Bromopsio variegatae-Festucetea ovinae* to unite subalpine meso-xeric and mesic grasslands, including one new order, three alliances and seven associations. None of the suggested units were published validly due to insufficient original diagnoses.

For the Northern Caucasus, Tsepkova (1987) proposed a new class of high-mountain arid grasslands with the provisional name *Bothryochloo-Salvietea*, which according to Vynokurov et al. (2021) is a syntaxonomic synonym of the *Festuco-Brometea*. Other steppic grasslands of the Northern Caucasus have been traditionally assigned to the class *Festuco-Brometea* (Tsepkova 2005; Demina et al. 2017; Vynokurov et al. 2021).

In Turkey, several high-level syntaxonomic units have been established for dry grasslands and thorn-cushion vegetation. Zohary (1973) united semi-desert and wormwood steppe grasslands into the class "*Artemisietea fragrantis anatolica*" Zohary 1973 nom. inv. (Art. 2b ICPN), and proposed the class "*Astragaletea armeno-turcica*" Zohary 1973 nom. inv. (Art. 2b ICPN) for subalpine tragacanthic vegetation in this region. Simultaneously, Quézel (1973) described another unit for hedgehog plant communities in the subalpine zone of the Taurus Mountains in Turkey, occurring at elevations 2000–2500 m a.s.l., beyond the tree line – *Astragalo-Brometea* Quézel 1973. In the same publication, Quézel (1973) also published another class of xero-mesophytic and mesophytic subalpine grasslands, occupying higher altitudes than tragacanth vegetation communities: *Trifolio anatolici-Polygonetea arenastri* Quézel 1973. In the eastern part of Turkey, in Eastern Anatolia, there were some syntaxonomic investigations of steppe vegetation (Çetik and Tatlı 1975; Tatlı 1991; Ocakverdi 1992; Hamzaoğlu 2006; Öztürk et al. 2015). Ocakverdi (1992) surveyed the vegetation (including steppe vegetation) in the region of Turkey bordering with Armenia. He distinguished two physiognomic types of steppe vegetation (grass steppe and tragacanth steppe) and three altitudinal variants: "plain" steppe (1,675–1,725 m a.s.l., mainly grass steppe vegetation), lower mountain steppe (1,750–1,850 m a.s.l., both grass steppe and tragacanth steppe) and high-mountain steppe (1,950–2,696 m a.s.l., grass steppe). He proposed four associations, none of them published validly (Art. 1 ICPN). Later, Ocakverdi et al. (2009) described 10 new associations from the same region (Kısır Mountain). Hamzaoğlu (2006) studied steppe communities of East Anatolia. He united the studied vegetation to a new order *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu 2006, subordinated to the class *Astragalo-Brometea* Quézel 1973.

In another bordering region, Iran, xerophilous grassland and scrub communities were first delineated by Zohary (1973), who proposed several vegetation classes: "*Artemisietea fragrantis anatolica*" Zohary 1973 nom. inv. (Art. 2b ICPN) for wormwood steppe grasslands in Northwestern Iran and Anatolia, "*Artemisietea herbae-albae iranica*" Zohary 1973 nom. inv. (Art. 2b ICPN) grouping wormwood semideserts in the Central Plateu of Iran, and "*Astragaletea iranica*" Zohary 1973 nom. inv. (Art. 2b ICPN) for tragacanth communities in Iran and Iraq. Later, the vegetation of the subalpine and alpine belts of the Alborz Mountains have been studied by Klein (1982, 1987). He described several new classes: *Onobrychidetea cornutae* Klein 1987 nom. inval. (Art. 2b ICPN) from the lower alpine belt of Alborz (3,200–3,500 m a.s.l.) and *Prangetea ulopterae* Klein 1987 nom. inval. (Art. 2b ICPN) from the subalpine belt of Alborz (2,500–3,200 m a.s.l.), aimed to unite high-mountain hedgehog communities and xeric tall-herb vegetation respectively. Also, from the subalpine belt of the northern macroslope of Alborz Mountains, Klein and Lacoste (1994) described one association subordinated to the *Festuco-Brometea*, *Alchemilletum plicatissimae* Klein et Lacoste 1994, but did not assign it to an alliance or order.

In general, the class *Astragalo-Brometea* is the most widely used name to unite the dry grasslands and thorn-cushion vegetation in the western part of the Irano-Turanian region. However, its conceptual boundaries have undergone significant changes over time, both geographically and physiognomically. Many researchers now extend its scope to include tragacanth vegetation not only from the subalpine belt but also from the lower elevations, as well as chamaephyte-dominated phryganoid vegetation, non-tragacanth dry grasslands at lower elevations, saline steppes, and gypsophilous rocky grasslands (Ketenoğlu et al. 1983; Akman et al. 1984; Aydoğdu et al. 1994; Aydoğdu et a. 2004; Hamzaoğlu et al. 2004; Kaya 2011). Additionally, xero-mesophytic and mesophytic grasslands at higher elevations, which were classified by Quézel (1973) as a separate class *Trifolio-Polygonetea*, are sometimes included within the *Astragalo-Brometea* (Eren et al. 2004; Parolly 2004). Some authors have proposed extending the concept of the class also to the northern part of Iran, synonymizing the *Onobrychidetea cornutae* and *Prangetea ulopterae* described there (Parolly 2004). Recently, the dry feather-grass steppes of Tajikistan also were provisionally included into the *Astragalo-Brometea* (Nowak et al. 2016, 2018).

Methods

Field sampling in Armenia

We sampled 111 plots of 10 m^2- size (Suppl. materials 1, 2) during the 13th Field Workshop of the Eurasian Dry Grassland Group (EDGG) in Armenia, from 26 June to 6 July 2019 (Aleksanyan et al. 2020; for distribution of sites, see Figure 1). Within each plot, we recorded vascular plants and terricolous bryophytes and lichens with the shoot presence method (Dengler 2008). Besides, we estimated their percentage cover on a continuous scale (for discussion of advantages of this method compared to ordinal scales, see Dengler and Dembicz 2023). Specimens that could not be determined in the field were dried and taken to the lab for further determination.

Other environmental and structural parameters that were recorded *in situ* following the EDGG sampling methodology (Dengler et al. 2016), included: geographical position (latitude, longitude), elevation (m), slope aspect (°), slope inclination (°), maximum microrelief (cm), soil depth (cm, mean and SD of five measurements per plot), vegetation covers (%; total vegetation, shrub layer, herb layer, cryptogam layer), cover of litter (%), covers of stones and rocks, gravel, and fine soil (all three fractions summing up to 100%), maximum height of shrubs (m), maximum height of herbs (cm), height of herb layer (cm, mean and SD of five measurements with a falling disc per plot), and land use details (grazing, mowing, burning, abandonment).

Soil was collected as mixed samples from the uppermost 15 cm of the soil in five random points inside each plot. After air drying and sieving to the fine-soil fraction, the following parameters were measured in the lab: pH (in H_2O), electrical conductivity (μS cm^{-1}), organic C content (%), humus content (%), N content (%), and C/N ratio. Southing was calculated from aspect as -cos (aspect).

The nomenclature of vascular plants was standardised to Euro+Med (2023) for vascular plants, Hodgetts et al. (2020) for bryophytes, Nimis et al. (2018) for lichens. For some groups of closely related species that could not always be distinguished, we defined additional species aggregates ("aggr."; see Suppl. material 3). The value distribution of all recorded and analysed numerical environmental, structural and biodiversity variables is given in Suppl. material 4. The complete data are stored in and available from the GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot) as dataset "AM_B".

Data from external sources

Plot data from the surrounding countries

To be able to identify the high-level syntaxonomic units, we digitised from literature and used for comparison relevés from the bordering regions, focusing on the original diagnosis of the high-level units of similar vegetation types: 230 plots from Anatolia (Turkey) and 51 plots from Northern Iran. Among them, the original diagnosis of the class *Astragalo-Brometea* Quézel 1973 with the type order *Astragalo-Brometalia* Quézel 1973 and the other orders *Drabo-Androsacetalia* Quézel 1973, *Hyperico linarioidis-Thymetalia scorpilii* Akman et al. 1987, *Onobrychido armenae-Thymetalia leucostomi* Akman et al. 1985, *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu 2006, and other lower rank units (Quézel 1973; Akman et al. 1984, 1987; Gümüs 1992; Klein and Lacoste 1994; Hamzaoğlu 2006; Ocakverdi et al. 2009). Also, 206 plots from Northern Caucasus (Russia) were taken from the Eastern European Steppe Database (Vynokurov et al. 2020). Combined with our own plots from Armenia, a dataset of 598 relevés resulted (Suppl. material 5). After the unification of the species taxonomy, removing the taxa determined to the genus level, and combining the aggregates, the final dataset contained 1,556 taxa.

Environmental data from external sources

Climatic data were extracted from the CHELSA Climate database (Karger et al. 2017, 2018). We used the following variables: BIO01 – mean annual air temperature, BIO07 – annual range of air temperature, BIO12 – annual precipitation amount, BIO17 – mean monthly precipitation amount of the driest quarter.

Maps were created using QGIS software (QGIS Development Team 2009). As basemaps, we used the map of main vegetation types of Armenia by Grossgeim (1928), and the SRTM (Shuttle Radar Topography Mission) elevation model for Armenia (EROS Center 2017).

Attributes for the Armenian species

In order to assess the distribution ranges of species, we analysed their distribution maps (according to GBIF 2023 and POWO 2023) and classified their distribution ranges into the following broad categories: European (occurring mainly in the temperate regions of Europe and Western Siberia), Mediterranean (covering the southern part of Europe in areas with Mediterranean climate), Irano-Turanian (occurring in Western and Central Asia), Transcaucasian (narrow endemics of Armenia and surrounding regions of Transcaucasia), Caucasian (broader endemics of the whole Caucasus Range, including the Northern Caucasus and adjacent parts of Eastern Anatolia in Turkey and North-Western Iran). If the species occurred predominantly in one of the mentioned regions, we assigned a value of one (1) to the corresponding category. In case that the species occurred in two regions simultaneously (European and Irano-Turanian, European and Mediterranean, or Mediterranean and Irano-Turanian), we assigned a value of 0.5 to the corresponding categories. If the species distribution covered three regions (European, Mediterranean and Irano-Turanian), we assigned a value '0.3' to each of these categories. In all other cases, when the species distribution area was greater than the mentioned categories (e.g., Palaearctic, Holarctic, etc.), we classified these species into the category 'Other'. The assigned distribution ranges of species are available in Suppl. material 6.

In addition, we classified all the species into one of the Raunkiær plant life forms: therophytes, geophytes, hemicryptophytes, chamaephytes, and phanerophytes. The data are also available in the Suppl. material 6.

Statistical analysis

Unsupervised classification

Unsupervised classification for both the West Asian and Armenian dataset was done in JUICE 7.0 (Tichý 2002) using the modified TWINSPAN method (Roleček et al. 2009) with three pseudospecies cut levels (0, 5, and 15), and Whittaker's beta-diversity index as a measure of internal cluster heterogeneity. Diagnostic species were determined based on phi values (Chytrý et al. 2002), standardised to equal plot numbers at association level (Tichý and Chytrý 2006). This was done hierarchically at the four syntaxonomic levels from association to class (García-Mijangos et al. 2021). Since this approach is not implemented in JUICE (Tichý 2002) yet, we had to do it in Microsoft Excel, which precluded the use of Fisher's exact test for significance. To avoid selecting non-significant diagnostic species, we put the thresholds for phi values rather high. For associations and alliances, we used > 0.4 for diagnostic species and > 0.6 for highly diagnostic species, while for orders and classes the thresholds were > 0.3 and > 0.5, respectively. Moreover, we also ensured that the phi values were at least 0.2 higher in the target syntaxon than the syntaxon of the same rank with the next-lower phi value (see García-Mijangos et al. 2021). If a species fulfilled the criteria to be diagnostic at several hierarchical levels, it was assigned to the level with the highest phi value. In case of monotypic syntaxa, diagnostic species were only assessed at the higher level.

Ordination

DCA-Ordination was performed with Canoco 5 (ter Braak and Šmilauer 2012) with log-transformed percent cover values of species and downweighting rare species and post hoc fitted variables (environmental, calculated or measured).

Comparison of syntaxon characteristics

Differences in variables between syntaxa were tested by univariate ANOVA using SPSS 22 (IBM, Armonk, NY, US). We tested whether the assumptions of ANOVA (normal distribution, equal variance) were sufficiently met by visually inspecting the frequency distribution of the residuals and by testing for homogeneity of variance according to Levene (Quinn and Keough 2002). Where ANOVA revealed a significant pattern, Tukey's post-hoc test at $p < 0.05$ was used to identify homogeneous groups of syntaxa. Results were presented as box-whisker plots with median and mean, and $25^{th}/75^{th}$ (boxes) and $10^{th}/90^{th}$ (whiskers) percentiles as well as outliers.

Syntaxonomic assignment

We selected a TWINSPAN resolution where the terminal clusters were floristically still well-characterised and not too small. These clusters were then assigned to the rank of association. Alliance, order and class levels were assigned to higher cut levels of the dendrogram, with the double aim to have floristically well differentiated and ecologically and chorologically interpretable units on a comparable level as these hierarchies have in Mucina et al. (2016).

After defining the hierarchical units, we carefully checked the syntaxonomic literature of the neighbouring countries to determine whether syntaxa with this content already existed. If this was the case, we took the established name. If not, we formally described new syntaxa according to the ICPN (Theurillat et al. 2021). Following Recommendation 7A of the ICPN, we refrained from establishing new associations when we had fewer than 10 relevés and instead treated the respective cluster as an informal community at association rank. Likewise, we refrained from a formal description of the new class that was supported by our analyses, suggesting that this should first be "validated" in a broader-scale analysis involving the neighbouring countries of Armenia.

Results

Unsupervised classification and ordination of the West Asian and Caucasian dataset

Modified TWINSPAN resulted into 16 clusters with five main groups of clusters: A (clusters 1–3), B (4–6), C (7), D (8–10) and E (11–16) (Figure 2). The synoptic table built with these five main groups is shown in Suppl. material 7.

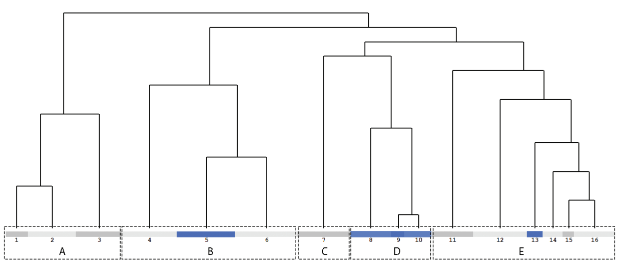

Figure 2. Results of the Modified TWINSPAN classification for the broad-scale comparison involving plots from the bordering countries (n = 598). The width of the bars is proportional to the number of included plots. The main groups (letters) and terminal clusters (numbers) are described in the text. Blue colour indicates clusters that predominantly or completely consisted of Armenian plots.

The group A (clusters 1–3) completely consisted of the relevés originally assigned to the class *Astragalo-Brometea*, including the type order *Astragalo-Brometalia* Quézel 1973 (in the cluster 2), described from the Taurus Mountains in South-Western Turkey (Quézel 1973). The plots assigned to the other orders of this class with their corresponding types were also included in this group of clusters: *Drabo-Androsacetalia* Quézel 1973 (cluster 2) from the same Taurus Mountain range; *Hyperico linarioidis-Thymetalia scorpilii* Akman et al. 1987 (cluster 1) from the Ilgaz Mountains in North-Western Turkey; *Onobrychido armenae-Thymetalia leucostomi* Akman et al. 1985 (cluster 3) described from Central Anatolia. Plots from Armenia did not fit into this group.

The second group B (clusters 4–6) comprised plots from the high-mountain steppe vegetation. Cluster 4 consisted mainly of relevés from the northern slope of the Alborz Mountains in Iran, assigned to the association *Alchemilletum plicatissimae* Klein et Lacoste 1994. Plots from the Northern Caucasus region assigned to the alliance *Artemisio chamaemelifoliae-Bromopsion variegatae* Vynokurov in Vynokurov et al. 2021 were classified into cluster 5, together with some plots from Armenia. Cluster 6 comprised plots sampled near the Kısır Mountain in Turkey, in Eastern Anatolia. They were originally assigned to several associations of the class *Astragalo-Brometea* but without placement in alliances and orders (Ocakverdi et al. 2009).

Thorn-cushion communities from Eastern Anatolia are combined in the group C (cluster 7). They were originally assigned to the order *Festuco oreophilae-Veronicetalia orientalis* Hamzaoğlu 2006 of the class *Astragalo-Brometea*, together with its type alliance *Festuco oreophilae-Veronicion orientalis* Hamzaoğlu 2006 and the respective association *Astragalo-Onobrychidetum cornutae* Gümüs 1992. Even though this cluster was not placed in the corresponding group A in the dendrogram (Figure 2), they seem closely related according to the ordination (Figure 3).

Clusters 8–10 formed group D. It consisted exclusively of plots from Armenia. Among them, cluster 8 contained the most xeric communities sampled in the driest parts of Armenia, followed by cluster 10. Cluster 9 was transitional between the groups D and E.

The group E (clusters 11–16) was formed by plots containing the more 'typical' *Festuco-Brometea* species, mostly from the region of the Northern Caucasus. Cluster 11 was comprised mainly of rocky grasslands belonging to the order *Asphodelino tauricae-Euphorbietalia petrophilae* Vynokurov in Vynokurov et al. 2021; cluster 12 contained grass steppes mostly of the *Festucetalia valesiacae*. Cluster 13 combined mountain steppes exclusively from Armenia. Clusters 14–16 comprised mostly meso-xeric communities of the order *Brachypodietalia pinnati* from the Northern Caucasus. A synoptic table with the five distinguished groups of clusters (A–E) is provided in Suppl. material 7.

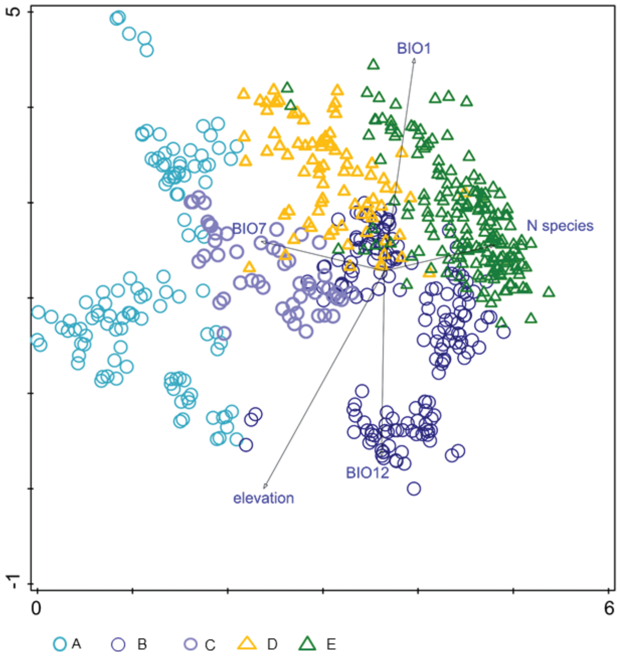

Figure 3. DCA of the West Asian dataset (DCA with supplementary variables, eigenvalues/gradient lengths/cumulative explained variation of axis 1: 0.6313/5,37/4.02, axis 2: 0.4207/4.94/6.69). Vectors (environmental variables): BIO1: annual mean temperature; BIO7: temperature annual range; BIO12: annual precipitation; elevation: elevation (m a.s.l.); N species: vascular plant richness.

General overview of the Armenian plots

In our 111 plots of 10 m^2, we recorded a total of 739 vascular plant, 40 bryophyte and 13 lichen taxa (subspecies, species, aggregates and sections, further as 'species'). The species richness per plot ranged from 21 to 85, with a mean of 47.3. On average there were 46.8 vascular plant, 0.4 bryophyte and 0.1 lichen species per plot. The most frequent vascular plant was *Galium verum* (in 72% of all plots), followed by *Thymus kotschyanus* (59%), *Teucrium capitatum* (58%), *Poa bulbosa* (55%), *Dactylis glomerata* (54%), *Scutellaria orientalis* aggr. (53%), *Koeleria macrantha* (51%), *Stachys recta* (50%) and *Potentilla recta* aggr. (50%). The most frequent bryophytes were *Syntrichia ruralis* (27%), *Ptychostomum imbricatulum* (19%) and *Syntrichia montana* (14%). Lichens were absent in most plots, with the most frequent one (*Cladonia foliacea*) reaching just 4%.

Classification of the Armenian dataset

The most meaningful modified TWINSPAN classification of the plots from Armenia resulted in the 12-cluster solution (Figure 4). The first cluster (X) had only a single relevé of scree vegetation recorded in the Vayots Dzor Province near Hermon. The rest of the clusters are interpreted at the community or association level. Clusters 1.1.1.1–1.1.3.2 consisted of the most xeric plots of the semi-desert, rocky and thorn-cushion vegetation in the lower elevations. Clusters 2.1.1.1 and 2.1.1.2 represent plots of mountain meadow steppes from the highest elevations. Clusters 2.2.1.1–2.2.1.4 consisted of plots of thorn-cushion and steppic grasslands of so-called mountain steppes.

Ordination of the Armenian dataset

Ordination of the plots with the assignment to one of these clusters revealed that the first axis of the DCA graph (Figure 5) corresponds to a gradient of moisture and temperature connected with the elevation range. The most mesic plots occupied higher altitudes (cluster 2.1.1.1), while the most xeric ones were distributed in the lower elevations (clusters 1.1.2.1–1.1.3.2). The climatic-elevation gradient and community parameters correlated with the differentiation of two higher classification units – *Ziziphora tenuior-Stipa arabica* grasslands and the class *Festuco-Brometea*.

Syntaxonomic scheme

Resulting from our analyses of the Armenian data and the comparison with the syntaxa of neighbouring territories, we propose the following syntaxonomic scheme

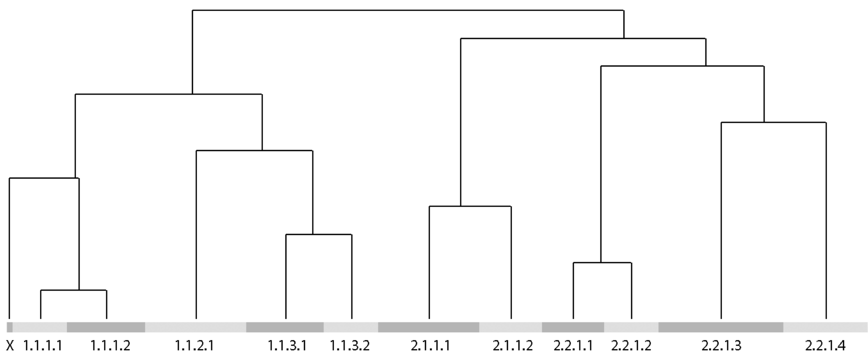

Figure 4. Results of the Modified TWINSPAN classification of the Armenian plots (n = 111). The terminal clusters were interpreted as associations or, if represented by too few plots, as informal communities at association rank. The first cluster (X) consisted only of one plot of scree vegetation. Codes at the tips of the other clusters correspond to Table 1.

for the dry grassland and thorn-cushion communities of Armenia, including a single plot with an unclear assignment (Table 1). According to our literature overview and the analysis of the West Asian and Caucasian dataset, we concluded that most of the syntaxa found are new to science. The formal descriptions of the new syntaxa ("Vynokurov et al. 2024") are provided in Appendix 1.

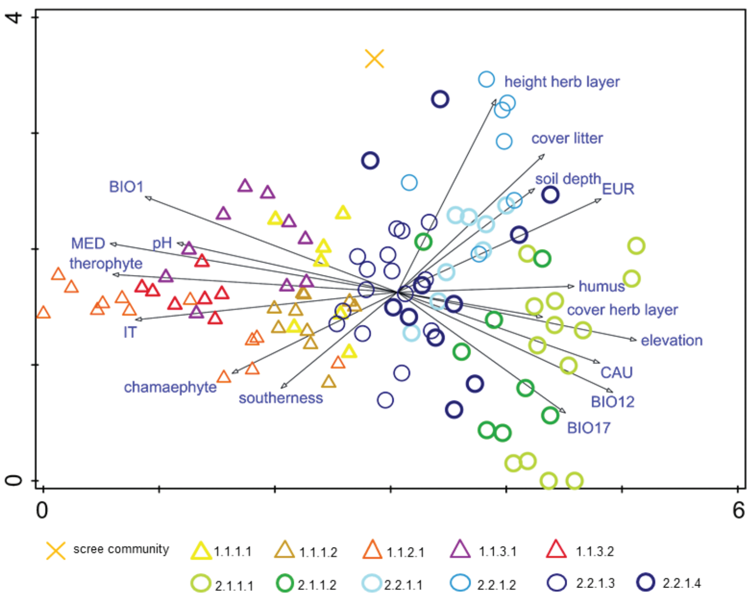

Figure 5. DCA ordination of the 111 Armenian plots with assignment to the 12 distinguished units at association level (DCA with supplementary variables, eigenvalues/gradient lengths/cumulative explained variation of axis 1: 0.5825/5.12/5.76, axis 2: 0.3160/3.64/8.89). Triangles indicate members of the class *Ziziphora tenuior-Stipa arabica* grasslands, circles members of the class *Festuco-Brometea*. Vectors: BIO1: annual mean temperature; BIO12: annual precipitation; BIO17: precipitation of driest quarter; CAU: cover of Caucasian species in %; chamaephytes: cover of chamaephytes in %; cover herb layer: cover of the herb layer in %; cover litter: cover of the litter; elevation: elevation in m a.s.l.; EUR: cover of European species in %; height herb layer: height of the herb layer; humus: soil humus content in %; IT: cover of Irano-Turanian species in %; MED: cover of Mediterranean species in %; pH: pH values of the plot soil samples; soil depth: mean soil depth of plot; southerness: -cos (aspect); therophyte: cover of therophytes in %.

Table 1. Syntaxonomic scheme for the dry grasslands and thorn-cushion communities of Armenia based on the 111 plots analysed in this paper.

Unclear class (scree communities)
Euphorbia orientalis-Melilotus officinalis community
Potential class 1 *Ziziphora tenuior-Stipa arabica* grasslands
Order 1.1 *Cousinio brachypterae-Stipetalia arabicae* Vynokurov et al. 2024
Alliance 1.1.1 *Onobrychido michauxii-Stipion capillatae* Vynokurov et al. 2024
1.1.1.1 *Stachys lavandulifolia-Astracantha condensata* community
1.1.1.2 *Marrubio parviflorae-Stipetum capillatae* Vynokurov et al. 2024
Alliance 1.1.2 *Artemision fragrantis* Vynokurov et al. 2024
1.1.2.1 *Noaeo mucronatae-Artemisietum fragrantis* Vynokurov et al. 2024
Alliance 1.1.3 *Acantholimono caryophyllacei-Stipion holosericeae* Vynokurov et al. 2024
1.1.3.1 *Acantholimono caryophyllacei-Stipetum holosericeae* Vynokurov et al. 2024
1.1.3.2 *Stachys inflata-Acantholimon vedicum* community
Class 2. *Festuco-Brometea* Br.-Bl. et Tx. ex Soó 1947
Order 2.1 *Plantagini atratae-Bromopsietalia variegatae* Vynokurov et al. 2024
Alliance 2.1.1 *Artemisio chamaemelifoliae-Bromopsion variegatae* Vynokurov in Vynokurov et al. 2021
2.1.1.1 *Ranunculo caucasici-Bromopsietum variegatae* Vynokurov et al. 2024
2.1.1.2 *Tragopogon reticulatus-Astracantha aurea* community
Order 2.2 *Onobrychido transcaucasicae-Stipetalia pulcherrimae* Vynokurov et al. 2024
Alliance 2.2.1. *Onobrychido transcaucasicae-Stipion pulcherrimae* Vynokurov et al. 2024
2.2.1.1 *Trisetum flavescens-Stachys macrostachys* community
2.2.1.2 *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community
2.2.1.3 *Globulario trichosanthae-Stipetum pulcherrimae* Vynokurov et al. 2024
2.2.1.4 *Seslerio phleoidis-Onobrychidetum cornutae* Vynokurov et al. 2024

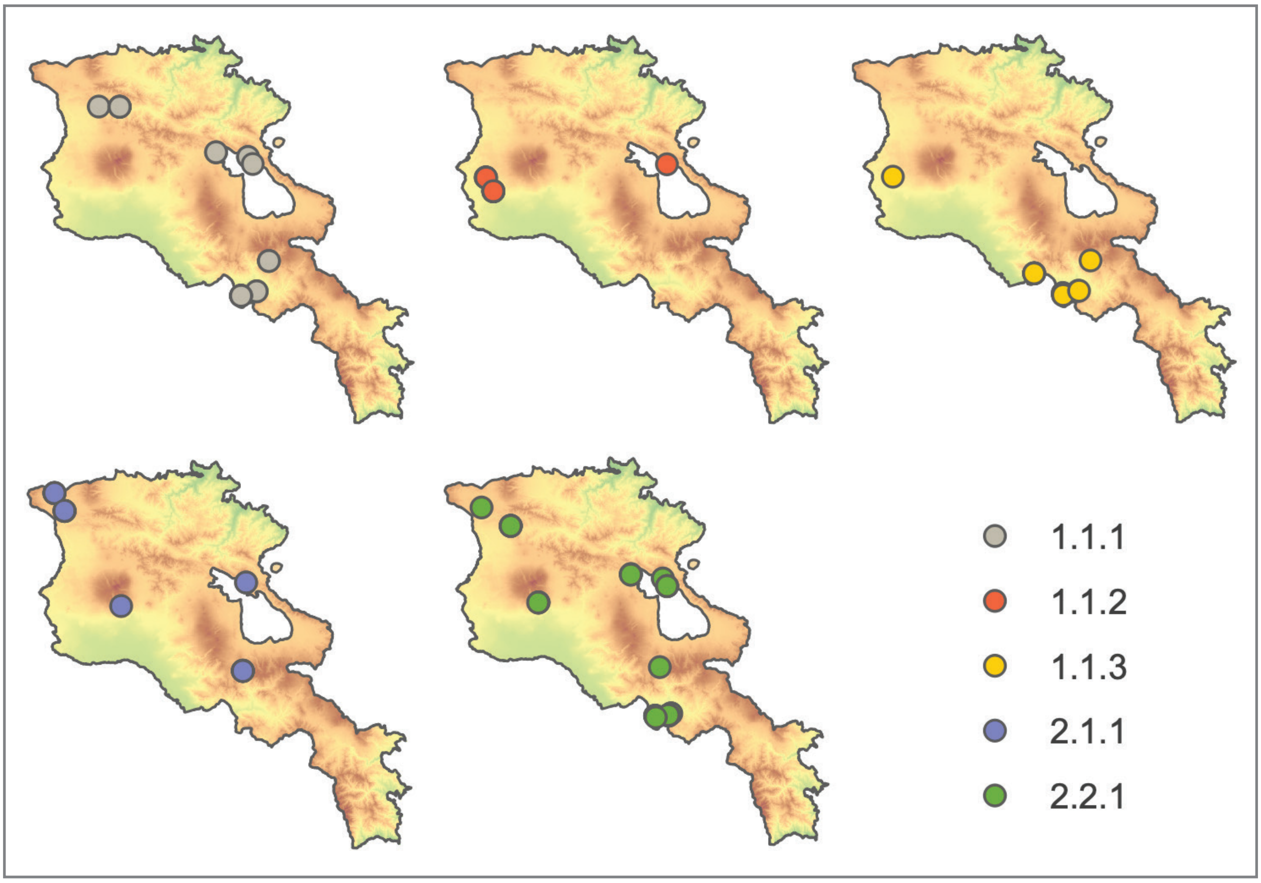

Figure 6. Distribution of five described vegetation alliances in Armenia based on sampled vegetation plots (*n* = 110). 1.1.1 – *Onobrychido michauxii-Stipion capillatae*, 1.1.2 – *Artemision fragrantis*, 1.1.3 – *Acantholimono caryophyllacei–Stipion holosericeae*, 2.1.1 – *Artemisio chamaemelifoliae–Bromopsion variegatae*, 2.2.1 – *Onobrychido transcaucasicae-Stipion pulcherrimae*. Basemap: SRTM elevation model for Armenia (obtained from Earth Resources Observation and Science (EROS) Center 2017).

Description of the syntaxa

The proposed classification of the Armenian dry grassland and thorn-cushion communities is shown in the synoptic table (abbreviated version: Table 2; full version: Suppl. material 2). The distribution of the alliances is shown in Figure 6, typical stands of the association-level units are visualised in two photo plates (Figures 7, 8), while the site conditions, structure and species richness of the syntaxa of the four hierarchical levels are compared in Figures 9–13. In the following, we provide brief descriptions of the diagnostic species and information on ecology and distribution for all syntaxonomic levels and additionally on the community structure for the association-level units. The diagnostic species are listed alphabetically, with the highly diagnostic ones highlighted in bold and bryophytes and lichens marked with B and L, respectively.

***Euphorbia orientalis-Melilotus officinalis* scree community** (Figure 7A)

One cluster in our analysis consisted of only a single relevé of scree vegetation. For this instance, we assume that a corresponding vegetation type needs to be described in the future in the rank of an order or even a class when enough relevant data is available. The aforementioned relevé was sampled in the Vayots Dzor Province, near Hermon (39.8812°N, 45.43254°E), 1,739 m a.s.l., aspect 135°, inclination 46°, 2 July 2019, total vegetation cover: 50%:

Alyssum alyssoides: 0.5, *Arenaria serpyllifolia* aggr.: 0.1, *Asperula arvensis*: 0.2, *Buglossoides arvensis*: 0.1, *Bupleurum commutatum*: 0.01, *Caucalis platycarpos*: 0.1, *Cerastium ruderale*: 3, *Chaerophyllum bulbosum*: 0.5, *Cleome ornithopodioides*: 0.01, *Convolvulus arvensis*: 0.1, *Coronilla coronata*: 2, *Crepis pulchra*: 2, *Euphorbia orientalis*: 15, *Galium spurium*: 1, *Galium tenuissimum*: 0.3, *Holosteum marginatum*: 0.1, *Lactuca viminea*: 0.5, *Lamium amplexicaule*: 0.01, *Medicago rigidula*: 0.1, *Melica taurica*: 1, *Melilotus officinalis*: 5, *Michauxia laevigata*: 0.5, *Nepeta trautvetteri*: 0.3, *Noccaea perfoliata*: 0.01, *Prangos ferulacea*: 1, *Reichardia dichotoma*: 0.3, *Salvia verticillata*: 30, *Sanguisorba minor*: 2, *Saponaria orientalis*: 0.2, *Secale vavilovii*: 2, *Stachys recta*: 0.5, *Valerianella uncinata*: 0.1, *Vicia sativa*: 0.3, *Zosima absinthiifolia*: 4.

Table 2. Abbreviated constancy table of the classes, orders, alliances and associations/communities distinguished among the Armenian dry grasslands and thorn-cushion communities. Dark grey indicates diagnostic species at the respective level, while this colour is copied to all subordinate levels. Light grey refers to transgressive diagnostic species at the higher level (only given if the sum of the phi values of the syntaxa at the lower level without the target syntaxon is > 0). Frames indicate differential species at the association level. Diagnostic species are sorted by decreasing phi values in their target unit, while companion species are sorted by decreasing total constancy. While all diagnostic species at the class level are shown, at the order, alliance and association level only the first seven plus all with a phi-value > 0.5 were kept. Additionally, all species with a total constancy of ≥ 20% were also kept. Species that did not meet any of these criteria are not shown here. The complete version of this table, including also the precise phi values and the individual relevés is available as Suppl. material 2.

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m² (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m² (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m² (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m² (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Cl. 1																						
Xeranthemum squarrosum	25	57	.	57	.	.	41	77	59	.	.	29	50	77	80	29	.	.	.	.	.	.
Teucrium capitatum	58	87	37	87	.	55	100	77	82	.	55	100	100	77	90	71	.	.	.	14	94	64
Taeniatherum caput-medusae subsp. crinitum	22	51	.	51	.	.	24	69	65	.	.	14	30	69	70	57	.	.	.	.	.	.
Holosteum umbellatum	24	51	3	51	.	5	41	54	59	.	5	14	60	54	50	71	.	.	.	.	.	18
Crupina vulgaris	18	40	2	40	.	2	6	69	53	.	2	14	.	69	40	71	.	.	.	.	6	.
Thymelaea passerina	15	34	2	34	.	2	35	38	29	.	2	14	50	38	20	43	.	.	.	.	6	.
Tanacetum aureum	23	40	10	40	.	14	47	31	41	.	14	86	20	31	10	86	.	.	.	14	6	36
Helichrysum plicatum	24	45	8	45	5	10	29	69	41	5	10	14	40	69	20	71	.	13	13	14	13	.
Marrubium parviflorum	15	32	2	32	.	2	41	23	29	.	2	.	70	23	50	.	.	.	.	.	6	.
Bromus danthoniae	10	23	.	23	.	.	18	15	35	.	.	14	20	15	30	43	.	.	.	.	.	.
Bromus squarrosus	15	30	3	30	.	5	12	38	41	.	5	14	10	38	50	29	.	.	.	.	6	9
Sideritis montana	22	40	8	40	.	12	53	69	6	.	12	71	40	69	10	.	.	.	.	14	13	18
Poa bulbosa	55	77	40	77	33	43	41	100	94	33	43	.	70	100	100	86	15	63	75	.	69	9
Achillea arabica	20	38	6	38	5	7	29	54	35	5	7	.	50	54	60	.	.	13	25	.	6	.
Anisantha tectorum	6	15	.	15	.	.	12	.	29	.	.	14	10	.	30	29	.	.	.	.	.	.
Centaurea aggregata	9	19	2	19	.	2	18	15	24	.	2	29	10	15	10	43	.	.	13	.	.	.
Dianthus orientalis	6	15	.	15	.	.	12	23	12	.	.	29	.	23	.	29	.	.	.	.	.	.
All. 1.1.1																						
Veronica multifida	23	26	21	26	19	21	65	8	.	19	21	57	70	8	.	.	31	.	13	29	25	18
Assoc. 1.1.1.1																						
Astracantha condensata	11	17	6	17	.	10	41	8	.	.	10	86	10	8	.	.	.	.	.	.	13	18
Stachys lavandulifolia	8	17	2	17	.	2	41	.	6	.	2	71	20	.	10	.	.	.	.	.	6	.
Gypsophila elegans	5	9	3	9	.	5	24	.	.	.	5	57	.	.	.	.	.	.	.	14	.	9
Onobrychis michauxii	11	17	6	17	.	10	41	8	.	.	10	71	20	8	.	.	.	.	13	.	19	.
Viola occulta	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Herniaria hirsuta	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Crepis ciliata	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Onosma setosa	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Centaurea phrygia subsp. abbreviata	2	4	.	4	.	.	12	.	.	.	.	29	.	.	.	.	.	.	.	.	.	.
Nepeta racemosa	8	13	5	13	.	7	29	.	6	.	7	57	10	.	10	.	.	.	.	14	.	18
Asperula arvensis	31	53	14	53	.	21	65	46	47	.	21	100	40	46	60	29	.	.	13	.	44	9
Assoc. 1.1.1.2																						
Stipa capillata	23	40	10	40	.	14	47	46	29	.	14	.	80	46	50	.	.	.	.	.	31	9

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m² (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m² (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m² (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m² (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Allium cardiostemon	2	4	.	4	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.	.	.
Euphorbia condylocarpa	7	9	6	9	.	10	24	.	.	.	10	.	40	.	.	.	.	.	13	.	6	18
All. 1.1.2																						
Noaea mucronata	10	23	.	23	.	.	.	77	6	.	.	.	.	77	.	14	.	.	.	.	.	.
Cousinia brachyptera	8	19	.	19	.	.	6	62	.	.	.	.	10	62	.	.	.	.	.	.	.	.
Astragalus hyalolepis	13	26	3	26	5	2	12	77	.	5	2	.	20	77	.	.	8	.	.	.	6	.
Allium pseudoflavum	16	36	2	36	.	2	12	85	24	.	2	29	.	85	20	29	.	.	.	.	6	.
Minuartia hamata	24	51	3	51	.	5	29	100	35	.	5	29	30	100	20	57	.	.	13	.	6	.
B Syntrichia caninervis	6	15	.	15	.	.	.	46	6	.	.	.	.	46	.	14	.	.	.	.	.	.
Androsace albana	4	9	.	9	.	.	.	31	.	.	.	.	.	31	.	.	.	.	.	.	.	.
Polygala hohenackeriana	4	9	.	9	.	.	.	31	.	.	.	.	.	31	.	.	.	.	.	.	.	.
Meniocus linifolius	16	38	.	38	.	.	24	77	24	.	.	14	30	77	.	57	.	.	.	.	.	.
Alyssum turkestanicum	9	21	.	21	.	.	12	54	6	.	.	29	.	54	10	.	.	.	.	.	.	.
Arenaria serpyllifolia aggr.	32	57	13	57	10	14	59	100	24	10	14	86	40	100	30	14	15	.	38	.	13	9
All. 1.1.3																						
Chardinia orientalis	11	26	.	26	.	.	12	15	47	.	.	.	20	15	40	57	.	.	.	.	.	.
Crepis sancta	15	34	2	34	.	2	12	31	59	.	2	.	20	31	70	43	.	.	13	.	.	.
Stipa holosericea	11	26	.	26	.	.	18	8	47	.	.	.	30	8	50	43	.	.	.	.	.	.
Aegilops cylindrica	7	17	.	17	.	.	.	15	35	.	.	.	.	15	30	43	.	.	.	.	.	.
Roemeria hybrida	4	9	.	9	.	.	.	.	24	.	.	.	.	.	20	29	.	.	.	.	.	.
Noccaea perfoliata	26	38	17	38	14	19	35	.	71	14	19	29	40	.	60	86	23	.	.	57	6	27
Bromus japonicus	15	30	5	30	.	7	24	15	47	.	7	14	30	15	40	57	.	.	13	.	6	9
Assoc. 1.1.3.1																						
Torilis arvensis	3	6	.	6	.	.	.	.	18	.	.	.	.	.	30	.	.	.	.	.	.	.
Acantholimon caryophyllaceum	5	9	2	9	.	2	.	.	24	.	2	.	.	.	40	.	.	.	.	14	.	.
Lomelosia rotata	7	15	2	15	.	2	.	23	24	.	2	.	.	23	40	.	.	.	.	.	6	.
Carduus hamulosus	2	4	.	4	.	.	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.
Stipa zalesskii subsp. pontica	2	4	.	4	.	.	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.
Geranium lucidum	2	4	.	4	.	.	.	.	12	.	.	.	.	.	20	.	.	.	.	.	.	.
Aegilops triuncialis	6	15	.	15	.	.	12	.	29	.	.	.	20	.	40	14	.	.	.	.	.	.
Assoc. 1.1.3.2																						
Acantholimon vedicum	5	11	.	11	.	.	.	.	29	.	.	.	.	.	.	71	.	.	.	.	.	.
Stachys inflata	11	21	3	21	.	5	6	.	53	.	5	14	.	.	20	100	.	.	25	.	.	.
Bunium microcarpum	8	13	5	13	.	7	.	.	35	.	7	.	.	.	.	86	.	.	25	.	.	9
Petrorhagia cretica	4	9	.	9	.	.	.	.	24	.	.	.	.	.	.	57	.	.	.	.	.	.
Helianthemum ledifolium	11	26	.	26	.	.	6	23	47	.	.	.	10	23	20	86	.	.	.	.	.	.
Gaudiniopsis macra	5	11	.	11	.	.	.	8	24	.	.	.	.	8	.	57	.	.	.	.	.	.
Ephedra procera	3	6	.	6	.	.	.	.	18	.	.	.	.	.	.	43	.	.	.	.	.	.
Papaver minus	3	6	.	6	.	.	.	.	18	.	.	.	.	.	.	43	.	.	.	.	.	.
Aethionema carneum	3	6	.	6	.	.	.	.	18	.	.	.	.	.	.	43	.	.	.	.	.	.
Arabis auriculata aggr.	9	19	2	19	.	2	6	15	35	.	2	.	10	15	10	71	.	.	.	.	.	9
Lamium amplexicaule	4	6	2	6	5	.	.	.	18	5	.	.	.	.	.	43	8	.	.	.	.	.
Camelina laxa	4	9	.	9	.	.	6	.	18	.	.	.	10	.	.	43	.	.	.	.	.	.

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m² (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m² (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m² (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m² (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Galium verticillatum	7	13	3	13	.	5	6	.	29	.	5	.	10	.	10	57	.	.	.	14	6	.
Ziziphora tenuior	13	30	.	30	.	.	6	38	47	.	.	14	.	38	30	71	.	.	.	.	.	.
Aegilops biuncialis	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Cuscuta pedicellata	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Valerianella coronata	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Onobrychis atropatana	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Cousinia daralaghezica	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Astragalus ornithopodioides	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Crucianella exasperata	2	4	.	4	.	.	.	.	12	.	.	.	.	.	.	29	.	.	.	.	.	.
Stipa arabica	14	30	2	30	.	2	18	31	41	.	2	29	10	31	20	71	.	.	.	.	6	.
Cl. 2																						
Lotus corniculatus	39	2	67	2	90	55	6	.	.	90	55	.	10	.	.	.	92	88	88	57	31	64
Achillea millefolium aggr.	47	13	73	13	95	62	29	.	6	95	62	43	20	.	10	.	92	100	75	57	63	55
Dactylis glomerata	55	26	76	26	57	86	47	.	24	57	86	43	50	.	40	.	54	63	100	86	88	73
Poa pratensis aggr.	33	11	49	11	71	38	18	15	.	71	38	.	30	15	.	.	69	75	50	86	13	36
Scabiosa bipinnata	34	6	54	6	38	62	12	8	.	38	62	29	.	8	.	.	54	13	63	43	63	73
Campanula glomerata aggr.	18	.	32	.	33	31	.	.	.	33	31	.	.	.	.	.	15	63	50	71	13	18
Potentilla recta aggr.	51	28	68	28	71	67	41	15	24	71	67	29	50	15	40	.	69	75	88	43	81	45
Galium verum	73	53	87	53	81	90	47	62	53	81	90	71	30	62	60	43	77	88	88	100	81	100
Phleum phleoides	25	6	40	6	52	33	6	.	12	52	33	14	.	.	20	.	54	50	25	71	31	18
Pimpinella saxifraga aggr.	17	.	30	.	48	21	.	.	.	48	21	.	.	.	.	.	69	13	13	.	6	64
Polygala anatolica	18	2	30	2	29	31	.	8	.	29	31	.	.	8	.	.	46	.	.	57	31	36
Leontodon hispidus	19	4	30	4	48	21	.	8	6	48	21	.	.	8	10	.	62	25	13	57	13	18
Bupleurum falcatum aggr.	13	.	22	.	19	24	.	.	.	19	24	.	.	.	.	.	31	.	.	43	19	36
Trifolium alpestre	12	.	21	.	29	17	.	.	.	29	17	.	.	.	.	.	38	13	50	.	.	27
Trisetum flavescens	13	2	21	2	29	17	.	.	6	29	17	.	.	.	10	.	8	63	63	14	.	9
Ord. 2.1																						
Trifolium ambiguum	13	.	22	.	62	2	.	.	.	62	2	.	.	.	.	.	46	88	13	.	.	.
Campanula stevenii	22	.	38	.	81	17	.	.	.	81	17	.	.	.	.	.	77	88	50	.	6	18
Plantago atrata	27	2	46	2	86	26	.	.	6	86	26	.	.	.	10	.	85	88	13	29	25	36
Trifolium trichocephalum	11	.	19	.	52	2	.	.	.	52	2	.	.	.	.	.	62	38	.	.	.	9
Bromopsis variegata	23	11	32	11	76	10	29	.	.	76	10	57	10	.	.	.	92	50	.	14	.	27
Myosotis alpestris	8	.	14	.	38	2	.	.	.	38	2	.	.	.	.	.	46	25	.	.	6	.
Koeleria albovii	12	.	21	.	43	10	.	.	.	43	10	.	.	.	.	.	38	50	.	.	25	.
[…]																						
Veronica denudata	21	9	30	9	57	17	12	8	6	57	17	.	20	8	10	.	54	63	25	14	13	18
[…]																						
Festuca ovina aggr.	20	11	27	11	52	14	.	31	6	52	14	.	.	31	10	.	54	50	13	.	19	18
[…]																						
Taraxacum sect. Taraxacum	23	6	35	6	62	21	12	.	6	62	21	14	10	.	10	.	69	50	25	43	6	27
Assoc. 2.1.1.1																						
Ranunculus caucasicus	6	.	11	.	33	.	.	.	.	33	.	.	.	.	.	.	54	.	.	.	.	.
Huynhia pulchra	5	.	10	.	29	.	.	.	.	29	.	.	.	.	.	.	46	.	.	.	.	.

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m² (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m² (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m² (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m² (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Lomelosia caucasica	5	.	10	.	29	.	.	.	.	29	.	.	.	.	.	.	46	.	.	.	.	.
Alchemilla sericea	7	.	13	.	33	2	.	.	.	33	2	.	.	.	.	.	54	.	.	.	.	9
Campanula collina	5	.	8	.	24	.	.	.	.	24	.	.	.	.	.	.	38	.	.	.	.	.
Polygonum cognatum	13	.	22	.	48	10	.	.	.	48	10	.	.	.	.	.	69	13	25	.	6	9
Phleum alpinum	6	.	11	.	29	2	.	.	.	29	2	.	.	.	.	.	46	.	13	.	.	.
Cirsium leucocephalum	15	.	27	.	52	14	.	.	.	52	14	.	.	.	.	.	77	13	13	43	.	18
Schedonorus pratensis	7	.	13	.	29	5	.	.	.	29	5	.	.	.	.	.	46	.	.	.	.	18
Stipa tirsa	8	.	14	.	29	7	.	.	.	29	7	.	.	.	.	.	46	.	.	.	19	.
B Tortula acaulon	4	.	6	.	19	.	.	.	.	19	.	.	.	.	.	.	31	.	.	.	.	.
Pedicularis condensata	4	.	6	.	19	.	.	.	.	19	.	.	.	.	.	.	31	.	.	.	.	.
Psephellus xanthocephalus	4	.	6	.	19	.	.	.	.	19	.	.	.	.	.	.	31	.	.	.	.	.
Arenaria blepharophylla aggr.	5	.	10	.	24	2	.	.	.	24	2	.	.	.	.	.	38	.	.	.	.	9
Rumex acetosella	5	.	10	.	24	2	.	.	.	24	2	.	.	.	.	.	38	.	13	.	.	.
Assoc. 2.1.1.2																						
Tragopogon reticulatus	11	4	16	4	24	12	6	8	.	24	12	.	10	8	.	.	.	63	13	.	.	36
Senecio pseudo-orientalis	4	.	6	.	14	2	.	.	.	14	2	.	.	.	.	.	.	38	13	.	.	.
Astracantha aurea	6	2	10	2	19	5	6	.	.	19	5	.	10	.	.	.	.	50	13	14	.	.
Lathyrus digitatus	5	.	8	.	19	2	.	.	.	19	2	.	.	.	.	.	8	38	.	.	6	.
Verbascum speciosum	2	.	3	.	10	.	.	.	.	10	.	.	.	.	.	.	.	25	.	.	.	.
Trifolium spadiceum	2	.	3	.	10	.	.	.	.	10	.	.	.	.	.	.	.	25	.	.	.	.
Gagea glacialis	2	.	3	.	10	.	.	.	.	10	.	.	.	.	.	.	.	25	.	.	.	.
Ord. 2.2																						
Stachys macrostachys	9	.	16	.	.	24	.	.	.	.	24	.	.	.	.	.	.	.	75	57	.	.
Stachys recta	50	32	63	32	33	79	65	8	18	33	79	57	70	8	30	.	54	.	38	100	88	82
Securigera varia	35	15	49	15	38	55	24	.	18	38	55	29	20	.	30	.	54	13	75	100	44	27
Cerinthe minor	16	6	24	6	.	36	12	.	6	.	36	.	20	.	10	.	.	.	.	57	44	36
Teucrium chamaedrys	16	4	25	4	5	36	12	.	.	5	36	14	10	.	.	.	8	.	13	43	38	45
Salvia verticillata	27	15	37	15	10	50	24	.	18	10	50	43	10	.	30	.	15	.	38	43	50	64
Stipa pulcherrima	24	15	30	15	.	45	6	8	29	.	45	.	10	8	20	43	.	.	13	57	56	45
Assoc. 2.2.1.1																						
Artemisia absinthium	12	.	21	.	19	21	.	.	.	19	21	.	.	.	.	.	23	13	75	14	.	18
Verbascum cheiranthifolium	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	25	.	.	.
Arenaria graminea	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	25	.	.	.
Chaerophyllum roseum	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	25	.	.	.
Assoc. 2.2.1.2																						
Klasea radiata	8	.	14	.	5	19	.	.	.	5	19	.	.	.	.	.	8	.	.	71	19	.
Linum nervosum	17	6	25	6	5	36	.	15	6	5	36	.	.	15	10	.	8	.	.	100	19	45
Origanum vulgare	13	.	22	.	10	29	.	.	.	10	29	.	.	.	.	.	15	.	13	86	6	36
Onobrychis transcaucasica	19	4	30	4	14	38	12	.	.	14	38	.	20	.	.	.	23	.	13	100	31	27
Thalictrum minus	9	.	16	.	14	17	.	.	.	14	17	.	.	.	.	.	15	13	25	71	.	.
B Campyliadelphus chrysophyllus	4	.	6	.	5	7	.	.	.	5	7	.	.	.	.	.	8	.	.	43	.	.
Helictochloa armeniaca	5	.	8	.	.	12	.	.	.	.	12	.	.	.	.	.	.	.	.	43	6	9
Vicia canescens subsp. variegata	18	6	27	6	14	33	6	.	12	14	33	14	.	.	20	.	23	.	25	86	13	36

Syntaxon	All	1	2	1.1	2.1	2.2	1.1.1	1.1.2	1.1.3	2.1.1	2.2.1	1.1.1.1	1.1.1.2	1.1.2.1	1.1.3.1	1.1.3.2	2.1.1.1	2.1.1.2	2.2.1.1	2.2.1.2	2.2.1.3	2.2.1.4
Number of plots	110	47	63	47	21	42	17	13	17	21	42	7	10	13	10	7	13	8	8	7	16	11
Mean species richness in 10 m² (all)	47.4	45.0	49.2	45.0	50.1	48.8	43.5	45.0	46.6	50.1	48.8	42.4	44.2	45.0	45.3	48.4	56.8	39.3	49.1	52.3	42.3	55.8
Mean species richness in 10 m² (vascular plants)	46.9	44.6	48.7	44.6	49.3	48.3	43.2	44.9	45.9	49.3	48.3	41.9	44.1	44.9	44.6	47.7	55.6	39.1	48.9	51.4	41.9	55.3
Mean species richness in 10 m² (byophytes)	0.4	0.2	0.5	0.2	0.6	0.4	0.3	0.1	0.3	0.6	0.4	0.6	0.1	0.1	0.3	0.3	0.9	0.0	0.3	0.7	0.3	0.5
Mean species richness in 10 m² (lichens)	0.1	0.1	0.1	0.1	0.2	0.0	0.0	0.0	0.4	0.2	0.0	0.0	0.0	0.0	0.4	0.4	0.2	0.1	0.0	0.1	0.1	0.0
Rhinanthus subulatus	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Lathyrus latifolius	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Valeriana officinalis aggr.	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Campanula bononiensis	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Melampyrum sp.	2	.	3	.	.	5	.	.	.	.	5	.	.	.	.	.	.	.	.	29	.	.
Seseli libanotis	8	.	14	.	14	14	.	.	.	14	14	.	.	.	.	.	15	13	13	57	6	.
Assoc. 2.2.1.4																						
Linum tenuifolium	15	.	25	.	.	38	.	.	.	.	38	.	.	.	.	.	.	.	13	.	44	73
Coronilla coronata	4	.	6	.	.	10	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	36
Asphodeline taurica	4	.	6	.	.	10	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	36
Androsace chamaejasme	4	.	6	.	.	10	.	.	.	.	10	.	.	.	.	.	.	.	.	.	.	36
B Hypnum cupressiforme	13	4	19	4	14	21	.	8	6	14	21	.	.	8	.	14	15	13	13	.	.	73
Campanula sibirica	9	6	11	6	.	17	18	.	.	.	17	43	.	.	.	.	.	.	.	.	.	64
Sesleria phleoides	6	2	10	2	5	12	.	8	.	5	12	.	.	8	.	.	8	.	.	.	.	45
Asperula affinis	5	.	8	.	.	12	.	.	.	.	12	.	.	.	.	.	.	.	.	.	6	36
Campanula rapunculoides	11	.	19	.	5	26	.	.	.	5	26	.	.	.	.	.	8	.	13	43	.	64
Pontechium maculatum	7	.	13	.	14	12	.	.	.	14	12	.	.	.	.	.	23	.	.	.	.	45
Fritillaria caucasica	3	.	5	.	.	7	.	.	.	.	7	.	.	.	.	.	.	.	.	.	.	27
Differential species in more than one association																						
Arenaria dianthoides	5	.	8	.	14	5	.	.	.	14	5	.	.	.	.	.	.	38	25	.	.	.
Gagea caroli-kochii	5	.	8	.	10	7	.	.	.	10	7	.	.	.	.	.	.	25	38	.	.	.
Silene cephalantha	5	.	8	.	10	7	.	.	.	10	7	.	.	.	.	.	.	25	38	.	.	.
Companion species																						
Thymus kotschyanus	60	66	56	66	48	60	59	69	71	48	60	43	70	69	60	86	31	75	50	71	56	64
Scutellaria orientalis aggr.	54	62	48	62	43	50	71	54	59	43	50	100	50	54	50	71	15	88	50	57	44	55
Koeleria macrantha	52	55	49	55	43	52	59	77	35	43	52	57	60	77	40	29	62	13	38	29	63	64
Elytrigia intermedia aggr.	47	49	46	49	19	60	65	46	35	19	60	71	60	46	50	14	8	38	88	57	44	64
Eryngium billardierei	38	43	35	43	5	50	24	46	59	5	50	14	30	46	60	57	.	13	50	43	69	27
Convolvulus lineatus	36	51	25	51	.	38	71	62	24	.	38	43	90	62	40	.	.	.	25	.	50	55
Medicago sativa	35	34	37	34	14	48	29	46	29	14	48	.	50	46	50	.	15	13	38	71	44	45
Alyssum alyssoides	35	43	29	43	19	33	41	38	47	19	33	43	40	38	40	57	23	13	50	.	56	9
Festuca valesiaca aggr.	35	23	43	23	48	40	41	8	18	48	40	14	60	8	20	14	54	38	75	.	38	45
Euphorbia seguieriana	32	40	25	40	10	33	24	62	41	10	33	43	10	62	50	29	8	13	13	29	56	18
Centaurea ovina aggr.	27	38	19	38	.	29	47	46	24	.	29	.	80	46	30	14	.	.	.	14	56	18
B Syntrichia ruralis	27	21	32	21	24	36	6	31	29	24	36	.	10	31	50	.	23	25	38	57	19	45
Dianthus cretaceus	26	21	30	21	52	19	29	31	6	52	19	14	40	31	.	14	54	50	13	29	6	36
Medicago x varia	26	26	27	26	29	26	41	23	12	29	26	43	40	23	20	.	8	63	13	.	44	27
Ziziphora clinopodioides	25	19	30	19	14	38	24	.	29	14	38	.	40	.	40	14	.	38	13	43	56	27
Hypericum scabrum	25	32	19	32	.	29	41	.	47	.	29	29	50	.	60	29	.	.	13	.	56	18
Leontodon asperrimus	25	13	33	13	33	33	29	.	6	33	33	14	40	.	10	.	23	50	25	14	38	45
Thesium ramosum	22	36	11	36	5	14	53	23	29	5	14	43	60	23	30	29	8	.	13	29	6	18
Plantago lanceolata	22	15	27	15	10	36	35	.	6	10	36	14	50	.	10	.	8	13	63	43	25	27
Onobrychis cornuta	21	19	22	19	.	33	29	8	18	.	33	.	50	8	20	14	.	.	.	29	44	45
Falcaria vulgaris	20	17	22	17	10	29	18	8	24	10	29	14	20	8	40	.	8	13	13	57	38	9

Potential class 1: *Ziziphora tenuior-Stipa arabica* grasslands – Western Asian dry grasslands and xeric thorn cushion communities

Diagnostic species: *Achillea arabica*, *Aegilops cylindrica*, *Agropyron cristatum*, *Allium pseudoflavum*, *Alyssum turkestanicum*, *Androsace maxima*, *Anisantha tectorum*, *Arabis auriculata* aggr., *Arenaria serpyllifolia* aggr., *Artemisia fragrans*, *Asperula arvensis*, *Bromus danthoniae*, *B. japonicus*, *B. squarrosus*, *Centaurea aggregata*, *Chardinia orientalis*, *Crepis sancta*, *Crupina vulgaris*, *Dianthus orientalis*, *Helianthemum ledifolium*, *Helichrysum plicatum*, *Holosteum marginatum*, ***H. umbellatum***, *Marrubium parviflorum*, *Meniocus linifolius*, ***Minuartia hamata***, *Noaea mucronata*, *Poa bulbosa*, *Sideritis montana*, *Stachys inflata*, *S. lavandulifolia*, *Stipa arabica*, *S. capillata*, *S. holosericea*, ***Taeniatherum caput-medusae* subsp. *crinitum***, *Tanacetum aureum*, ***Teucrium capitatum***, *Thymelaea passerina*, ***Xeranthemum squarrosum***, *Ziziphora tenuior.*

Ecology and distribution. Communities of the potential new class occur in the lower elevations in dry conditions and include semi-desert vegetation, xeric thorn-cushion communities, and xeric grasslands. Within Armenia, it is represented by one order and three alliances.

Order 1.1: *Cousinio brachypterae-Stipetalia arabicae* – Western Asian dry grasslands and xeric thorn cushion communities

Diagnostic species: Identical with those of the monotypic class.

Ecology and distribution. Communities of this order are distributed in Transcaucasia and possibly even broader within Western Asia. We expect them to occur throughout Western Asia in dry conditions (semi-deserts, dry steppe-like communities, low-elevation thorn-cushion communities). Also, according to our analysis, communities of this order may occur even in higher elevations on rocky substrates.

Alliance 1.1.1: *Onobrychido michauxii-Stipion capillatae* – Transcaucasian rocky dry grasslands

Diagnostic species: *Astracantha condensata*, *Onobrychis michauxii*, *Salvia aethiopis*, *Stachys lavandulifolia*, *Teucrium capitatum*, *Veronica multifida* (mainly negatively differentiated central alliance).

Ecology and distribution. Communities of this alliance are distributed in higher elevations than those of the other two alliances included in this order. This alliance is a transitional unit between this order and the order *Onobrychido transcaucasicae-Stipetalia pulcherrimae*, comprising Transcaucasian mountain steppes (see below).

1.1.1.1: *Stachys lavandulifolia-Astracantha condensata* community (Figure 7B)

Diagnostic species: *Asperula arvensis*, ***Astracantha condensata***, *Centaurea phrygia* subsp. *abbreviata*, *Crepis ciliata*, *Euphorbia orientalis*, ***Gypsophila elegans***, *Herniaria hirsuta*, *Leptunis trichodes*, *Melica taurica*, *Nepeta racemosa*, *Onobrychis michauxii*, *Onosma setosa*, *Salvia aethiopis*, *Sempervivum transcaucasicum*, ***Stachys lavandulifolia***, *Tanacetum aureum*, *Teucrium orientale*, *Tragopogon dubius*, *Viola occulta*, *Zosima absinthiifolia.*

Structure, ecology and distribution. We sampled this vegetation type in the Gegharkunik (vicinity of the town of Sevan, Shorja) and Vayots Dzor (Hermon, vicinity of Gnishik and Khachik) provinces. These communities were located at the most south-facing rocky slopes with shallow soil and low humus content. The herb layer was sparse and with a high representation of Irano-Turanian species, e.g. *Astracantha condensata*, *A. microcephala*, *Stachys lavandulifolia*, *Teucrium orientale*.

1.1.1.2: *Marrubio parviflorae-Stipetum capillatae* (Figure 7C)

Diagnostic species: *Allium cardiostemon*, *Centaurea ovina* aggr., *Euphorbia condylocarpa*, *Marrubium parviflorum*, *Stipa capillata.*

Structure, ecology and distribution: These communities were sampled on slopes with shallow rocky substrates in Gegharkunik (Ardanish), Lori (near Shirakamut) and Vayots Dzor (vicinity of Gnishik and Khachik) provinces. The association differed by a higher herb layer cover compared to the previous community and the highest participation of hemicryptophytes among all associations of the class. The dominant species were *Festuca valesiaca* aggr., *Onobrychis cornuta* and *Teucrium capitatum*.

Alliance 1.1.2: *Artemision fragrantis* – Transcaucasian wormwood semi-deserts

Diagnostic species: *Agropyron cristatum*, ***Allium pseudoflavum***, *Alyssum turkestanicum*, *Androsace albana*, *Arenaria serpyllifolia* aggr., *Artemisia fragrans*, ***Astragalus hyalolepis***, *Bromopsis riparia*, *Ceratocephala falcata*, ***Cousinia brachyptera***, *Crupina vulgaris*, *Cuscuta araratica*, *Consolida hispanica*, *Didymodon tophaceus* (B), *Meniocus linifolius*, *Minuartia hamata*, ***Noaea mucronata***, *Peganum harmala*, *Polygala hohenackeriana*, *Sclerocaryopsis spinocarpos*, *Syntrichia caninervis* (B).

Ecology and distribution: *Artemisia fragrans* semi-deserts in Armenia are distributed in the lowest elevations in the country. We did not sample other semi-desert types, but we can expect that Armenian loamy and sandy semi-deserts will also be probably included in this unit. In our dataset, this alliance is represented by a single association.

1.1.2.1: *Noaeo mucronatae-Artemisietum fragrantis* (Figure 7D)

Diagnostic species: identical with those of the monotypic alliance.

Structure, ecology and distribution: This association is typical for the Aragatsotn province (vicinity of Dashtadem and Tatool). The sampled plots were distributed at the lowest elevations with the highest mean annual temperature and lowest mean annual precipitation compared to the other studied associations. The communities were dominated by *Artemisia fragrans*, *Poa bulbosa*, and *Taeni-*

atherum caput-medusae subsp. *crinitum*. The herb layer is relatively sparse and with a high representation of therophytes (e.g. *Alyssum turkestanicum*, *Bromus squarrosus*, *Ceratocephala falcata*, *Crupina vulgaris*, *Sclerocaryopsis spinocarpos*) and characteristic chamaephytes (*Artemisia fragrans*, *Noaea mucronata*).

Alliance 1.1.3: *Acantholimono caryophyllacei-Stipion holosericeae* – Transcaucasian dry grasslands and xeric thorn-cushion communities

Diagnostic species: *Acantholimon vedicum*, *Aegilops cylindrica*, *Aethionema carneum*, *Arabis auriculata* aggr., *Bromus japonicus*, *Bunium microcarpum*, *Chardinia orientalis*, *Crepis sancta*, *Crupina vulgaris*, *Ephedra procera*, *Galium verticillatum*, *Gaudiniopsis macra*, *Helianthemum ledifolium*, *Noccaea perfoliata*, *Papaver minus*, *Roemeria hybrida*, ***Stachys inflata***, *Stipa arabica*, *S. holosericea*, *Taeniatherum caput-medusae* subsp. *crinitum*, *Petrorhagia cretica*, *Ziziphora tenuior*.

Ecology and distribution: This unit comprises vegetation traditionally known as 'highland xerophytic vegetation'. It includes dry grasslands and xeric tragacanth communities distributed above the semi-desert belt and below the mountain steppe altitudinal belt. We distinguish one association and one community within this alliance.

1.1.3.1: *Acantholimono caryophyllacei-Stipetum holosericeae* (Figure 7E)

Diagnostic species: *Acantholimon caryophyllaceum*, *Aegilops triuncialis*, *Carduus hamulosus*, *Crepis sancta*, *Geranium lucidum*, *Lomelosia rotata*, *Noccaea annua*, *Stipa zalesskii* subsp. *pontica*, *Torilis arvensis*, *Xeranthemum squarrosum*.

Structure, ecology and distribution: We sampled this association mainly in the Vayots Dzor province (Hermon, vicinities of Areni, Gnishik and Khachik), and also in one locality in Aragatsotn province (near Tatool). The communities were distributed on shallow soils, but with higher humus content and lower gravel cover compared to the other associations of this class. *Acantholimon caryophyllaceum*, *Stipa holosericea*, and *Taeniatherum caput-medusae* subsp. *crinitum* are the dominant species in this association. Among other species, Irano-Turanian elements often occur, such as *Achillea arabica*, *Eryngium billardierei*, *Hypericum scabrum*, and *Thymus kotschyanus*.

1.1.3.2: *Stachys inflata-Acantholimon vedicum* community (Figure 7F)

Diagnostic species: ***Acantholimon vedicum***, *Aegilops biuncialis*, *A. cylindrica*, ***Aethionema carneum***, *Androsace maxima*, ***Arabis auriculata* aggr.,** *Artemisia fragrans*, *Aspicilia hispida* (L), *Astragalus ornithopodioides*, ***Bunium microcarpum***, *Callipeltis cucullaria*, *Camelina laxa*, *Chardinia orientalis*, *Cousinia daralaghezica*, *Crossidium squamiferum* (B), *Crucianella exasperata*, *Crupina vulgaris*, *Cuscuta pedicellata*, ***Ephedra procera***, *Galium verticillatum*, ***Gaudiniopsis macra***, ***Helianthemum ledifolium***, *Holosteum marginatum*, *Lactuca tuberosa*, *Lamium amplexicaule*, *Onobrychis atropatana*, ***Papaver minus***, ***Petrorhagia cretica***, ***Stachys inflata***, *Stipa arabica*, *Tanacetum aureum*, *Trinia glauca*, *Valerianella coronata*, *Ziziphora tenuior*.

Structure, ecology and distribution: We sampled this vegetation type in Ararat (vicinity of Tigranashen) and Vayots Dzor (vicinity of Gnishik) provinces. Communities were distributed at lower elevations with high mean annual temperature and low mean annual precipitation. The substrate differed by the most alkaline soil reaction (mean pH: 8). The herb layer was sparse and with a high representation of Irano-Turanian and Mediterranean therophyte species (*Aegilops* spp., *Crupina vulgaris*, *Petrorhagia cretica*, *Ziziphora tenuior*), while the cover of hemicryptophytes was the lowest among all studied communities. These communities did not have clear dominants, but *Chardinia orientalis*, *Stachys inflata*, *Stipa arabica*, and *S. sareptana* subsp. *anisotricha* occurred with higher cover than the other species. The species richness of vascular plants, bryophytes and lichens was higher compared to the other associations of the class.

Class 2: *Festuco-Brometea* – Mesoxeric and xeric basiphilous grasslands of temperate Europe and adjacent regions

Diagnostic species: *Abietinella abietina* (B), ***Achillea millefolium* aggr.,** *Artemisia absinthium*, *Bupleurum falcatum* aggr., *Campanula glomerata* aggr., *C. rapunculoides*, *C. stevenii*, *Cirsium leucocephalum*, ***Dactylis glomerata***, *Galium verum*, *Koeleria albovii*, *Leontodon hispidus*, *Linum nervosum*, *L. tenuifolium*, ***Lotus corniculatus***, *Onobrychis transcaucasica*, *Origanum vulgare*, *Phleum phleoides*, *Pimpinella saxifraga* aggr., *Plantago atrata*, *Poa pratensis* aggr., *Polygala anatolica*, *Polygonum cognatum*, *Potentilla recta* aggr., *Scabiosa bipinnata*, *Securigera varia*, *Stachys macrostachys*, *Taraxacum* sect. *Taraxacum*, *Thalictrum minus*, *Trifolium alpestre*, *T. ambiguum*, *T. trichocephalum*, *Trisetum flavescens*.

Ecology and distribution: Within Armenia, this class comprises meso-xeric grasslands and mountain steppes at higher elevations. We distinguish two orders representing different altitudinal belts.

Order 2.1: *Plantagini atratae-Bromopsietalia variegatae* – High-mountain meso-xeric grasslands of the Caucasus

Diagnostic species: *Achillea millefolium* aggr., *Ajuga orientalis*, *Alchemilla sericea*, *Arenaria blepharophylla* aggr., *A. gypsophiloides*, *Aster alpinus*, *Brachypodium pinnatum*, ***Bromopsis variegata***, *Campanula collina*, ***C. stevenii***, *Cirsium leucocephalum*, *Festuca ovina* aggr., *Schedonorus pratensis*, *Festuca rubra* aggr., *Filipendula vulgaris*, *Gagea glacialis*, *Galium cordatum*, *Gentiana septemfida*, *Huynhia pulchra*, ***Koeleria albovii***, *Lathyrus digitatus*, *Lomelosia caucasica*, *Lotus corniculatus*, *Luzula multiflora*, *Medicago papillosa*, *Muscari armeniacum*, ***Myosotis alpestris***, *Ornithogalum sigmoideum*, *Papaver orientale*, *Pedicularis condensata*, *Phleum alpinum*, *Pilosella officinarum* aggr., *Pimpinella saxifraga* aggr., ***Plantago atrata***, *Poa pratensis* aggr., *Pohlia nutans* (B), *Polygonum cognatum*, *Potentilla argentea*, *Psephellus xanthocephalus*, *Pseudoleskella tectorum* (B), *Pulsatilla albana*, *Ranunculus caucasicus*, *Rumex acetosella*, *Senecio pseudo-orientalis*, *Stachys macrantha*, *Stipa tirsa*, *Taraxacum* sect. *Taraxacum*, *Thymus collinus*, *Tortula acaulon* (B), ***Trifolium ambiguum***, *T. spadiceum*, ***T. trichocephalum***, *Verbascum speciosum*, *Veronica denudata*, *V. gentianoides.*

Ecology and distribution: Communities of this order occupy the highest sampled elevations in Armenia: upper subalpine and lower alpine belts. They form a particular unit recognized in the dominant approach typology: mountain meadow steppes. Beyond this elevation belt, they are replaced by the alpine grasslands which possibly belong to the class *Juncetea trifidi* Hadač in Klika et Hadač 1944 (*Festucetalia woronowii* Tsepkova 1987).

Alliance 2.1.1: *Artemisio chamaemelifoliae-Bromopsion variegatae* – Caucasian subalpine and lower-alpine meso-xeric grasslands

Diagnostic species: *Achillea millefolium* aggr., *Alchemilla sericea*, *Arenaria gypsophiloides*, *Bromopsis variegata*, *Campanula collina*, ***C. stevenii***, *Festuca ovina* aggr., *F. rubra* aggr., *Huynhia pulchra*, *Koeleria albovii*, *Lathyrus digitatus*, *Lomelosia caucasica*, *Lotus corniculatus*, *Myosotis alpestris*, ***Plantago atrata***, *Polygonum cognatum*, *Potentilla argentea*, *Ranunculus caucasicus*, *Taraxacum sect. Taraxacum*, ***Trifolium ambiguum***, ***T. trichocephalum***, *Veronica denudata*, *V. gentianoides.*

Ecology and distribution: This unit was described from the Main Range of the North Caucasus (Vynokurov et al. 2021) in the elevations of 1,800–2,200 m a.s.l. In Armenia, it occurs mainly higher than 2,000 m a.s.l., and shares multiple species with the Northern Caucasus unit. Thus, we are classifying mountain meadow steppes of Armenia within the same alliance. Here we distinguish one association and one informal community within it.

2.1.1.1: *Ranunculo caucasici-Bromopsietum variegatae* (Figure 8A)

Diagnostic species: *Alchemilla sericea*, *Arenaria blepharophylla* aggr., *Artemisia chamaemelifolia*, *Aster alpinus*, *Avenula pubescens*, *Brachypodium pinnatum*, *Bromopsis variegata*, ***Campanula collina***, *C. stevenii*, *Carex caryophyllea*, *Cirsium leucocephalum*, *Schedonorus pratensis*, *Galium cordatum*, ***Huynhia pulchra***, ***Lomelosia caucasica***, *Luzula multiflora*, *Medicago papillosa*, *Muscari armeniacum*, *Myosotis alpestris*, *Pedicularis condensata*, *Phascum cuspidatum* (B), *Phleum alpinum*, *Pilosella officinarum* aggr., *Pimpinella saxifraga* aggr., *Plantago atrata*, *Polygonum cognatum*, *Psephellus xanthocephalus*, *Pulsatilla albana*, ***Ranunculus caucasicus***, *Rumex acetosella*, *Stachys macrantha*, *Stipa tirsa*, *Tragopogon graminifolius*, *Trifolium trichocephalum*, *Veronica gentianoides.*

Structure, ecology and distribution: We sampled this vegetation type at the steep north-facing slopes at elevations around 2,100 m, mainly in the Shirak province (vicinities of Amasia and Zorakert), and also in Gegharkunik province (Ardanish). The localities were characterised by a high mean annual precipitation (around 700–900 mm). The soil reaction was slightly acidic (mean pH: 6.5). The association differed by high species richness and the highest participation of Caucasian species, e.g. *Dianthus cretaceus*, *Lomelosia caucasica*, *Stachys macrantha*, and *Trifolium trichocephalum*, among all studied communities. Graminoids were dominant, particularly *Brachypodium pinnatum*, *Bromopsis variegata*, *Carex humilis*, and *Phleum alpinum*.

2.1.1.2: *Tragopogon reticulatus-Astracantha aurea community* (Figure 8B)

Diagnostic species: *Arenaria dianthoides*, *A. gypsophiloides*, *Astracantha aurea*, *Campanula stevenii*, *Elytrigia repens*, *Gagea glacialis*, *Koeleria albovii*, *Lathyrus digitatus*, *Papaver orientale*, *Plantago atrata*, *Senecio pseudo-orientalis*, *Tragopogon reticulatus*, ***Trifolium ambiguum***, *T. spadiceum*, *Trisetum flavescens*, *Verbascum speciosum.*

Structure, ecology and distribution: We sampled this community mainly in the Gegharkunik province (Selim pass), and also in the Aragatsotn province (near the fortress of Amberd). Most of the localities were situated at 2,300–2,400 m a.s.l. and represented the highest elevations among all studied sites. The soil reaction was slightly acidic. These communities are characterised by low species richness with a high participation of Transcaucasian and Caucasian species, e.g. *Arenaria dianthoides*, *Astracantha aurea*, *Koeleria albovii*. *Festuca ovina* aggr. and *Plantago atrata* were the dominant species.

Order 2.2: *Onobrychido transcaucasicae-Stipetalia pulcherrimae* – Transcaucasian mountain steppes

Diagnostic species: *Artemisia absinthium*, *Bupleurum falcatum* aggr., *Campanula glomerata* aggr., *C. rapunculoides*, *Cerinthe minor*, *Dactylis glomerata*, *Euphrasia pectinata*, *Galium verum*, *Globularia trichosantha*, *Helictochloa armeniaca*, *Hypericum perforatum*, *Klasea radiata*, *Linum nervosum*, *L. tenuifolium*, *Lotus corniculatus*, *Nepeta nuda*, *Onobrychis transcaucasica*, *Origanum vulgare*, *Phlomis tuberosa*, *Polygala anatolica*, *Rosa spinosissima*, *Salvia verticillata*, *Scabiosa bipinnata*, *Securigera varia*, *Stachys macrostachys*, *S. recta*, *Stipa pennata*, *S. pulcherrima*, *Teucrium chamaedrys*, *Thalictrum minus*, *Vicia canescens* subsp. *variegata*, *Viola ambigua.*

Ecology and distribution: Mountain steppes in the Transcaucasus form a distinct altitudinal belt above highland xerophyte vegetation (*Cousinio brachypterae-Stipetalia arabicae*) and below mountain meadow steppes (*Plantagini atratae-Bromopsietalia variegatae*). In our dataset, the order is represented by one alliance.

Alliance 2.2.1: *Onobrychido transcaucasicae-Stipion pulcherrimae* – Transcaucasian mountain steppes

Diagnostic species: *Campanula rapunculoides*, *Cerinthe minor*, *Dactylis glomerata*, *Linum nervosum*, *L. tenuifolium*, *Onobrychis transcaucasica*, *Origanum vulgare*, *Scabiosa bipinnata*, *Securigera varia*, *Stachys macrostachys*, *S. recta.*

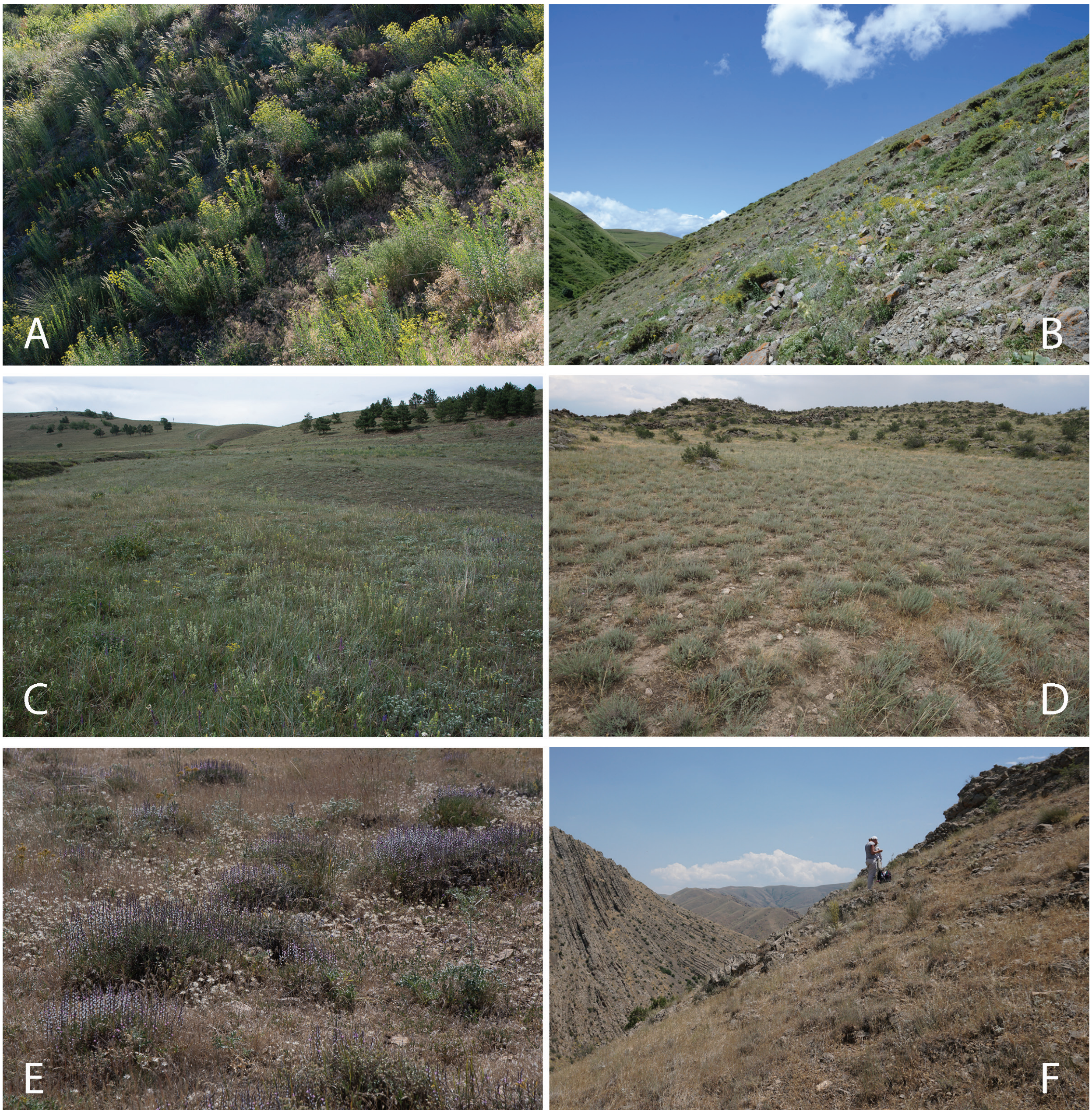

Figure 7. Dry grassland and thorn-cushion communities of Armenia that do not belong to the *Festuco-Brometea*. **A.** *Euphorbia orientalis-Melilotus officinalis* scree community near Hermon (Vayots Dzor Province); **B.** *Stachys lavandulifolia-Astracantha condensata* community (alliance 1.1.1); **C.** *Marrubio parviflorae-Stipetum capillatae* (alliance 1.1.1); **D.** Semi-deserts of the association *Noaeo mucronatae-Artemisietum fragrantis* (alliance 1.1.2); **E.** Highland xerophytic vegetation of the *Acantholimono caryophyllacei-Stipetum holosericeae* (alliance 1.1.3); **F.** *Stachys inflata-Acantholimon vedicum* community (alliance 1.1.3) (Photos: A, C, E: Jürgen Dengler; B: Thomas Becker; D: Denys Vynokurov; F: Dariia Borovyk).

Ecology and distribution: Despite its high floristic heterogeneity, we unite all mountain steppes into one alliance. We distinguish two informal communities and two associations.

2.2.1.1: *Trisetum flavescens-Stachys macrostachys* community (Figure 8C)
Diagnostic species: *Arenaria graminea*, *Artemisia absinthium*, *Chaerophyllum roseum*, *Gagea caroli-kochii*, *Silene cephalantha*, ***Stachys macrostachys***, *Trisetum flavescens*, *Verbascum cheiranthifolium.*

Structure, ecology and distribution: We sampled this vegetation type at the elevations 1,950–2,300 m a.s.l. in Aragatsotn (near Amberd fortress), Gegharkunik (Selim pass, Shorja) and Shirak (vicinity of Amasia) provinces. These communities develop on soils with high humus content. The herb layer is relatively dense with dominance of grasses (*Elytrigia intermedia* aggr., *Phleum nodosum*, *Poa pratensis* aggr., *Trisetum flavescens*) and legumes (*Securigera varia*, *Trifolium alpestre*, *Vicia tenuifolia* subsp. *variabilis*, *V. canescens* subsp. *variegata*).

2.2.1.2: *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community (Figure 8D)
Diagnostic species: *Arabis hirsuta*, *Campanula bononiensis*, *Campyliadelphus chrysophyllus* (B), *Chaerophyllum aureum*, *Daphne oleoides* subsp. *kurdica*, *Helictochloa armeniaca*, ***Klasea radiata***, *Lathyrus latifolius*, ***Linum nervosum***, *Nepeta nuda*, ***Onobrychis transcaucasica***, ***Origanum vulgare***, *Phlomis tuberosa*, *Primula veris* subsp. *macrocalyx*, *Rhinanthus subulatus*, *Salvia nemorosa*, *Securigera varia*, *Seseli libanotis*, *Stachys macrostachys*, *Stipa zalesskii* subsp. *canescens*, ***Thalictrum minus***, *Valeriana officinalis* aggr., *Vicia canescens* subsp. *variegata*, *Viola ambigua*.

Structure, ecology and distribution: We recorded relevés of this community only in the Vayots Dzor province, at north-facing slopes (inclination 10–40°) in the vicinity of Gnishik and between Khachik and Areni. Communities differed by closed herb layer and high litter cover. The species composition is characterised by a high participation of forbs with European distribution, such as *Campanula bononiensis*, *Klasea radiata*, and *Securigera varia*. The dominant species is *Vicia canescens* subsp. *variegata*.

2.2.1.3: *Globulario trichosanthae-Stipetum pulcherrimae* (Figure 8E)
Diagnostic species: central association (no diagnostic species)

Structure, ecology and distribution: We sampled this vegetation type at elevations around 1,900–2,200 m a.s.l. in the provinces of Gegharkunik (Ardanish and vicinity of the town of Sevan), Shirak (Jajur pass) and Vayots Dzor (vicinities of Gnishik, Khachik and Areni). In the species composition, prevailing groups of species were European (*Potentilla recta* aggr., *Stachys recta*, *Stipa pulcherrima*) and Irano-Turanian (*Eryngium billardierei*, *Onobrychis michauxii*, *Thymus kotschyanus*, *Ziziphora clinopodioides*), followed by Caucasian endemics (*Astragalus cancellatus*, *Centaurea pseudoscabiosa*, *Scabiosa bipinnata*). The dominant species of the association was *Stipa pulcherrima*.

2.2.1.4: *Seslerio phleoidis-Onobrychidetum cornutae* (Figure 8F)
Diagnostic species: *Abietinella abietina* (B), *Adonis volgensis*, *Androsace chamaejasme*, *Asperula affinis*, *Asphodeline taurica*, *Briza media*, *Campanula rapunculoides*, *C. sibirica*, *Coronilla coronata*, *Euphorbia esula* aggr., *Euphrasia pectinata*, *Fritillaria caucasica*, *Homalothecium lutescens* (B), *Hypnum cupressiforme* (B), *Leucanthemum vulgare*, *Linum tenuifolium*, *Pimpinella saxifraga* aggr., *Pinus sylvestris*, *Pontechium maculatum*, *Psephellus karabaghensis*, *Sesleria phleoides*, *Spiraea crenata*, *Thalictrum foetidum*, *Viola alba*.

Structure, ecology and distribution: We sampled this association at elevations 1,940–2,070 m a.s.l. in Gegharkunik (Ardanish, Shorja, vicinity of the town of Sevan) and Shirak (Jajur pass) provinces. The association differed by the highest mean total species richness and richness of bryophytes across all studied communities. The species composition is represented by a high participation of European species of grasses and forbs, such as *Briza media*, *Campanula rapunculoides*, *Galium verum*, *Pimpinella saxifraga* aggr., and *Stachys recta*. *Carex humilis*, *Onobrychis cornuta* and *Teucrium chamaedrys* are the dominant species.

Differentiation of the syntaxa with respect to ecology, structure and biodiversity

Topography, climate and soil

Communities within the *Festuco-Brometea* predominantly thrived at higher elevations, especially those of *Plantagini atratae-Bromopsietalia variegatae*, reaching up to 2,400 m a.s.l. (Figure 9A). Generally, they occurred within the elevation range of 1,900–2,400 m a.s.l., with some exceptions, like in the case of the *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community, which were found between 1,700 to 2,100 m a.s.l. These low elevation occurrences were compensated by local topographic preferences, particularly avoidance of drier slopes with a southerly aspect. This community exhibited the lowest southerness index among all syntaxa (Figure 9B).

In contrast, communities of the *Ziziphora tenuior-Stipa arabica* grasslands with its order *Cousinio brachypterae-Stipetalia arabicae* occurred at lower elevations, primarily below 2,000 m a.s.l. Among its three alliances, *Artemision fragrantis*, which comprises wormwood semi-deserts, thrived at the lowest altitudes, ranging from 1,300 to 1,600 m a.s.l. Additionally, the *Stachys inflata-Acantholimon vedicum* community, which belongs to the alliance *Acantholimono caryophyllacei–Stipion holosericeae*, also occupied comparably low elevations, at about 1,600 m a.s.l. Other units of this order generally occupy elevations not exceeding 2,000 m a.s.l.

The altitudinal zonation reflected the climatic preferences of the communities. The *Cousinio brachypterae-Stipetalia arabicae* communities tended to prefer warmer and drier conditions, while the class *Festuco-Brometea* thrived in more mesic and cooler environments (Figure 9C, D).

Regarding soil characteristics, most communities preferred neutral or slightly alkaline soils, except for the order *Plantagini atratae-Bromopsietalia variegatae*, which occurred in slightly acidic soil conditions with a pH around 6.5 (Figure 10A). This variation aligns with the altitudinal zonation, reflecting different soil compositions and vegetation types across elevation levels. Lower and medium elevations (montane and lower subalpine belt) were characterised by kastanozems and chernozems, which hosted semi-desert and steppe vegetation, and had neutral or slightly alkaline reaction. We classified them within the orders *Cousinio brachypterae-Stipetalia arabicae* and *Onobrychido transcaucasicae-Stipetalia pulcherrimae* respectively. Upper subalpine and lower alpine belts were home to meadow-steppe soils and mountain-meadow soils, which were characterised by slightly acidic to acidic reaction. Here, mountain meadow steppe vegetation thrived, which we summarised in the order *Plantagini atratae-Bromopsietalia variegatae*. At even higher altitudes, mountain steppes were replaced by acidophilous alpine grasslands, which were not covered in our study.

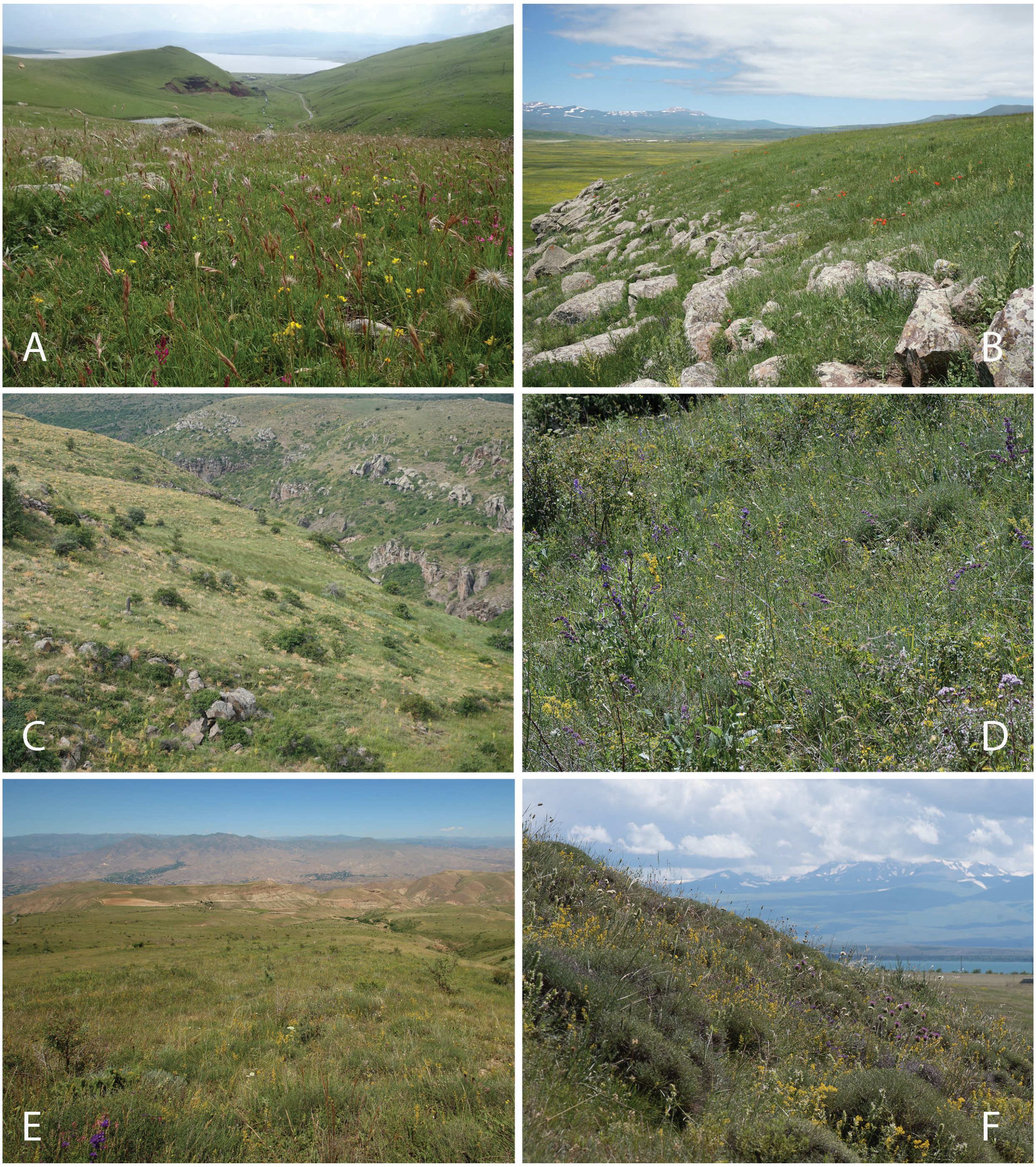

Figure 8. Dry grasslands of Armenia classified within the *Festuco-Brometea*. **A.** Mountain meadow steppes in the Lake Arpi National Park with the association *Ranunculo caucasici-Bromopsietum variegatae* (alliance 2.1.1); **B.** *Tragopogon reticulatus-Astracantha aurea* community (alliance 2.1.1); **C.** *Trisetum flavescens-Stachys macrostachys* community (alliance 2.2.1); **D.** *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* community (alliance 2.2.1); **E.** *Globulario trichosanthae-Stipetum pulcherrimae* (alliance 2.2.1); **F.** mountain steppes near the Sevan Lake with the association *Seslerio phleoidis-Onobrychidetum cornutae* (alliance 2.2.1). (Photos: A: Philipp Kirschner; B, C: Dariia Borovyk; D, F: Jürgen Dengler; E: Denys Vynokurov).

In terms of skeleton content, communities of the *Ziziphora tenuior-Stipa arabica* grasslands generally tended to occur on sites with shallower soils and higher skeleton content (Figure 10B, C). Among them, *Stachys lavandulifolia-Astracantha condensata* community and *Stachys inflata-Acantholimon vedicum* community represent rocky grasslands, and occurred on sites with the highest proportion of gravel in the upper soil level, reaching up to 80% and 90% respectively. Among the communities classified into the class *Festuco-Brometea*, we observed higher heterogeneity. Both units of the order *Plantagini atratae-Bromopsietalia variega-*

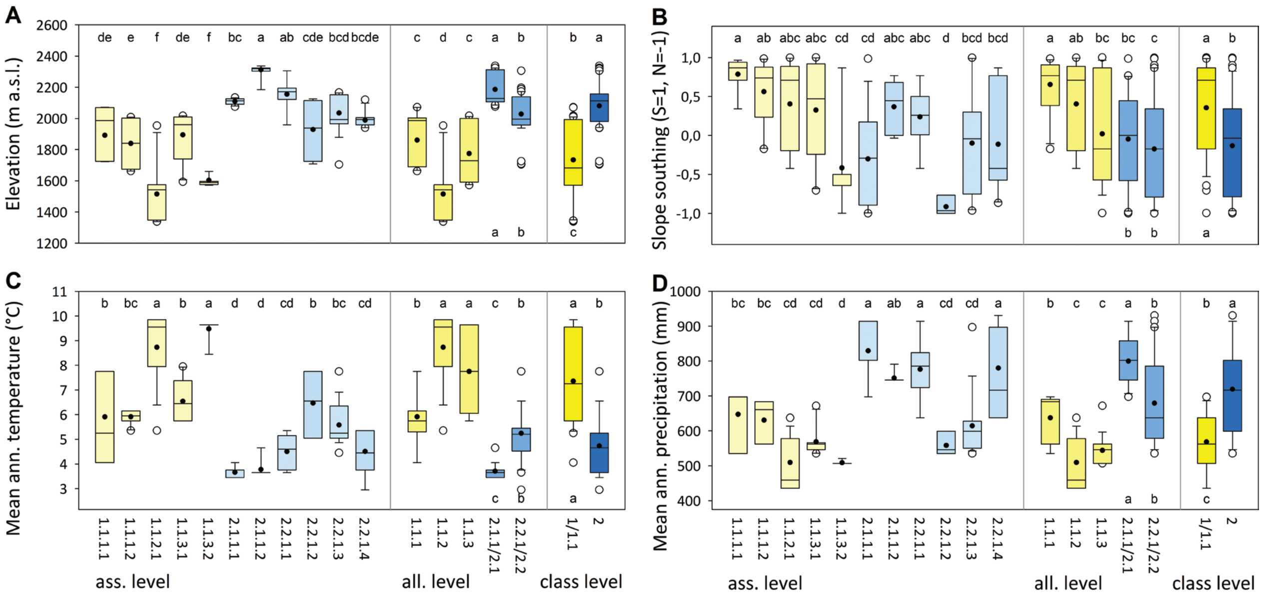

Figure 9. Site characteristics of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

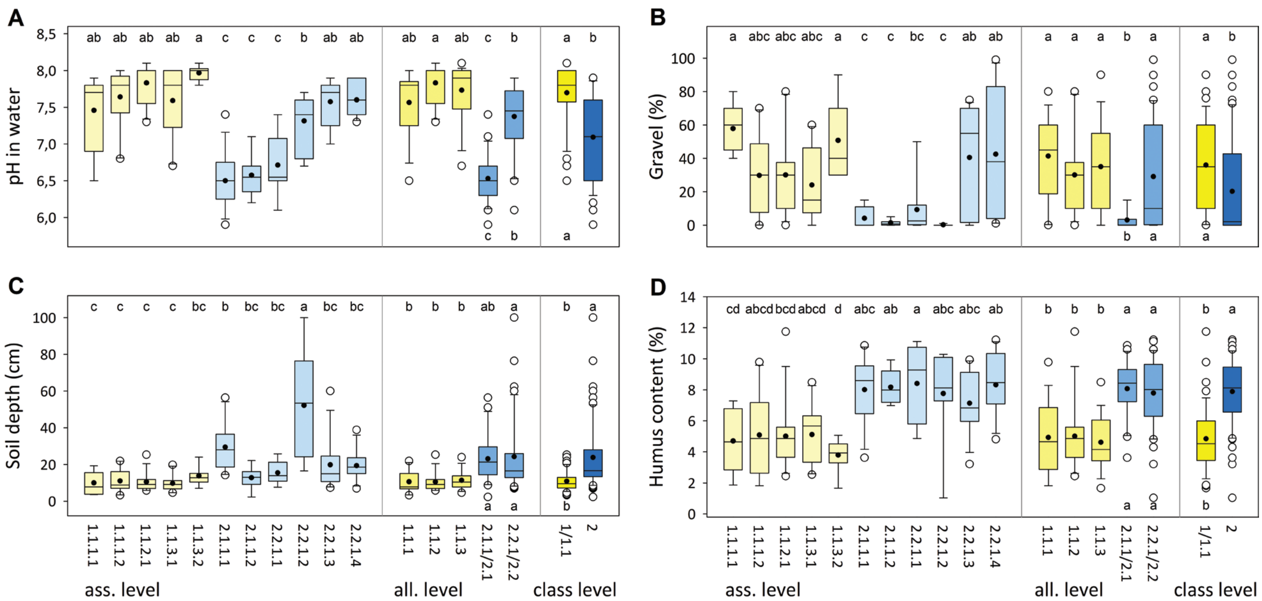

Figure 10. Soil characteristics of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

tae occurred on sites with low gravel content. Among them, *Ranunculo caucasici-Bromopsietum variegatae* was distributed on deeper soils. Mountain steppes of the order *Onobrychido transcaucasicae-Stipetalia pulcherrimae* seemed to occur on sites with varying skeleton proportion. While the *Trisetum flavescens-Stachys macrostachys* and *Onobrychis transcaucasica-Vicia canescens* subsp. *variegata* communities occurred on sites with low gravel proportions, the associations *Globulario trichosanthae-Stipetum pulcherrimae* and *Seslerio phleoidis-Onobrychidetum cornutae* were distributed mainly on rocky sites.

All communities of the class *Festuco-Brometea* tended to occur on sites with high humus content, with mean values within a narrow range of 7.5–8.1%. The tentative *Ziziphora tenuior-Stipa arabica* grasslands occurred on sites with significantly lower humus content, with mean values of 3.9–4.5% (Figure 10D).

Structure and species composition

Herb layer cover and litter cover, proxies for ecosystem productivity, were notably higher in the communities belonging to the class *Festuco-Brometea* (Figure 11A, B).

Regarding the dominant life forms, we observed a strong differentiation between the two classes. Communities belonging to the class *Festuco-Brometea* had a significantly higher proportion of hemicryptophytes, which was highest in the case of the *Ranunculo caucasici-Bromopsietum variegatae* association (Figure 11D). On the contrary, communities of the tentative new class '*Ziziphora tenuior-Stipa arabica* grasslands' had much lower proportions of hemicryptophytes, but a much higher proportion of therophytes (Figure 11C). The proportion of therophytes was particularly high in the case of the alliances *Artemision fragrantis* and *Acantholimono caryophyllacei-Stipion holosericeae*, which represent wormwood desert steppes and xerophytic thorn-cushions respectively. The proportion of chamaephytes was also significantly higher in the case of the latter class (not shown).

The proportion of species' range types also showed a strong differentiation between the two classes (Figure 12). The class *Festuco-Brometea* was characterised by a significantly higher proportion of species with European distribution (Figure 12A). This suggests that the class *Festuco-Brometea* comprises exclusively Euro-Siberian steppe vegetation and that its distribution range reaches a limit in Armenia. This is also well reflected by the co-occurrence of two biogeographic regions: the Euro-Siberian and the Irano-Turanian. On the contrary, the new tentative class '*Ziziphora tenuior-Stipa arabica* grasslands' represents communities with a lower presence of species with European distribution, and significantly higher proportions of species with Mediterranean and Irano-Turanian distribution (Figure 12B, E).

The presence of endemic species in the studied communities was also remarkable. While there were no significant differences detected between the two classes concerning narrow Transcaucasian endemics (Figure 12D), a distinct pattern emerged for the broader Caucasian endemics. These species, ranging across the Caucasus region, including the North Caucasus, were more prevalent in the *Festuco-Brometea* compared to the *Ziziphora tenuior-Stipa arabica* grasslands (Figure 12C). Among the two recognized orders of the *Festuco-Brometea*, the proportion of Caucasian endemics was higher in the *Plantagini atratae-Bromopsietalia variegatae*, which comprises mountain meadow steppes of higher elevations. Overall, we observed an increasing proportion of endemic species alongside elevation. Interestingly, the proportion of species with other distribution ranges, namely, broader than the listed above, was also significantly higher in the case of the *Festuco-Brometea* plant communities (Figure 12F).

Plot-scale species richness

Total species richness in 10 m² did not differ significantly among the higher syntaxa (Figure 13). At the association level, there was no strong differentiation either, with only the *Ranunculo caucasici-Bromopsietum variegatae* and the *Seslerio phleoidis-Onobrychidetum cornutae* being above average and *Tragopogon reticulatus-Astracantha aurea* community below. For vascular plant species richness, the pattern largely matched that of total species richness, while for lichens there were no significant differences at any level. Only bryophytes showed a weak richness pattern at the order and alliance level, with the monotypic order *Plantagini atratae-Bromopsietalia variegatae* being the richest.

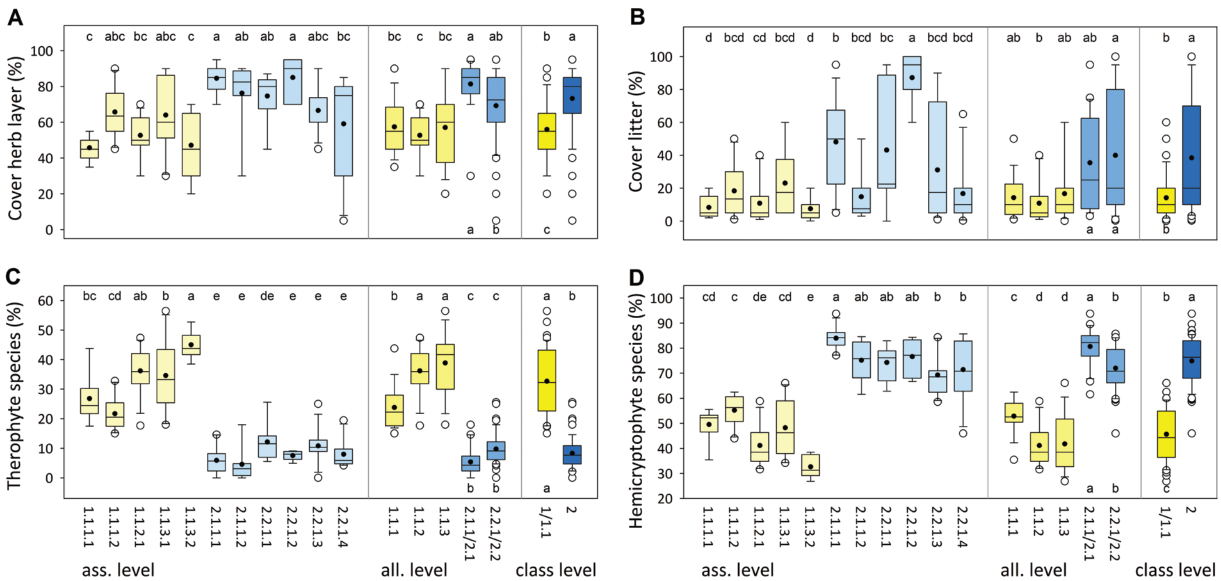

Figure 11. Structure and dominant life forms of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

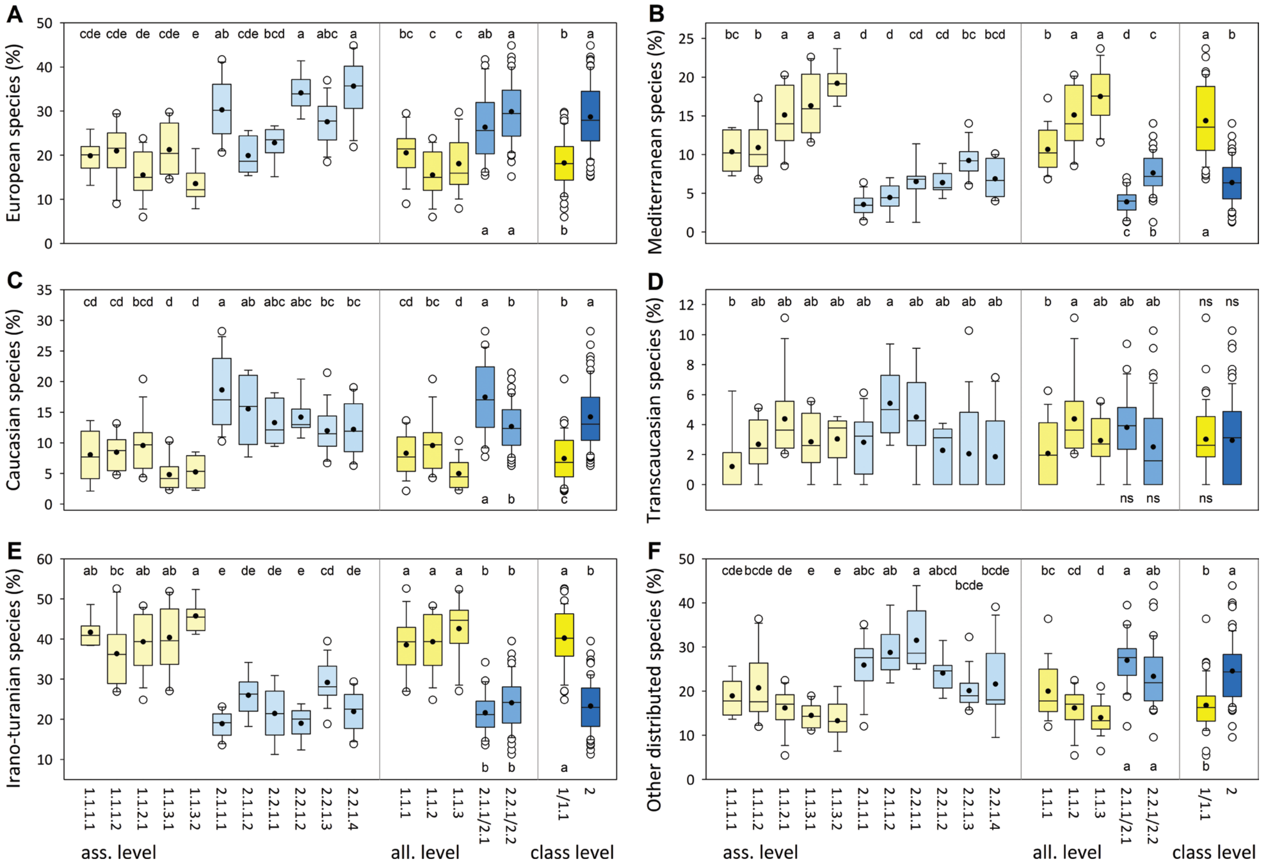

Figure 12. Proportions of range types of the grassland types at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

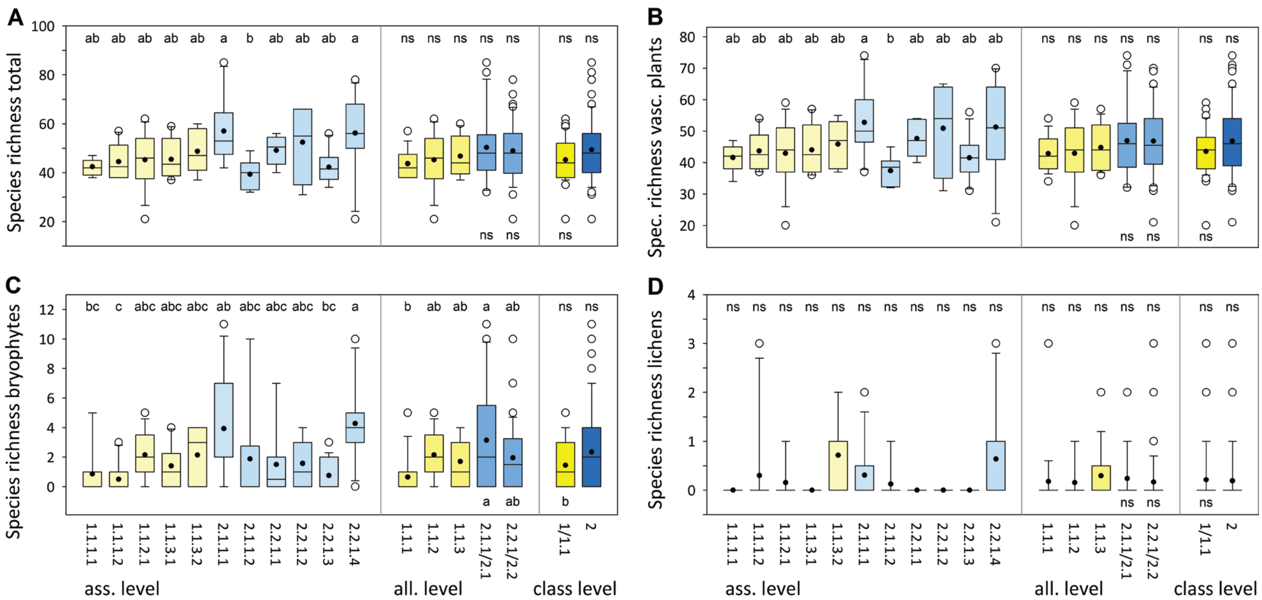

Figure 13. Species richness in 10 m^2-plots for different taxonomic groups compared at different syntaxonomic levels. Box plots (median, interquartile range, range and outliers) as well as arithmetic means (black points) are shown. For the codes of syntaxa, see Table 1. Different letters within one syntaxonomic level indicate significant differences at $p < 0.05$ according to Tukey's test following a significant ANOVA. For orders, the two-digit codes after the slashes and the letters below the boxplots apply.

Discussion

Higher-level units of the dry grasslands and thorn-cushion communities of Armenia

The type of the class *Astragalo-Brometea*, namely the order *Astragalo-Brometalia*, along with other orders traditionally associated with it (*Drabo-Androsacetalia*, *Hyperico linarioidis-Thymetalia scorpilii*, *Onobrychido armenae-Thymetalia leucostomi*), were grouped together as "group A" in the Twinspan analysis (Figure 2). This suggests that these clusters collectively represent the vegetation of the class *Astragalo-Brometea*. Furthermore, although cluster 7 forms a separate group C, it is positioned closer to group A on the DCA ordination. Hence, the order *Festuco oreophilae-Veronicetalia orientalis* may also be considered part of the class *Astragalo-Brometea*, as originally described (Hamzaoğlu 2006). However, more comprehensive data analysis would be needed to clarify if *Festuco oreophilae-Veronicetalia orientalis* belongs to *Astragalo-Brometea* or should form a distinct class uniting Eastern Anatolian tragacanth communities.

Groups B and E comprised plots from meso-xeric, xeric, and rocky grasslands that can be categorised as belonging to the class *Festuco-Brometea*. Whereas plots within group E were previously assigned to order-level units (*Asphodelino tauricae-Euphorbietalia petrophilae*, *Festucetalia valesiacae*, *Brachypodietalia pinnati*), group B did not have any assignments to any syntaxonomic order. Considering the clear separation between group B and group E at the very basis of the dendrogram, and the fact that group B is, in contrast to group E, positioned above the Y-axis in the DCA ordination (Figure 3), we propose establishing a distinct order-level unit for group B. This unit would encompass high-mountain xero-mesic meadow-steppe grassland communities found in the Caucasus, Eastern Anatolia, and Northern Iran, and we suggest naming it "*Plantagini atratae-Bromopsietalia variegatae*" (see below).

Group D encompasses the driest communities sampled in Armenia, particularly cluster 8. The species present in this group are predominantly distributed in the Irano-Turanian region, such as *Artemisia fragrans*, *Eryngium billardierei*, *Noaea mucronata*, *Stipa arabica*, *S. holosericea*, and others. This species composition suggests that similar vegetation types may also exist in other regions of Western Asia. Since there is no suitable class-level unit available, we propose that in the future, a new class should be established. To do so a comprehensive comparison involving more data from the surrounding regions would be needed. For now, in this paper, we refer to this unit as "*Ziziphora tenuior-Stipa arabica* grasslands", combining the dry grassland, semi-desert and xeric thorn-cushion vegetation of Western Asia.

To summarise, we can classify all the vegetation plots of the bigger dataset into three classes: *Astragalo-Brometea* (groups A and C), *Festuco-Brometea* (groups B and E), and a tentative new class, "*Ziziphora tenuior-Stipa arabica* grasslands". This was well supported by the DCA ordination (Figure 3), in which the plots categorised as *Festuco-Brometea* were positioned to the right of the Y-axis, while *Astragalo-Brometea* was positioned on the bottom-left corner of the plot, and "*Ziziphora tenuior-Stipa arabica* grasslands" on the upper-right corner. The chorological analysis (Figure 12) suggests that the "*Ziziphora tenuior-Stipa arabica* grasslands" are an Irano-Turanian vegetation type and may be found in other parts of this region, especially in Western Asia.

Lower-level syntaxonomic units

We can identify two distinct vegetation classes in Armenia: *Festuco-Brometea* and a novel class meant to encompass drier grasslands and thorn-cushion communities found at lower elevations. This finding aligns well with the outcomes of the TWINSPAN analysis of the Armenian plots (Figure 4).

Cluster X in the TWINSPAN dendrogram corresponds to scree vegetation that currently cannot be assigned to any existing vegetation class. It appears to be similar to the *Thlaspietea rotundifolii* Br.-Bl. 1948 from temperate Europe or *Drypidetea spinosae* Quézel 1964 from the Mediterranean. In the North Caucasus, a class of high-altitude scree vegetation on siliceous outcrops, *Lamio tomentosi-Chaerophylletea humilis* Belonovskaya et al. 2014, exists. However, the latter mainly consists of subnival belt vegetation with a completely different floristic composition. Therefore, we cannot currently assign the aforementioned Armenian scree community to any existing class and leave it unassigned.

The remaining clusters in the left part of the dendrogram (clusters 1.1.1.1–1.1.3.2 in Figure 4) can be linked to the proposed new class, informally named '*Ziziphora tenuior-Stipa arabica* grasslands'. The clusters on the right side of the dendrogram (clusters 2.1.1.1–2.2.1.4) are clearly associated with the class *Festuco-Brometea*.

Further examination of the drier part of Armenian plots (clusters 1.1.1.1–1.1.3.2 on the dendrogram, Figure 4) revealed three distinct units corresponding to alliance-level syntaxa. Cluster 1.1.1.1 represented rocky grasslands, cluster 1.1.1.2 consisted of dry grasslands at higher elevations with Irano-Turanian influences, and cluster 1.1.2.1 was related to stony semi-deserts. Clusters 1.1.3.1 and 1.1.3.2 correspond to 'highland xerophytic vegetation' or Minor-Asian thorny-cushion shrubs (as per Makagian 1941). We propose interpreting these units as five associations and communities within three different alliances and one order.

Relevés from clusters 2.1.1.1–2.1.1.2 were previously categorized under group B in the earlier section (broad-scale comparison), together with plots from the North Caucasus belonging to the alliance *Artemisio chamaemelifoliae-Bromopsion variegatae*. Given their separation from the other clusters at a high level (Figure 2), we suggest uniting clusters 2.1.1.1–2.1.1.2 into a new order-level unit named *Plantagini atratae-Bromopsietalia variegatae* (see below). This new order is ecologically similar to the *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (Willner et al. 2019; Dengler and Willner 2023). Both unite meso-xeric grasslands and share several common diagnostic species, such as *Brachypodium pinnatum*, *Filipendula vulgaris*, *Pimpinella saxifraga* aggr., *Stipa tirsa*, as well as several mesophilic species, including *Achillea millefolium* aggr., *Schedonorus pratensis*, *Festuca rubra* aggr., *Lotus corniculatus*, and *Potentilla argentea*. However, the new order is clearly distinguished by the presence of numerous Caucasian endemics and species of Irano-Turanian distribution among the diagnostic species, such as *Bromopsis variegata*, *Campanula collina*, *Gentiana septemfida*, *Huynhia pulchra*, *Koeleria albovii*, *Psephellus xanthocephalus*, *Pulsatilla albana*, *Ranunculus caucasicus*, and others. Additionally, this order is distinguished by the presence of high-mountain species of broader distribution, such as *Aster alpinus*, *Phleum alpinum*, and *Plantago atrata*.

Clusters 2.2.1.1–2.2.1.4 corresponded to the so-called mountain steppes, following the classification of Makagian (1941). These clusters are linked to the class *Festuco-Brometea* within a new order *Onobrychido transcaucasicae-Stipetalia pulcherrimae* and a new alliance *Onobrychido transcaucasicae-Stipion pulcherrimae*, which unite the Transcaucasian mountain steppes.

Biodiversity and ecology of the studied communities

With an average of 46.8 vascular plants in 10 m^2, the dry grasslands of Armenia were significantly richer than the Palaearctic average of the three relevant ecological-physiognomic vegetation types (A.3 - Xeric grasslands and steppes; B.2 - Meso-xeric grasslands; D.3 - Garrigues and thorn-cushion communities) in the high-quality database GrassPlot (v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; see Biurrun et al. 2021) with 35.8 species. By contrast, bryophytes (0.4 vs. 3.0 species) and lichens (0.1 vs. 0.9 species) were clearly poorer than in dry grasslands elsewhere. The difference is even more pronounced when comparing with the dry grasslands of the central valleys of the Alps, where Bergauer et al. (2022) reported averages of 35.1 vascular plant, 3.9 bryophyte and 1.9 lichen species in the same plot size. For the inneralpine dry grasslands of Austria, Magnes et al. (2021) reported even a slightly lower richness of vascular plants (34.2), but a slightly higher of bryophytes and lichens combined (6.1) than in Switzerland. Thus, it is astonishing why the Armenian dry grasslands deviate so strongly by higher small-scale vascular plant richness and lower bryophyte and lichen richness not only from the Palaearctic average but also from the dry grasslands in the central valleys of the Alps that should share similarities with the central valleys of the Caucasus. One explanation for the higher density of species in Armenia and also in the Italian Apennines (49.5 species in 10 m^2, Filibeck et al. 2018) could lie in the glaciations (Bergauer et al. 2022). While during the Pleistocene the valleys of the Alps were almost entirely filled by glaciers, in the case of the Caucasus and the Apennines only local glaciers on mountain tops occurred (Aseev et al. 1984), which could mean that the vascular plant flora of the Alpine valleys is simply so impoverished that no more species for higher plot-scale richness are available. By contrast, bryophytes and lichens should be much less affected by the glaciations as their spores are so much lighter than seeds of vascular plants, that they hardly suffer from dispersal limitations. One potential explanation for the very low richness of non-vascular taxa in Armenia could be that the majority of bryophyte and lichen taxa is adapted to cooler climate, while the mean annual temperature in Armenia is higher than in the Alps. However, both potential explanations are not much more than speculations at present. Moreover, while essentially in any region where EDGG studied dry grasslands before, the meso-xeric types were much richer at plot scale than the xeric types (Dengler et al. 2012; Magnes et al. 2021), we did not find a significant richness difference between our more xeric class 1 (*Ziziphora tenuior-Stipa arabica* grasslands) and the less xeric class 2 (*Festuco-Brometea*) (Figure 13). All these unexpected patterns and our *ad hoc* explanations call to be tested with a comprehensive dataset that contains standardized richness data for dry grasslands in many different situations in the Palaearctic, such as the GrassPlot database (Dengler et al. 2018).

Conclusions and outlook

Despite having compiled the available vegetation plot data, particularly the type relevés, of the relevant syntaxa described in the other countries of the Caucasus as well as Anatolia and Northern Iran, we found low correspondence of the Armenian dry grassland communities with these. It appears that only one of our five alliances had been described before, the *Artemisio chamaemelifoliae-Brompsion variegatae* from the Northern Caucasus, Russia (Vynokurov et al. 2021). We thus had to describe most of the syntaxa from associations to orders as new to science, and it will be interesting to see whether some of them will also be found in the future in neighbouring countries. To make these findings accessible in the updates of the EuroVegChecklist (Mucina et al. 2016; Preislerová et al. 2022; see https://floraveg.eu/vegetation/), we have prepared an application to the EuroVegChecklist Committee (EVCC) (Suppl. material 8) for consideration (for the procedure, see Biurrun and Willner 2020).

Even at the class level we found that the more xeric dry grassland of the lower elevations in Armenia are floristically so profoundly different from either the Euro-Siberian *Festuco-Brometea* or the Anatolian-Iranian *Astragalo-Brometea* that they might be a class of their own. However, a formal description should wait for a plot-based broad-scale classification of all the dry grasslands in the Caucasus, Anatolia and Northern Iran, similar to the studies of Eastern and Central Europe by Willner et al. (2017, 2019). Such an attempt would be facilitated in the future by the growing Iranian Vegetation Plot database (A. Naqinezhad, pers. comm.), the Turkish Non-Forest database (B. Güler, pers. comm.) and the Transcaucasian Vegetation Database (Novák et al. 2023a). If the "*Ziziphora tenuior-Stipa arabica* grasslands" should turn out to be a valid class also from the supra-national perspective, this would also impact the current European consensus vegetation classification system, which also includes the three South Caucasus countries (EuroVegChecklist; Mucina et al. 2016; with updates at https://floraveg.eu/vegetation/). It would add additional higher-rank syntaxa, but also several species currently considered as sole diagnostic species of the class *Festuco-Brometea* (Mucina et al. 2016) would not be that anymore as they are equally or even more frequent in the *Ziziphora tenuior-Stipa arabica* grasslands, for example, *Stipa capillata* or *Festuca valesiaca* aggr.

Within Armenia, the next logical step would be to compile more plot data of dry grasslands with the same methodology to ensure that the system is complete and all the determined diagnostic species can be confirmed. Then the system could be translated into an electronic expert system that enables the automatic and unequivocal classification of new dry grassland plots (see the example by Garcia-Míjangos et al. 2021). We hope that our pioneer survey will motivate Armenian researchers to apply similar approaches to other main vegetation types to allow comparable diverse analyses as well as the integration into the European habitat classification system EUNIS (Chytrý et al. 2020). While it is still a long way, ultimately a comprehensive plot-based vegetation typology as it exists in other countries of the Western Palaearctic (e.g. Schaminée et al. 1995 et seq.; Berg et al. 2001 et seq.; Chytrý 2007 et seq.) could become a powerful tool for conservation, applied and fundamental research.

Finally, our collected data of biodiversity, species composition and in situ environmental variables are also valuable for broad-scale analyses on biodiversity patterns and their drivers, global change projections and biogeographic analyses. For this purpose, we have already contributed them to the relevant international plot databases, namely EVA (Chytrý et al. 2016), sPlot (Bruelheide et al. 2019) and GrassPlot (Dengler et al. 2018).

Data availability

All original data from Armenia (species composition and header data as well as derived metrics of the plots) are provided in the Supplementary materials of this article.

Author contributions

A.A. and G.F. organised the 13th EDGG Field Workshop in Armenia, and together with A.B., A.H., D.F., D.B, D.V., I.B., I.G.-M., I.V., J.D., M.M., M.O., P.K., S.P., T.B. and U.B. collected the field data. A.A. and G.F. determined vascular plant specimens collected during the Field Workshop, I.D. critical Festuca species, D.B and D.V *Stipa* species, B.C.-M. bryophytes and H.M. lichens. A.B., D.B., D.V., I.B., I.V. and S.P. digitised the field forms and harmonised the data. D.V. performed the literature search and digitised vegetation plots from neighbouring countries. D.V. classified the relevés of the national and the supranational dataset and together with J.D. and developed the classification system for Armenia. J.D. determined the diagnostic species in the Armenian dataset and prepared the synoptic tables. T.B. assigned the life forms; D.V., T.B., and G.F. classified species distribution ranges. D.B. prepared the maps; T.B. performed the ANOVAs and prepared the boxplots and M.M. performed the ordinations. The manuscript was drafted by D.V. and J.D. with significant inputs by A.A., D.B., I.B., I.G.-M. and T.B. All authors checked, improved and approved the manuscript.

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Appendix 1

Formal descriptions of the new syntaxa according to the ICPN

For the diagnostic species we refer to the main text as well as Table 2 and Suppl. material 2.

1.1 *Cousinio brachypterae-Stipetalia arabicae* ord. nov. hoc loco

Holotypus hoc loco: *Artemision fragrantis* Vynokurov et al. 2024 (this paper)

2.1 *Plantagini atratae-Bromopsietalia variegatae* ord nov. hoc loco

Holotypus hoc loco: *Artemisio chamaemelifoliae-Bromopsion variegatae* Vynokurov in Vynokurov et al. 2021 (page 186)

2.2 *Onobrychido transcaucasicae-Stipetalia pulcherrimae* ord. nov. hoc loco

Holotypus hoc loco: *Onobrychido transcaucasicae-Stipion pulcherrimae* Vynokurov et al. 2024 (this paper)

1.1.1 *Onobrychido michauxii-Stipion capillatae* all. nov. hoc loco

Holotypus hoc loco: *Marrubio parviflorae-Stipetum capillatae* Vynokurov et al. 2024 (this paper)

1.1.2 *Artemision fragrantis* all. nov. hoc loco

Holotypus hoc loco: *Noaeo mucronatae-Artemisietum fragrantis* Vynokurov et al. 2024 (this paper)

1.1.3 *Acantholimono caryophyllacei-Stipion holosericeae* all. nov. hoc loco

Holotypus hoc loco: *Acantholimono caryophyllacei-Stipetum holosericeae* Vynokurov et al. 2024 (this paper)

2.2.1 *Onobrychido transcaucasicae-Stipion pulcherrimae* all. nov. hoc loco

Holotypus hoc loco: *Seslerio phleoidis-Onobrychidetum cornutae* Vynokurov et al. 2024 (this paper)

1.1.1.2 *Marrubio parviflorae-Stipetum capillatae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 81 in Suppl. material 2 (original code AMR008); Armenia, Lori Province, vicinity of Shirakamut, 40.85801°N, 44.19223°E, altitude: 1,662 m a.s.l., aspect: 210°, inclination: 40°, 27 June 2019, authors of the relevé: Dieter Frank, Salza Palpurina, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Elytrigia intermedia* aggr. 10, *Marrubium parviflorum* 10, *Achillea arabica* 5, *Teucrium polium* 5, *Onobrychis michauxii* 4, *Artemisia austriaca* 3, *Thymus sipyleus* 3, *Medicago x varia* 2, *Cota melanoloma* 1, *Festuca valesiaca* aggr. 1, *Iris pumila* 1, *Isatis steveniana* 1, *Psephellus zuvandicus* 1, *Xeranthemum longepapposum* 1, *Ajuga chamaepitys* subsp. *chia* 0.5, *Asperula arvensis* 0.5, *Dactylis glomerata* 0.5, *Odontarrhena muralis* 0.5, *Stachys recta* 0.5, *Viola ambigua* 0.5, *Holosteum umbellatum* 0.3, *Nonea pulla* 0.3, *Scleranthus annuus* 0.3, *Convolvulus lineatus* 0.2, *Euphorbia condylocarpa* 0.2, *Stipa capillata* 0.2, *Zeravschania pauciradiata* 0.2, *Centaurea ovina* aggr. 0.1, *Salvia nemorosa* 0.1, *Stipa arabica* 0.1, *Thesium arvense* 0.1, *Falcaria vulgaris* 0.01, *Meniocus linifolius* 0.01, *Nepeta racemosa* 0.01, *Noccaea perfoliata* 0.01, *Reseda lutea* 0.01, *Veronica multifida* 0.01, *Viola arvensis* aggr. 0.01.

1.1.2.1 *Noaeo mucronatae-Artemisietum fragrantis* ass. nov. hoc loco

Holotypus hoc loco: plot ID 65 in Suppl. material 2 (original code AM11NE); Armenia, Aragatsotn Province, vicinity of Dashtadem, 40.32428°N, 43.85075°E, altitude: 1,357 m a.s.l., aspect: 265°, inclination: 7°, 29 June 2019, authors of the relevé: Alla Aleksanyan, Jürgen Dengler, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Poa bulbosa* 20, *Artemisia fragrans* 17, *Peganum harmala* 10, *Taeniatherum caput-medusae* subsp. *crinitum* 10, *Stipa arabica* 1, *Androsace albana* 0.5, *Koelpinia linearis* 0.5, *Stipa x kolakovskyi* 0.5, *Allium pseudoflavum* 0.2, *Crupina vulgaris* 0.2, *Minuartia hamata* 0.2, *Noaea mucronata* 0.2, *Arenaria serpyllifolia* aggr. 0.1, *Alyssum turkestanicum* 0.1, *Astragalus hyalolepis* 0.1, *Cousinia brachyptera* 0.1, *Erysimum gelidum* 0.1, *Odontarrhena tortuosa* 0.1, *Sclerocaryopsis spinocarpos* 0.1, *Syntrichia caninervis* 0.1, *Xeranthemum squarrosum* 0.1, *Aegilops cylindrica* 0.01, *Ceratocephala falcata* 0.01, *Cota triumfettii* 0.01, *Dianthus crinitus* 0.01, *Draba verna* 0.01, *Euphorbia seguieriana* 0.01, *Helichrysum plicatum* 0.01, *Hohenackeria exscapa* 0.01, *Holosteum umbellatum* 0.01, *Linaria simplex* 0.01, *Medicago medicaginoides* 0.01, *Meniocus linifolius* 0.01, *Minuartia meyeri* 0.01, *Polygala hohenackeriana* 0.01, *Thesium szovitsii* 0.01, *Thymus collinus* 0.01.

1.1.3.1 *Acantholimono caryophyllacei-Stipetum holosericeae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 71 in Suppl. material 2 (original code AMR035); Armenia, Vayots Dzor Province, vicinity of Khachik, 39.659529°N, 45.201325°E, altitude: 2,017 m a.s.l., aspect: 315°, inclination: 9°, 4 July 2019, authors of the relevé: Alla Aleksanyan, Idoia Biurrun, Dariia Borovyk. Floristic composition (species sorted by their cover in percent): *Chardinia orientalis* 35, *Acantholimon caryophyllaceum* 25, *Taeniatherum caput-medusae* subsp. *crinitum* 20, *Poa bulbosa* 15, *Anisantha tectorum* 10, *Syntrichia ruralis* 6, *Eryngium billardierei* 5, *Onobrychis cornuta* 3, *Medicago sativa* 2, *Stipa ehrenbergiana* 0.5, *Stipa holosericea* 2, *Teucrium polium* 2, *Achillea arabica* 0.5, *Convolvulus lineatus* 0.5, *Gagea germainae* 0.5, *Xeranthemum squarrosum* 0.3, *Ziziphora capitata* 0.3, *Centaurea virgata* 0.2, *Hypericum scabrum* 0.2, *Rochelia disperma* 0.2, *Alyssum turkestanicum* 0.1, *Asperula arvensis* 0.1, *Bromus danthoniae* 0.1, *Bromus japonicus* 0.1, *Ceratocephala falcata* 0.1, *Crepis sancta* 0.1, *Euphorbia iberica* 0.1, *Hordeum bulbosum* 0.1, *Marrubium parviflorum* 0.1, *Odontarrhena tortuosa* 0.1, *Potentilla recta* aggr. 0.1, *Thymus kotschyanus* 0.1, *Alyssum alyssoides* 0.01, *Arenaria serpyllifolia* aggr. 0.01, *Caucalis platycarpos* 0.01, *Holosteum umbellatum* 0.01, *Minuartia meyeri* 0.01, *Noccaea perfoliata* 0.01, *Veronica denudata* 0.01.

2.1.1.1 *Ranunculo caucasici-Bromopsietum variegatae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 18 in Suppl. material 2 (original code AM06NW); Armenia, Shirak Province, vicinity of Zorakert, 41.10135°N, 43.66933°E, altitude: 2,114 m a.s.l., aspect: 255°, inclination: 35°, 28 June 2019, authors of the relevé: Elena Belonovskaya, Jürgen Dengler, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Thymus sipyleus* 25, *Achillea millefolium* aggr. 15, *Phleum alpinum* 15, *Koeleria macrantha* 12, *Festuca ovina* aggr. 10, *Astragalus incertus* 8, *Carex humilis* 8, *Trifolium ambiguum* 7, *Bromopsis variegata* 5, *Hypnum cupressiforme* 5, *Lotus corniculatus* 5, *Medicago falcata* 5, *Abietinella abietina* 2, *Myosotis alpestris* 2, *Poa pratensis* aggr. 2, *Bryum caespiticium* 1, *Plantago atrata* 1, *Securigera varia* 1, *Weissia brachycarpa* 1, *Avenula pubescens* 0.5, *Streblotrichum convolutum* 0.5, *Cirsium leucocephalum* 0.5, *Gelasia rigida* 0.5, *Huynhia pulchra* 0.5, *Lomelosia caucasica* 0.5, *Rumex acetosella* 0.5, *Scabiosa bip-

innata 0.5, *Stachys recta* 0.5, *Carex caryophyllea* 0.3, *Hypericum linarioides* 0.3, *Poa badensis* 0.3, *Potentilla argentea* 0.3, *Schedonorus pratensis* 0.3, *Taraxacum* sect. *Taraxacum* 0.3, *Teucrium orientale* 0.3, *Veronica denudata* 0.3, *Galium verum* 0.2, *Papaver monanthum* 0.2, *Pimpinella saxifraga* aggr. 0.2, *Potentilla recta* aggr. 0.2, *Ajuga orientalis* 0.1, *Alyssum alyssoides* 0.1, *Arenaria blepharophylla* aggr. 0.1, *Arenaria gypsophiloides* 0.1, *Artemisia absinthium* 0.1, *Bupleurum falcatum* aggr. 0.1, *Campanula stevenii* 0.1, *Cirsium obvallatum* 0.1, *Colchicum trigynum* 0.1, *Galium cordatum* 0.1, *Linaria schelkownikowii* 0.1, *Pedicularis condensata* 0.1, *Phascum cuspidatum* 0.1, *Ranunculus caucasicus* 0.1, *Scleranthus perennis* 0.1, *Silene bupleuroides* 0.1, *Silene chlorantha* 0.1, *Syntrichia montana* 0.1, *Bryum argenteum* 0.01, *Crepis alpina* 0.01, *Draba nemorosa* 0.01, *Encalypta vulgaris* 0.01, *Herniaria incana* 0.01, *Muscari armeniacum* 0.01, *Polygala alpicola* 0.01, *Polygonum cognatum* 0.01, *Sedum acre* 0.01.

2.2.1.3 *Globulario trichosanthae-Stipetum pulcherrimae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 93 in Suppl. material 2 (original code AM42SE); Armenia, Vayots Dzor Province, vicinity of Gnishik, 39.675269°N, 45.30616°E, altitude: 2,136 m a.s.l., aspect: 80°, inclination: 23°, 3 July 2019, authors of the relevé: Asun Berastegi, Idoia Biurrun, Denys Vynokurov. Floristic composition (species sorted by their cover in percent): *Ziziphora clinopodioides* 15, *Koeleria macrantha* 7, *Stipa capillata* 7, *Dactylis glomerata* 5, *Stipa pulcherrima* 5, *Hypericum scabrum* 4, *Onobrychis cornuta* 4, *Helichrysum graveolens* 3, *Lotus corniculatus* 2, *Odontarrhena tortuosa* 2, *Teucrium chamaedrys* 2, *Teucrium polium* 2, *Centaurea ovina* aggr. 1, *Daphne oleoides* subsp. *kurdica* 1, *Eryngium billardierei* 1, *Galium verticillatum* 1, *Galium verum* 1, *Linum tenuifolium* 1, *Medicago sativa* 1, *Stipa pennata* 1, *Cichorium intybus* 0.5, *Cruciata laevipes* 0.5, *Cuscuta epithymum* 0.5, *Euphorbia seguieriana* 0.5, *Hypericum linarioides* 0.5, *Plantago lanceolata* 0.5, *Scabiosa bipinnata* 0.5, *Securigera varia* 0.5, *Stipa tirsa* 0.5, *Tanacetum polycephalum* subsp. *argyrophyllum* 0.5, *Globularia trichosantha* 0.3, *Leontodon hispidus* 0.3, *Stachys lavandulifolia* 0.3, *Stachys recta* 0.3, *Ajuga chamaepitys* subsp. *chia* 0.2, *Cerinthe minor* 0.2, *Leontodon asperrimus* 0.2, *Linum nervosum* 0.2, *Phleum phleoides* 0.2, *Poa bulbosa* 0.2, *Tragopogon sosnowskyi* 0.2, *Verbascum chaixii* subsp. *austriacum* 0.2, *Astragalus cancellatus* 0.1, *Bupleurum falcatum* aggr. 0.1, *Carlina vulgaris* 0.1, *Sanguisorba minor* 0.1, *Silene bupleuroides* 0.1, *Thesium arvense* 0.1, *Trinia glauca* 0.1, *Veronica microcarpa* 0.1, *Achillea millefolium* aggr. 0.01, *Agrimonia eupatoria* 0.01, *Crepis pulchra* 0.01, *Euphrasia pectinata* 0.01, *Odontites aucheri* 0.01, *Polygala alpicola* 0.01.

2.2.1.4 *Seslerio phleoidis-Onobrychidetum cornutae* ass. nov. hoc loco

Holotypus hoc loco: plot ID 13 in Suppl. material 2 (original code AMR076); Armenia, Gegharkunik Province, vicinity of Shoghakat, 40.49547°N, 45.29575°E, altitude: 1,959 m a.s.l., aspect: 305°, inclination: 30°, 1 July 2019, authors of the relevé: George Fayvush, Salza Palpurina, Iulia Vasheniak. Floristic composition (species sorted by their cover in percent): *Carex humilis* 20, *Onobrychis cornuta* 15, *Elytrigia intermedia* aggr. 8, *Primula veris* subsp. *macrocalyx* 7, *Thymus kotschyanus* 7, *Stipa pulcherrima* 6, *Onobrychis transcaucasica* 5, *Scutellaria orientalis* aggr. 5, *Galium verum* 4, *Inula aspera* 4, *Helianthemum nummularium* 2, *Sesleria phleoides* 2, *Teucrium chamaedrys* 2, *Abietinella abietina* 1, *Bromus scoparius* 1, *Campanula sibirica* 1, *Euphorbia iberica* 1, *Homalothecium lutescens* 1, *Hypnum cupressiforme* 1, *Linum tenuifolium* 1, *Lotus corniculatus* 1, *Medicago sativa* 1, *Syntrichia ruralis* 1, *Ziziphora clinopodioides* 1, *Achillea millefolium* aggr. 0.5, *Astracantha stenonychioides* 0.5, *Campanula rapunculoides* 0.5, *Dianthus cretaceus* 0.5, *Filipendula vulgaris* 0.5, *Linum nervosum* 0.5, *Plantago media* 0.5, *Polygala anatolica* 0.5, *Scabiosa bipinnata* 0.5, *Stachys recta* 0.5, *Thalictrum foetidum* 0.5, *Jurinea squarrosa* 0.3, *Viola ambigua* 0.3, *Phleum phleoides* 0.2, *Poa badensis* 0.2, *Psephellus karabaghensis* 0.2, *Tanacetum aureum* 0.2, *Convolvulus lineatus* 0.1, *Festuca valesiaca* aggr. 0.1, *Pontechium maculatum* 0.1, *Tragopogon reticulatus* 0.1, *Xanthoparmelia camtschadalis* 0.1, *Asperula prostrata* 0.01, *Carum caucasicum* 0.01, *Cetraria ericetorum* 0.01, *Euphrasia sevanensis* 0.01, *Hypericum scabrum* 0.01, *Orobanche alsatica* 0.01, *Teucrium orientale* 0.01.

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Supplementary material

Supplementary material 1
Complete header data of the Armenian plots (*.xlsx)
Link: https://doi.org/10.3897/VCS.119253.suppl1

Supplementary material 2
Complete synoptic table of 110 classified Armenian plots with percent constancies and phi values for the syntaxa of all levels as well as the individual plots (*.xlsx)
Link: https://doi.org/10.3897/VCS.119253.suppl2

Supplementary material 3
Definition of additional species aggregates (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl3

Supplementary material 4
Value distribution of all recorded and analysed numerical environmental, structural and biodiversity variables (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl4

Supplementary material 5
Data sources of the West Asian and Caucasian dataset (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl5

Supplementary material 6
List of the vascular plants from the Armenian dataset with assignment of life forms and distribution ranges (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl6

Supplementary material 7
Synoptic table of the West Asian and Caucasian dataset with the results of the broad-scale comparison with five distinguished groups of clusters (A–E) (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl7

Supplementary material 8
Planned applications to the EuroVegChecklist Committee (EVCC) (*.pdf)
Link: https://doi.org/10.3897/VCS.119253.suppl8