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Abstract

Aims: Developing a hierarchical classification system for classes, orders and alliances of the diverse dry grasslands of the Central and Eastern Balkan Peninsula and translating this into an electronic expert system (ES) for the automatic assignment of plots.

Location: Serbia, Kosovo, North Macedonia, Bulgaria and northern Greece.

Methods: We extracted 5734 plots from the Balkan Dry Grassland Database corresponding to eight classes of dry grasslands reported from the region, using the EuroVegChecklist ES. This data set and later the plots within each derived subunit were subjected to a new numerical approach: starting with an initial partitioning (expert-interpreted TWINSpan classification), diagnostic species were determined based on their phi-values for the target vegetation type and the differences in phi-values to the next similar types. These diagnostic species were fed into an ES to create a new partitioning, a procedure which was iterated until diagnostic species and species of the ES converged. Then the same approach was applied within each of the derived units to define the units of the next-lower level.

Results: The iterative cluster optimisation (ICO) converged in all cases. The resulting hierarchical expert system (HES) classified 95% of all plots to alliances. We distinguished

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four classes with eight orders and 12 alliances: (1) *Tuberarietea guttatae* (*Romuleion*); (2) *Stipo-Brachypodietea distachyi* (*Clinopodio alpini-Thymion striati*); (3) *Festuco-Brometea* with *Brachypodietalia pinnati* (*Chrysopogono-Danthonion calycinae* and *Cirsio-Brachypodion pinnati*), *Festucetalia valesiaca* (*Festucion valesiaca*), an unnamed order of rocky steppes (with *Pimpinello-Thymion zygioidis*) and *Koelerietalia splendentis* (*Centaureo-Bromion fibrosi*, *Saturejion montanae* and *Diantho haematocalycis-Festucion hirtovaginatae*); (four) *Koelerio-Corynephoretea* with *Sedo acris-Festucetalia* (*Festucion vaginatae*) and *Trifolio arvensis-Festucetalia ovinae* (*Armerio rumelicae-Potentillion* and *Minuartio montanae-Poion molinerii* all. nov.).

Conclusions: We created a unified hierarchical classification with an electronic ES using diagnostic species defined by phi-values. Our new approach (ICO-HES: iterative cluster optimisation for hierarchical expert systems) allows dividing large data sets into meaningful units at several hierarchical levels, and thus has high potential for complex classifications. Importantly, it overcomes the divide between ES species and diagnostic species and re-unites them into one concept.

KEYWORDS

Balkan, diagnostic species, dry grassland, *Festuco-Brometea*, iterative cluster optimisation for hierarchical expert systems (ICO-HES), *Koelerio-Corynephoretea*, phytosociological nomenclature, semisupervised classification, *Stipo-Brachypodietea distachya*, *Tuberarietea guttatae*, TWINSpan, vegetation classification

1 | INTRODUCTION

The Balkan Peninsula is a biodiversity hotspot of Europe, both in terms of species richness and number of endemics (Stevanović et al., 2007). The Balkan dry grasslands harbour high plot-scale species richness (' α -diversity'; e.g. Pedashenko et al., 2013; Palpurina et al., 2015, Dembicz et al., 2021). They occur on various bedrock types and under different climatic conditions at the intersection of continental (steppic), nemoral (Central European), Mediterranean and alpine biogeographical influences (Horvat et al., 1974; Palpurina et al., 2015). Thus, Balkan dry grasslands show enormous variation in species composition and can be assigned to many different vegetation types (' β -diversity'; e.g. Horvat et al., 1974; Pedashenko et al., 2013; Ačić et al., 2015; Matevski et al., 2018). The traditional land use that was pivotal for the development of semi-natural dry grasslands on the Balkan Peninsula remains important for their maintenance, especially considering that this region is one of the few in Europe where high-value grasslands with significant ecological value have survived to date over large areas (Veen et al., 2009; Török et al., 2018, 2020).

The first phytosociological studies of dry grasslands in the Central and Eastern Balkans were conducted from the 1950s onwards (e.g. Serbia: Jovanović-Dunjić, 1955; Bulgaria: Velchev, 1962; North Macedonia: Micevski, 1971a, 1971b). In a monograph of the vegetation of the Balkan Peninsula, Horvat et al. (1974) synthesised the hitherto disparate and mainly local studies to a Southeast European overview. In subsequent decades, only few studies dealt with grassland classification in the region. A renewed interest in

syntaxonomy and better international mobility of vegetation ecologists in the Balkans in the early 21st century led to a series of local and regional studies of individual dry-grassland types (e.g. Millaku et al., 2011; Čušterevska et al., 2012; Kabaš et al., 2013; Fotiadis et al., 2014; Pirini et al., 2014; Sopotlieva & Apostolova, 2014). Up to now, however, only few studies have revised a group of dry-grassland types for a larger region or a whole country based on the analysis of plot data. Most notable are Ačić et al. (2014, 2015: all dry grasslands of Serbia), Bergmeier et al. (2009: serpentine grasslands in N Greece), Matevski et al. (2015: rocky grasslands in SW and W North Macedonia), Pedashenko et al. (2013: all types of dry grasslands in parts of NW Bulgaria), Tzonev et al. (2006: *Pimpinello-Thymion* in NE Bulgaria) and Vassilev, Apostolova, and Pedashenko (2012: *Festuco-Brometea* in W Bulgaria). Only Kuzmanović et al. (2016: serpentine grasslands of large parts of the Balkans), Matevski et al. (2018: basiphilous grasslands of the Central Balkans) and Willner et al. (2019: mesoxeric grasslands of Central and Eastern Europe, including the Balkans) presented transboundary plot-based analyses of dry grasslands. Despite these valuable contributions to the knowledge of dry-grassland diversity in the region, there are still numerous geographic and syntaxonomic gaps, and the proposed regional solutions are inconsistent. The first comprehensive overview of the syntaxa of Europe (Mucina et al., 2016) mentions several high-rank syntaxa of dry grasslands from the Balkans, sometimes for the first time, but is not always supported by published analyses of vegetation data. Also, the European Red List of Habitats (Janssen et al., 2016), as well as successive attempts to parameterise European grassland types (Schaminée et al., 2016; Chytrý et al., 2020), have indicated that

the delimitation and distribution of these types across the Balkan Peninsula is unclear, even at the highest syntaxonomic levels (classes and orders). Such information would be important both for basic ecological research and conservation purposes.

With the recent emergence of large national and supranational vegetation-plot databases in Europe (Dengler et al., 2011; Chytrý et al., 2016) a major impediment to data-driven, consistent supranational classification has been overcome. Using the European Vegetation Archive (EVA; Chytrý et al., 2016), it is now feasible to extract all plots consistently and reproducibly across the continent that meet certain criteria. Schaminée et al. (2016) and later Chytrý et al. (2020), for example, used an approach based on the prevalence of species groups combined with dominance criteria to analyse the distribution and floristic composition of coarsely classified grassland types (roughly corresponding to phytosociological orders). Peterka et al. (2017) used Cocktail species groups (Bruehlheide, 1995, 1997) to define and characterise the alliances of fen vegetation in Europe. However, such approaches of *supervised classification* (for terminology see De Cáceres et al., 2015) are only meaningful when there is an existing and widely accepted a priori classification scheme. If there is no such scheme available, or none has proven appropriate for the geographical and ecological range, a *de novo* classification must be developed based solely on the data (*unsupervised classification* sensu De Cáceres et al., 2015). A recent analysis of coastal dune vegetation in Europe and adjacent regions by Marcenò et al. (2018) combined both aspects, that is, an unsupervised classification with TWINSpan, followed by the creation of formal assignment rules in JUICE (Tichý, 2002). However, the hierarchy of syntaxonomic levels is not commonly implemented in current formalised classification procedures, although it constitutes a highly informative aspect of phytosociological classifications (Braun-Blanquet, 1964; Dengler et al., 2008; Guarino et al., 2018). Either researchers restrict themselves to a single syntaxonomic level whose units are defined without hierarchy (e.g. Peterka et al., 2017), or they start at a lower syntaxonomic level and then group these basic units into a hierarchical system (e.g. Chytrý, 2007; Marcenò et al., 2018). Only very recently, syntaxonomic hierarchies have been fully implemented in such numerical workflows (García-Mijangos et al., 2021; Kaçki et al., 2021).

In this study, we aimed at (a) developing a classification approach that is capable of creating hierarchical phytosociological classification systems in a transparent manner and translating this directly into formal assignment rules (i.e., an expert system) and (b) testing the newly developed methodology using the dry grasslands of the Central and Eastern Balkan Peninsula as a complicated real-world example.

2 | STUDY AREA

The study area comprises the central and eastern parts of the Balkan Peninsula, here defined as the territories of Serbia, Kosovo, North Macedonia, Bulgaria and the three northernmost regions of

Greece (East Macedonia and Thrace, Central Macedonia and West Macedonia). Encompassing approximately 268,000 km², the investigated area covers about 47% of the whole peninsula (Figure 1). It stretches from 39.3° to 46.2° N and from 18.8° to 28.7° E.

Most of the study area is mountainous, including the Balkan (Stara Planina), Rhodope, Pirin, Rila and Šar Mts (Horvat et al., 1974). The highest peaks are located in the Rila Mts (2925 m a.s.l.) and Pirin Mts (2914 m a.s.l.), while the mean elevation is about 540 m a.s.l. Flat terrain is relatively common in the eastern part, most extensively in the Danube Plain in northern Bulgaria and in the Thracian Plain. Other large flat territories include parts of the Pannonian Basin (Vojvodina) in the north and the Vardar valley in the south.

The diverse relief of the Balkan Peninsula, especially the orientation of the main mountain chains and long river valleys, causes a large variation in climatic conditions. Thus, the mean annual temperature in the northern parts of the study area is around 11–12°C, but about 16°C in the region of Thessaloniki (northern Greece) (Lieth et al., 1999). A more continental climate, characterised by cold winters (mean January temperature below 0°C) and warm summers (mean July temperature: 23°C) dominates in Vojvodina and Morava in Serbia, West Bulgaria and the Danubian Plain in Bulgaria (Glovnyá & Blagoeva, 1989). The precipitation maximum generally occurs in summer (June), and the minimum in winter (February). Only a small fraction of the study area (southern parts of North Macedonia and northern Greece) belongs to the Mediterranean climate zone, with warm moist winters (mean January temperature above 5°C) and hot and dry summers (Ivanov, 2016). A transitional subcontinental–sub-Mediterranean climate can be found on the plains of Tetovo and Skopje in North Macedonia, the Upper Thracian Plain, the easternmost parts of the Sredna Gora Mts and Balkan Range (Stara Planina) in Bulgaria and east of the northern Pindus Mts in Greece. In these regions, the winter is less cold than in the continental climate zone, and precipitation has two maxima (in June and November) and two minima (in August and February) (Velev, 2002; Bohn et al., 2004; Strid et al., 2020).

Carbonate bedrock (limestone, dolomite, marble) dominates in the mountains, especially in the western and central parts of the study area (e.g. Northern Pindus, Šar, Galičica, Suva Planina, Rtanj, Pirin, Slavyanka Mts and the mountains west of Sofia). The mountains along the border between Bulgaria and Serbia and the Rhodope Mts are composed of Palaeozoic rocks. The main igneous bedrock in the Balkan range and most mountains of the Macedonia–Thrace Massif is granite. Large serpentine areas occur in southern Bulgaria (especially East Rhodope Mts) and northwestern Greece. Loess, sandy loess and aeolian sands are found in the middle and lower Danube Basin (i.e., Vojvodina and Danubian Plain) (Fitzsimmons et al., 2012).

Chernozems are typical soil types for base-rich loess substrates in Vojvodina and the Danubian Plain. Chromic soils prevail in regions with Mediterranean and transitional Mediterranean climate, while Luvisols are typical for territories with continental climate. In the mountains, the main soil types are Cambisols (Ninov, 2002; Ivanov, 2016).



FIGURE 1 Study area (bright colours) on the Balkan Peninsula. Countries are indicated by their ISO code, and main geographic features are named.

3 | METHODS

3.1 | Balkan Dry Grassland Database

The Balkan Dry Grassland Database (BDGD; GIVD ID: EU-00-013; Vassilev, et al., 2012) was established in 2012 by a consortium of researchers to collect plot data of dry-grassland vegetation from the whole Balkan Peninsula for joint analyses. This steadily growing collaborative database is aimed at comprehensive compilation of such data from both published and unpublished sources. It is maintained using the TURBOVEG software (Hennekens & Schaminée, 2001) and is a part of EVA (Chytrý et al., 2016).

Among other criteria, the standardisation in BDGD involved geographic coordinates and the spatial accuracy of plot locations. Plots lacking coordinates were georeferenced a posteriori using Google Earth based on the locality description included in the respective publications. While in most of the plots species cover was estimated in percent or using the Braun-Blanquet cover-abundance scale (Braun-Blanquet, 1964), or a variant thereof, there was also a considerable fraction using the dominance approach (Aleksandrova, 1973), in which the cover estimation of species is based on Hult's scale with five classes (Shennikov, 1964). The cover values of these plots were transformed to the seven-grade Braun-Blanquet scale following the suggestion of Meshinev and Apostolova (2002). For each plot, we indicated whether bryophytes and/or lichens were recorded. Since most dry grasslands harbour bryophytes and lichens, we assumed that they were not recorded

when no such species were listed, except when the authors explicitly stated their absence.

3.2 | Preparation of the initial data set

On 1 November 2014, we extracted all plots from BDGD within Serbia, Kosovo, North Macedonia, Bulgaria and northern Greece ($n=8251$). Half of them came from 137 published sources, while the other half were unpublished at the time of inclusion in the database (Appendix S1). Since strongly diverging plot sizes can confound classification results (Dengler et al., 2009), we checked plot-size distributions in the individual countries (Appendix S2). We accordingly chose a plot-size range of 15–100 m² as a compromise between maximising spatial coverage and minimising the distorting effects of diverging plot sizes. Smaller or larger plots or plots without size information were removed, resulting in a selection of 7320 plots. Then we removed plots with a combined cover of shrub and tree species greater or equal to 30% ($n=7178$ plots). Finally, we further excluded duplicates and multiple plots from nested-plot series, resulting in a final data set of 6924 plots.

This data set was then exported to the JUICE software (Tichý, 2002) for harmonisation of taxonomic concepts and nomenclature. The taxa identified only to the genus level were deleted from further analysis. Vascular plant taxonomy was standardised to Euro+Med (2019), mosses to Hill et al. (2006), liverworts to Grolle and Long (2000) and lichens to Nimis et al. (2018). We accepted a

few additional vascular plant taxa missing from Euro+Med (2019) (Table S3.1 in Appendix S3). Taxa identified with different taxonomic precision were merged to the wider concept, that is, subspecies to species and species to aggregates, respectively. To this end, we defined several additional aggregates not included in the taxonomic references (Table S3.2 in Appendix S3).

We applied the 'EuroVegChecklist Expert System' function of JUICE. This expert system (ES) contains diagnostic species of European phytosociological classes (based on Mucina et al., 2016) and assigns each plot to the class whose diagnostic species prevail. We quantified the representation of diagnostic species of individual classes using the sum of square-root-transformed percentage cover values across species of each class as an intermediate approach between species counts and sums of untransformed percentage covers. When a species was considered diagnostic in more than one vegetation type, it received full weight in each of these types.

We derived a priori diagnostic species lists for each of the eight dry-grassland classes which, according to EuroVegChecklist (Mucina et al., 2016), were expected to occur in the region (i.e., *Festuco-Brometea*, *Helianthemetea guttati*, *Helichryso-Crucianelletea maritimae*, *Koelerio-Corynephoretea canescentis* s.l. including *Sedo-Scleranthetea*, *Lygeo sparti-Stipetea tenacissimae*, *Poetea bulbosae*, *Stipo giganteae-Agrostietea castellanae*, *Stipo-Trachynietea distachyae*), as well as for the floristically most closely related classes of herbaceous vegetation (i.e., *Ammophiletea*, *Artemisietea vulgaris* s.l. including *Epilobietea angustifolii*, *Asplenietea trichomanis*, *Cakiletea maritimae*, *Callunoulicetea* s.l. including *Nardetea strictae*, *Carici rupestris-Kobresietea bellardii*, *Daphno-Festucetea*, *Elyno-Seslerietea*, *Festuco-Puccinellietea*, *Juncetea maritimi*, *Juncetea trifidi*, *Molinio-Arrhenatheretea*, *Mulgedio-Aconitetea*, *Polygono-Poetea annuae*, *Saginetea maritimae*, *Scheuchzerio palustris-Caricetea fuscae*, *Stellarietea mediae* s.l. including *Papaveretea rhoeadis*, *Sisymbrietea*, *Chenopodietea* and *Digitario sanguinalis-Eragrostietea minoris*, *Thlaspietea rotundifolii*, *Trifolio-Geranietea sanguinei*). The initial lists of the a priori diagnostic taxa were taken from Mucina et al. (2016), using the combined lists of the included classes in case of 's.l.' classes, and applied to the data set using the EuroVegChecklist ES. In cases where this original outcome led to class assignments in strong disagreement with common phytosociological practice, we fine-tuned the species lists of the ES iteratively. This involved both adding species not evaluated by Mucina et al. (2016) and modifying the diagnostic values of already included species, based on the knowledge of the authors of this article and existing statistically tested lists of diagnostic species at the class level (e.g. Berg et al., 2001; Dengler, 2003; Michl et al., 2010; Pedashenko et al., 2013; Fotiadis et al., 2014; for full list, see Appendix S4). The 'consensus list' of diagnostic species for classes of the herbaceous vegetation on the Balkan Peninsula forms the first hierarchical step of our ES (Figure 2). Appendix S5 shows the resulting changes of plot assignment compared to the ES of Mucina et al. (2016). Plots assigned by the ES to one of the eight dry-grassland classes listed above were considered to represent dry grasslands (6230 plots). It should be noted that this part of the ES is only intended to separate dry-grassland classes as defined above from the rest of all other

non-woodland vegetation types; thus, we optimised the species lists for optimal discrimination between both groups of classes, but only marginally for discrimination among the classes of each group.

From this point onwards, we excluded bryophytes and lichens from the data set because they had been identified only in a subset of plots (1039 plots with 160 non-vascular plant taxa). To avoid undue effects of spatially unequal sampling intensity, we further stratified the data with the heterogeneity-constrained resampling (HCR) procedure (Lengyel et al., 2011). To this end, we used a grid with a cell size of 15' latitude \times 25' longitude (ca 750 km²) and selected a minimum of 50 and a maximum of 100 plots per grid cell depending on the beta diversity of plots within the grid cell following Wisser and De Cáceres (2013). If less than 50 plots were available, we selected all of them. HCR was applied with the Bray-Curtis similarity coefficient and square-root-transformed percentage cover values. This resulted in 5734 plots with 2440 vascular plant taxa for further analysis.

3.3 | Classification of the dry grasslands

For further classification, we developed a formal implementation of the idea presented in Luther-Mosebach et al. (2012; see also Michl et al., 2010). These authors used modified TWINSpan (Roleček et al., 2009) 'followed by manual re-arrangement of a subset of plots with the aim of increasing floristic distinctiveness of the vegetation types'. They used the phi coefficient (Chytrý et al., 2002) to identify diagnostic species for each vegetation type, reassigned those plots in which diagnostic species of another vegetation type prevailed, recalculated phi-values and iterated this procedure. However, since they did this largely manually, they were restricted to a few rounds of iteration and had to rely on expert assessment of the species groups in the plot tables to decide on potential reassignment. The second innovation of Michl et al. (2010) and Luther-Mosebach et al. (2012) was the consistent application of the concept of numerically determined diagnostic species in a top-down hierarchical approach across the syntaxonomic levels.

Our new approach, which we term ICO-HES (iterative cluster optimisation for hierarchical expert systems), works as follows (Figure 2): It can start with any partition of a set of vegetation plots. For example, this can be a certain level of a TWINSpan classification that is considered a first approximation of syntaxa of a certain rank. For these units, diagnostic species are determined within the context of the superior unit, that is, the next higher level of the hierarchy, with phi-values standardised to an equal group size (Tichý & Chytrý, 2006). However, we modified the phi-value use compared to common practice as follows: while phi-values per se compare the concentration of species' occurrence in the target vegetation type to that in the rest of the data set (Chytrý et al., 2002), possibly the more relevant question for distinguishing vegetation types within established classification systems is how much more concentrated the species is compared to the vegetation type with the next-highest frequency among all units (Luther-Mosebach et al., 2012; see Tsiripidis et al., 2009 for a similar approach). This means that a

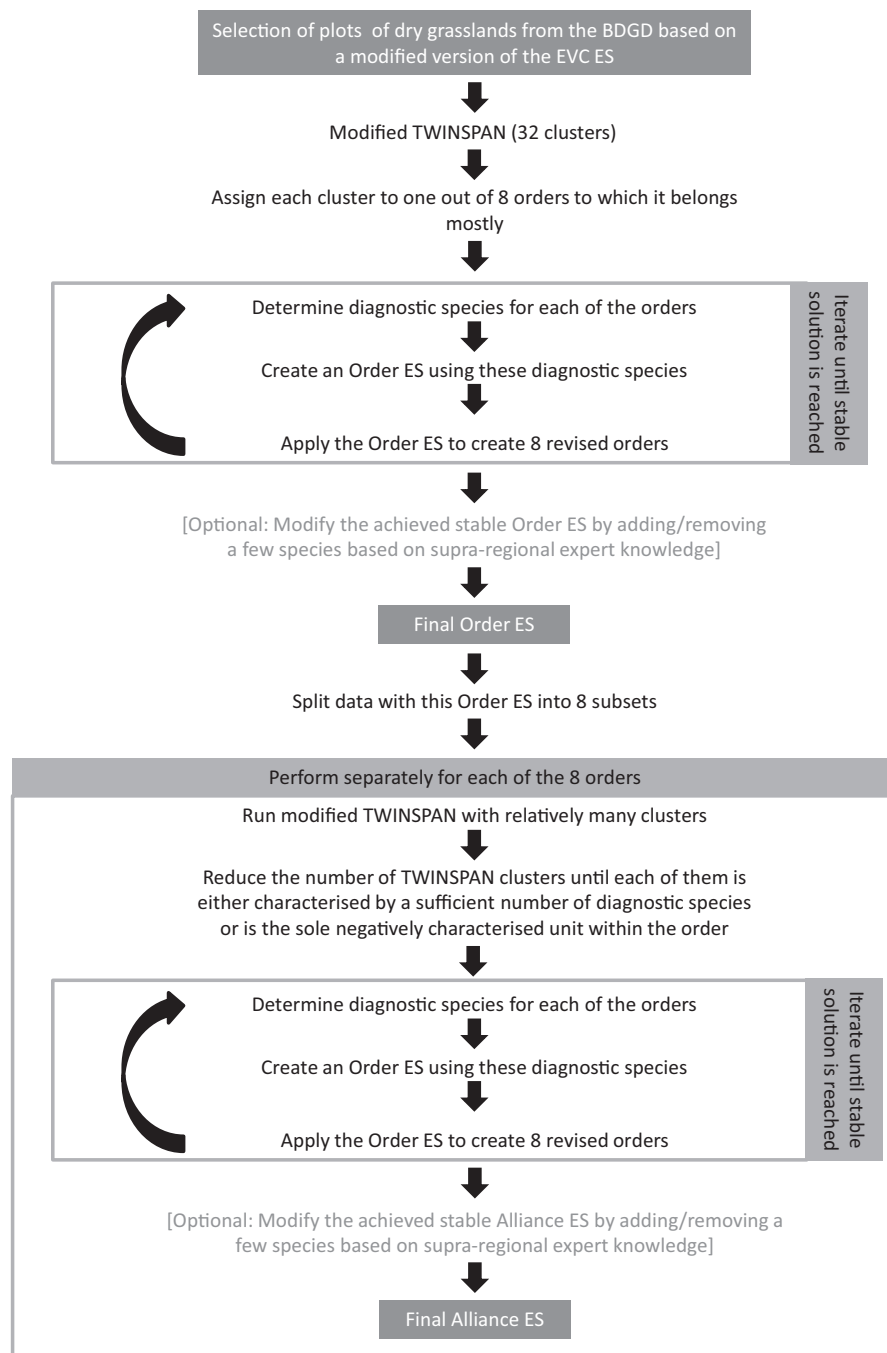


FIGURE 2 Flow chart of our methodological approach, which we call ICO-HES (iterative cluster optimisation for hierarchical expert systems).

subjective decision is not only needed for the absolute value of ϕ (see Chytrý, 2007), but also for the minimum difference. After trials with various combinations, we opted in our study for the following settings: the threshold of a diagnostic species was set to a ϕ -value of 0.20 or more in the unit with its highest frequency, but at the same time the ϕ -value had to be at least 0.15 higher than the one in the unit with the next-highest frequency. If a species had ϕ -values that differed by less than 0.15 between two or more units, it was assigned as a diagnostic species for all of these, except if it had a negative ϕ -value in the unit with the lowest frequency in such a group of units. In the latter case, the species was not considered diagnostic at all. These calculations were done in Excel. The set of identified diagnostic species was then used to create an ES with the

'EuroVegChecklist ES' function of JUICE, which in turn was used to reclassify the data set. The new partition of the data set was then exported again to Excel to determine a new set of diagnostic species. We assumed that this approach would result in a stable solution or oscillate around such after a few iterative rounds. If this point is reached, one has obtained an ES that contains lists of diagnostic species for particular vegetation types that are (almost) identical to the diagnostic species resulting from the application of this ES. The whole procedure was then repeated in the same way at the next lower hierarchical level of classification, separately within each unit determined at the higher level.

In our case specifically, we started with a modified TWINSpan classification (Roleček et al., 2009) of the whole stratified

dry-grassland data set to 32 clusters (Table S6.1 in Appendix S6). We used three cut levels of species cover (0%, 5%, 25%), a minimum group size for division of two and total inertia as similarity measure. It is well known that any clustering approach is sensitive to situations where certain units are overrepresented (in terms of number of plots, but particularly if only certain subunits are present). Thus, similarly to Willner et al. (2017), we evaluated the content of the original 32 clusters regarding their floristic composition, their floristic separation from each other and their geographic distribution (Figure S6.1 in Appendix S6). Our aim was to decide to which of the classes and orders of the European syntaxonomic system each of the clusters mainly belongs, and to merge such clusters to form roughly delimited units of equal rank with which to start the above-described iterative procedure. Once the iteration had reached a more or less stable solution, we evaluated the resulting units in terms of diagnostic species, ecological meaning and coherent spatial distribution. Having tested this mainly with solutions of four classes, seven orders and eight orders, we decided for the last option because this was the only one that resulted in a division reasonably corresponding to the European syntaxonomic classification system (see Section 4 and details in Appendix S7).

We essentially repeated this iterative analysis within each of the delimited orders. The TWINSpan settings were the same as those for the whole data set, except that we started with a lower maximum number of clusters. Starting with this finest resolution, we checked whether the resulting units (a) were floristically well separated from each other and (b) occupied a contiguous geographical and ecological space. For (a) we counted the number of final diagnostic species and how many of them on average occurred in each plot. Our understanding is that an alliance should have several diagnostic species, a subset of which should occur in each plot belonging to this alliance. Of these species, a significant portion should qualify as character species, meaning that their main occurrence should be in the respective alliance when taking all alliances into account (Dengler et al., 2005, 2008), not only dry-grassland alliances. For example, units in which the determined diagnostic species largely or exclusively consist of ruderal species or species of mesic grasslands, would not be retained as separate alliances of the dry-grassland vegetation. Within each order, we allowed one 'central alliance' (Dengler, 2003; Dengler et al., 2005) if the TWINSpan division had resulted in one or several subunits with numerous plots with only few of their own diagnostic species. If such a pattern appeared, we ran the iteration by assigning all the plots that had fewer diagnostic species of any other alliance of the order than a certain threshold (e.g. one species per plot) to this central alliance. For (b) we checked the resulting distribution map and interpreted the units ecologically (based on species composition and site descriptions from the original sources). To be accepted as a meaningful alliance (whether positively defined or central), a unit should be geographically and/or ecologically distinct within the geographic-ecological space of the order. If the finest partition of the order did not meet both criteria (a) and (b), we reverted to a partition with fewer units. Once we found a partitioning meeting these two criteria, we ran our iterative optimisation procedure

on it. If the resulting stable solution after several rounds still met these two criteria, we accepted these units on an alliance level, otherwise we went back to a coarser subdivision (or eventually decided to accept only one alliance within the order in the region).

3.4 | Interpretation and presentation of syntaxa

Once we had reached a subdivision fulfilling the two criteria (a) and (b) as well as an ES for the three levels of hierarchy (classes of dry grasslands within all herbaceous vegetation, orders within dry grasslands and alliances within each of the orders), we characterised the defined units following De Cáceres et al. (2015). We also present the class level, although classes could not be meaningfully derived with our approach using the regional data set only.

We prepared a synoptic table depicting the three hierarchical levels class, order and alliance, with percentage frequencies of the species for the alliance level and mean values of percentage frequencies in the alliances for the orders, classes and all included dry grasslands plots. This way of calculating frequencies for higher units considers the alliances as equivalent units and accounts for their potentially unequal representation in the data set. The evaluation of the diagnostic species was done with the above-described implementation of phi-values, and species were sorted according to decreasing phi-values in the syntaxon they characterise. Since bryophytes and lichens had been recorded only in about one fifth of all plots, they were not used in the ES. Instead, we added them post hoc to the synoptic table by calculating their frequency within the subset of plots per each alliance in which they were recorded. We were thereby able to assess bryophyte and lichen species frequencies and diagnostic values in most of the units, except three alliances that had none or only one plot with bryophyte and lichen records.

To translate our hierarchical classification system into a section of the standard European system of syntaxa (i.e., to inform possible updates of Mucina et al., 2016; see <http://euroveg.org/evc-committee>), we verified whether our units had already been validly described according to the International Code of Phytosociological Nomenclature (ICPN) (Theurillat et al., 2021). We adopted the oldest valid syntaxon name or, if such a name was not available, we described a new syntaxon according to Theurillat et al. (2021). To do this in a transparent way, we subjected all available type relevés of associations described from or used in the region, and particularly those of the type associations of the alliances to our hierarchical ES. When several floristically and ecologically similar units of the same rank had been described in neighbouring regions, we used published synoptic tables to compare them with the synoptic tables from our region to join our unit with the most similar one. If the available information was inconclusive, we left the final placement of a unit open and discussed possible solutions.

Finally, we prepared a standardised comparison and characterisation of the distinguished alliances using boxplots. We used elevation and slope inclination as the only two ecological variables available for nearly all plots as well as total vegetation cover and

vascular plant species richness as two informative vegetation variables. To get a more comprehensive picture, we additionally inferred site conditions via the Ecological Indicator Values for Europe (EIVE), which cover nearly 15,000 vascular plant taxa of Europe and thus have a good coverage also for the study region (Dengler et al., 2023). EIVE 1.0 provides information on continuous scales from 0 to 10 for five of the most relevant niche dimensions. We calculated unweighted mean EIVE values for soil moisture, soil nitrogen, soil reaction, light and temperature.

4 | RESULTS

4.1 | Overview of the resulting classification scheme

The hierarchical ES for the Balkan dry-grassland vegetation resulting from our analyses is provided in Appendices S8–S18, with detailed explanations (Appendix S8) and all files needed to run it in JUICE (Appendices S9–S18). The placement of type relevés of many dry-grassland associations described from the region by our hierarchical ES and the resulting syntaxonomic correspondence of alliances and orders is given in Appendix S19. The confusion matrix of the initial unsupervised TWINSpan classification and our final supervised ES is presented in Appendix S20. While our ES-based orders 2.1 (*Astragalo onobrychidis-Potentilletalia*), 3.1 (*Brachypodietalia pinnati*), 3.3 (unnamed order comprising the *Pimpinello-Thymion zygoidis*) and 4.1 (*Sedo acris-Festucetalia*) largely (around 75% up to 97%) matched the originally assigned TWINSpan cluster(s), the correspondence was somewhat lower for the other orders.

The resulting scheme for higher syntaxa is given in Table 1 and the corresponding synoptic table (abridged version: Table 2, complete version: Appendices S21–S22). Based on our hierarchical classification scheme (Table 1) and the application of our ES to the type relevés of the relevant associations from the region (Appendix S19), combined with extensive literature review on dry-grassland syntaxa from the region, we conclude that a range of higher syntaxa should be merged (Table 1), while one alliance is described as new to science (Appendix 1). Further, to ensure consistency and clarity of the system, we propose to modify some syntaxon names (Appendix 2) and provide missing lectotypifications (Appendix 3) in agreement with the ICPN, which are already reflected in Table 1. To facilitate future implementation in the EuroVegChecklist we prepared the key arguments for the necessary nomenclatural applications to the Committee for Change and Conservation of Names (CCCN) (Appendix S23) and for the modification of the EuroVegChecklist (Appendix S24 for syntaxon names; Appendix S25 for the syntaxonomic hierarchy).

4.2 | General performance of the approach

The EuroVegChecklist ES as implemented in JUICE was generally able to separate the classes of herbaceous vegetation. However,

using the original species lists led to about 10%–20% of plots being misclassified based on individual assessment of plot assignment by the lead authors. After these species lists were modified based on various published sources and our own experience (see Appendix S4), the algorithm was able to provide a rather convincing separation of the classes. It is noteworthy that both with the original species lists and with our improved species lists only two of the ‘Mediterranean’ classes were ‘found’ with more than very few plots (Appendix S5).

We applied our iterative approach to the whole data set, to different subsets and to numerous initial partitions of the data. In each case, the iterative procedure converged quickly, often yielding a solution in which species of the ES and resulting diagnostic species matched 100% within a few rounds. In cases where the remaining changes in plots between units became lower than 2% after 10 rounds at the latest, we accepted this as a quasi-stable solution (for details, see Appendix S26). Sometimes, the iterative procedure led to the dissolution of certain units after a few rounds due to the successive assignment of plots to other units. We considered this an indication of a poor original delimitation of the unit.

In practice, our approach left very few plots unassigned. All 6924 plots could be successfully assigned by our Class ES to one of the 21 included classes (Appendix S5). Within the dry grasslands, our Order ES was able to classify 5538 out of 5734 plots (96.6%), and the three Alliance ESs for the orders with more than one alliance in the region had success rates of 93.6% (*Brachypodietalia pinnati*), 99.3% (*Koelerietalia splendentis*) and 96.9% (*Trifolio-Festucetalia*), respectively (Appendix S21). With an average success rate of 98.2%, the assignment of plots to alliances within orders was even better than for orders within all dry grasslands, and the overall success rate of the combined hierarchical ES was still 94.9%. A closer look revealed that the few unclassified plots typically had very low numbers of species, indicating either very untypical situations or incomplete sampling (Appendix S21).

4.3 | Hierarchical classification

Having calculated a 32-cluster TWINSpan analysis of the 5734 dry-grassland plots, we assigned each of the clusters to the class (i.e., *Festuco-Brometea*, *Koelerio-Coryneporetea* s.l., *Helianthemetea guttati* and *Stipo-Brachypodietea*) to which the majority of the plots belonged according to our expert opinion. Accordingly, we combined the clusters to four initial groups and then ran our iterative procedure. While the iterations did converge, the results were not convincing, as the resulting units did not fit into the European syntaxonomic system (likely because the four classes were very unequally represented).

Thus, we continued to seek a direct division into orders by assigning each of the clusters to one of the orders reported from the region based on our interpretation. We generally recognised seven orders known from the literature (i.e., the orders of our final solution shown in Table 1, except order 3.3). Since the placement of the *Pimpinello-Thymion zygoidis*—which corresponded to two

TABLE 1 Hierarchical overview of the higher syntaxa of dry grasslands found in the Central and Eastern Balkan Peninsula as accepted in this paper, including major synonyms from the region in brackets.

Class 1: *Tuberarietea guttatae* Rivas Goday et Rivas-Martinez 1963 mut. Vassilev et al. 2024 – Mediterranean and sub-Mediterranean therophyte-dominated dry grasslands on acidic soils

Order 1.1: *Tuberarietalia guttatae* Br.-Bl. in Br.-Bl. et al. 1940 mut. Vassilev et al. 2024 – Mediterranean and sub-Mediterranean therophyte-dominated dry grasslands on inland acidic soils

Alliance 1.1.1: *Romuleion* Oberdorfer 1954 (*Trifolion cherleri* Micevski 1972 syntax. syn., *Scabioso-Trifolion dalmatici* Horvatić et N. Radelović in N. Radelović 1977 syntax. syn., *Aethionemion saxatilis* Bergmeier et al. 2009 syntax. syn., *Diantho pinifolii-Jasionion heldreichii* Bergmeier et al. 2009 syntax. syn.) – Therophyte-rich, sub-Mediterranean dry grasslands on siliceous soils of the Balkan Peninsula

Class 2: *Stipo-Brachypodietea distachyi* S. Brullo in S. Brullo et al. 2001 mut. Vassilev et al. 2024 – Mediterranean and sub-Mediterranean therophyte-dominated dry grasslands on base-rich soils

Order 2.1: *Astragalo onobrychidis-Potentilletalia* Micevski 1971 (*Ptilostemonea stellati-Vulpietalia ciliatae* Mucina in Mucina et al. 2016 nom. ined.) – Mediterranean and sub-Mediterranean therophyte-dominated dry grasslands on base-rich soils of the Central and Eastern Mediterranean Basin

Alliance 2.1.1: *Clinopodio alpini-Thymion striati* Micevski 1971 mut. Vassilev et al. 2024 (*Xeranthemion annui* Oberd. 1954 nom. prov.) – Therophyte-rich, sub-Mediterranean dry grasslands on base-rich soils of the Balkan Peninsula

Class 3: *Festuco-Brometea* Br.-Bl. & Tx. ex Soó 1947 – Temperate dry grasslands on loamy base-rich soils

Order 3.1: *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (*Brometalia erecti* W. Koch 1926 nom. rejic. propos.; *Scorzoneretalia villosae* Kovačević 1959 nom. rejic. propos.; see Dengler & Willner, 2023) – Mesoxeric basiphilous grasslands of the sub-Mediterranean to hemiboreal zones of Europe

Alliance 3.1.1: *Chrysopogono grylli-Danthonion alpinae* Kojić 1959 mut. Vassilev et al. 2024 – Mesoxeric subneutrophilous grasslands of the submontane belt in the Central Balkan Peninsula

Alliance 3.1.2: *Cirsio-Brachypodion pinnati* Hadač & Klika in Klika and Hadač 1944 – Mesoxeric basiphilous grasslands of Eastern Central and Eastern Europe and in the montane belt of the Balkan Peninsula

Order 3.2: *Festucetalia valesiaca* Br.-Bl. et Tx. ex Br.-Bl. 1950 nom. cons. propos. (*Festucetalia* Soó 1947 nom. rejic. propos., *Festucetalia valesiaca* Soó 1947 nom. illeg.; see Willner et al., 2021) – Continental steppes on deep, loamy soils

Alliance 3.2.1: *Festucion valesiaca* Klika 1931 nom. cons. propos. (*Festucion sulcatae* Soó 1930 nom. rejic. propos.) – Steppes and steppic grasslands in the lowlands of Eastern Central and East Europe

Order 3.3: NA – Rocky grasslands in the lowlands in the European steppe biome

Alliance 3.3.1: *Pimpinello lithophilae-Thymion zygioidis* Dihoru & Donița 1970 – Rocky limestone grasslands of the western Black Sea lowlands

Order 3.4: *Koelerietalia splendentis* Horvatić 1973 nom. cons. propos. (*Scorzoneretalia villosae* Kovačević 1959 p.p., typo excl.; *Halacsyetalia sendtneri* Ritter-Studnička 1970 nom. rejic. propos.; see Appendix S23) – Calcareous and serpentine rocky mountain grasslands of the Balkan and Apennine Peninsulas

Alliance 3.4.1: *Centaureo kosaninii-Bromopsis fibrosae* Blečić et al. 1969 mut. Vassilev et al. 2024 – Rocky dry grasslands on ultramafic rocks of the Central Balkan Peninsula

Alliance 3.4.2: *Saturejion montanae* Horvat in Horvat et al. 1974 – Subcontinental rocky dry grasslands of the mountain ranges in the Northeast Balkan Peninsula

Alliance 3.4.3: *Diantho haematocalycis-Festucion hirtovaginatae* Matevski et al. 2018 – Submediterranean rocky and gravelly dry grasslands of the mountain ranges in the Central Balkan Peninsula

Class 4: *Koelerio-Corynephoretea* Klika in Klika & Novák 1941 – Temperate dry grasslands on sandy or shallow skeletal soils

Order 4.1: *Sedo acris-Festucetalia* Tx. 1951 nom. invers. (*Festucetalia vaginatae* Soó 1957 syntax. syn.) – Subcontinental and continental sand steppes in Europe

Alliance 4.1.1: *Festucion vaginatae* Soó 1929 – Sand steppes of the Pannonian Basin and the western Black Sea coast

Order 4.2: *Trifolio arvensis-Festucetalia ovinae* Moravec 1967 (*Armerietalia rumelicae* V. Radelović et N. Radelović in V. Radelović et Zlatković ex Mucina et Čarni in Di Pietro et al. 2015 syntax. syn.) – Mesoxeric sandy and siliceous grasslands of sub-Mediterranean to boreal Europe

Alliance 4.2.1: *Armerio rumelicae-Potentillion* Micevski 1978 – Perennial-dominated dry grasslands of siliceous soils of the Balkan Peninsula

Alliance 4.2.2: *Minuartio montanae-Poion molinerii* Vassilev et al. 2024 (*Thymion jankae* Kojić et al. 1992 nom. inval.) – Pioneer dry grasslands on eroded serpentines of the Central Balkan Peninsula

Note: All deviations from the classification system of the EuroVegChecklist (Mucina et al., 2016) are documented in the Appendices S24 and S25.

subordinate TWINSpan clusters – is controversial in the literature, we joined it with the other clusters of the *Festucetalia valesiaca* or with the other clusters of the rocky grasslands (for details, see Appendix S7). In any case, the respective plots always ended up in the cluster of the Mediterranean calcareous grasslands after a few rounds of iteration, even after settings such as the phi-value thresholds were modified. Since the placement of zonal steppe vegetation in a Mediterranean order would not make sense, we finally defined the *Pimpinello-Thymion zygioidis* as its own starting cluster, that is, as a separate, eighth order. Here, the iteration soon converged to a stable solution with eight units, including one for the *Pimpinello-Thymion zygioidis* with a broader definition compared to the traditional view, but where the inclusion of the additional plots was floristically and ecologically meaningful (see Appendix S7).

Within each of the eight orders, we started the same procedure as described previously for the full data set, this time not referring to previously published classifications. Essentially, we retained those subdivisions that were sufficiently supported floristically to justify designation as separate alliances from our point of view, and which could be interpreted ecologically and/or chorologically. For five of the eight orders (1.1, 2.1, 3.2, 3.3, 4.1), the possible subdivisions either overlapped strongly in ecological and geographic space or the floristic differences were not substantial enough to separate alliances. We decided to consider these orders to be monotypic within the study area, that is, all plots of the respective orders were automatically assigned to the sole alliance. In the cases of 3.1, 3.4 and 4.2 we could separate two, three and two alliances, respectively, which are ecologically, chorologically and floristically meaningful.

TABLE 2 Shortened synoptic table of the alliances, orders and classes of dry grassland vegetation.

	Classes													Orders													Alliances												
	All	1	2	3	4	1.1	2.1	3.1	3.2	3.3	3.4	4.1	4.2	1.1.1	2.1.1	3.1.1	3.1.2	3.2.1	3.3.1	3.4.1	3.4.2	3.4.3	4.1.1	4.2.1	4.2.2														
Syntaxonomic unit		1	2	3	4	4.1	4.2	1.1	2.1	3.1	3.2	3.3	3.4	4.1	4.2	1.1.1	2.1.1	3.1.1	3.1.2	3.2.1	3.3.1	3.4.1	3.4.2	3.4.3	4.1.1	4.2.1	4.2.2												
Number of plots included	5440	1248	487	3333	372	1248	487	1220	1069	250	794	120	252	1248	487	866	354	1069	250	158	431	206	120	202	50														
Mean plot size [m ²]	52.7	51.2	41.9	59.1	41.7	51.2	41.9	59.4	49.0	75.8	56.8	24.1	50.5	51.2	41.9	59.9	58.9	49.0	75.8	61.0	45.1	64.1	24.1	52.3	48.8														
Mean vascular plant species richness	34.0	44.8	38.0	37.2	21.5	44.8	38.0	41.2	35.6	36.9	35.1	15.0	24.7	44.8	38.0	41.4	41.0	35.6	36.9	31.6	34.3	39.4	15.0	27.8	21.6														
Order 1.1 (54 taxa, 47 exclusive)																																							
<i>Psilurus incurvus</i>	7.0	46	16	2	4	46	16	1	1	5	1	3	4	4	46	16	1	1	5	1	1	2	3	6	2														
<i>Vulpia ciliata</i>	3.8	33	6	1	0	33	6	2	1	2	1	1	1	1	33	6	2	1	1	2	1	2	1	1	1														
<i>Trifolium arvense</i>	15.6	62	9	9	17	62	9	15	16	1	6	3	25	62	9	24	5	16	1	12	5	1	3	39	10														
<i>Taeniatherum caput-medusae</i>	4.5	34	8	2	0	34	8	1	4	4	1	1	1	1	34	8	1	4	4	1	1	1	1	1	1														
<i>Trifolium cherleri</i>	2.3	22	2	0	1	22	2	1	1	1	1	1	1	1	22	2	1	1	1	1	1	1	1	1	2														
<i>Anthemis ruthenica</i>	3.3	26	3	1	2	26	3	1	1	1	1	1	4	1	26	3	1	1	1	1	1	1	1	4	1														
<i>Trifolium angustifolium</i>	4.7	31	14	1	1	31	14	2	3	1	1	1	1	1	31	14	3	1	3	1	1	1	1	1	2														
<i>Trifolium campestre</i>	14.3	52	14	11	9	52	14	27	19	2	14	14	14	14	52	14	42	11	19	3	1	2	22	6															
<i>Petrorhagia prolifera</i>	8.1	41	18	4	2	41	18	2	13	6	3	4	4	4	41	18	2	1	13	6	3	5	1	7															
<i>Gallium divaricatum</i>	6.2	31	6	2	9	31	6	3	1	2	1	13	13	13	31	6	3	2	1	2	1	2	1	26															
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]														
<i>Poa bulbosa</i>	28.3	75	48	17	32	75	48	8	20	28	19	47	25	75	48	9	6	20	28	11	7	38	47	48	2														
<i>Eryngium campestre</i>	38.1	80	79	38	11	80	79	28	77	54	26	9	12	80	79	43	12	77	54	18	28	33	9	24															
Order 2.1 (36 taxa, 28 exclusive)																																							
<i>Brachypodium distachyon</i>	5.1	10	40	1	0	10	40	1	2	4	1	1	1	10	40	1	2	4	1	2	4	1	2	1	1														
<i>Thymus striatus</i>	10.3	21	50	7	1	21	50	1	5	2	13	2	2	21	50	1	1	5	2	22	17	4	4	4															
<i>Medicago minima</i>	15.6	34	65	11	5	34	65	2	19	26	9	13	1	34	65	2	1	19	26	14	12	13	1	1															
<i>Aegilops neglecta</i>	5.5	23	32	2	2	23	32	1	1	5	1	1	1	23	32	1	1	5	1	1	5	1	2	1	2														
<i>Bothriochloa ischaemum</i>	28.3	46	79	24	17	46	79	7	72	37	14	38	6	46	79	12	2	72	37	6	19	17	38	10	2														
<i>Ziziphora capitata</i>	1.7	1	15	1	1	1	15	1	2	0	0	1	1	1	15	1	1	2	0	1	1	1	1	1	1														
<i>Lomelosia divaricata</i>	1.5	2	14	0	0	2	14	1	1	0	0	1	1	2	14	1	1	1	1	1	1	1	1	1	1														
<i>Crupina vulgaris</i>	10.1	10	37	10	1	10	37	2	8	23	12	2	2	10	37	2	1	8	23	5	16	16	1	2															
<i>Bombacilena erecta</i>	5.2	12	26	3	1	12	26	1	3	8	3	1	1	12	26	1	1	3	8	1	8	1	8	2															
<i>Convulvulus holosericeus</i>	0.8	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]														
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]														
<i>Xeranthemum annuum</i>	12.9	25	37	12	2	25	37	3	30	28	8	6	1	25	37	4	1	30	28	5	8	10	6	1															
Order 3.1 (46 taxa, 43 exclusive)																																							
<i>Leucanthemum vulgare</i> agg.	8.1	1	14	0	1	1	14	0	1	2	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1														
<i>Briza media</i>	8.3	1	14	1	1	1	14	1	1	1	3	2	1	1	1	1	1	1	1	6	2	1	1	1	2														
<i>Trifolium montanum</i>	6.8	1	1	11	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1														

TABLE 2 (Continued)

	All			Classes			Orders			Alliances										
<i>Agrostis capillaris</i>	12.3	2	16	10	2	53	6	1	1	15	2	61	45	6	1	1	1	1	20	10
<i>Anthoxanthum odoratum</i>	13.8	6	2	18	10	6	2	55	7	1	3	64	46	7	1	6	3	29	2	
<i>Trifolium alpestre</i>	12.3	1	1	17	8	1	1	48	3	7	1	32	64	3	7	14	7	21	4	
<i>Hypochaeris maculata</i>	6.5	1	1	10	2	1	1	34	1	0	1	35	32	1	1	1	1	2	4	
<i>Filipendula vulgaris</i>	15.0	3	2	24	2	3	2	54	12	13	12	70	38	12	13	23	13	1	5	
<i>Stachys officinalis</i>	5.1	1	8	0	1	27	1	1	1	1	1	29	25	1	1	2	1	1	1	
<i>Trifolium pratense</i>	7.6	2	11	4	2	35	7	0	0	6	2	34	36	7	1	1	1	7	4	
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]
<i>Lotus corniculatus</i>	19.7	10	4	25	15	10	4	57	29	4	10	65	48	29	4	20	9	1	16	30
<i>Gallium verum</i>	21.8	12	11	27	17	12	11	63	31	11	7	63	63	31	11	11	7	2	30	18
<i>Achillea millefolium</i> aggr.	26.3	30	13	31	18	30	13	65	55	12	8	63	66	55	12	11	12	38	16	
<i>Helianthemum nummularium</i>	13.9	1	7	18	11	1	7	32	3	1	19	19	44	3	1	2	31	25	8	14
<i>Pilosella piloselloides</i> aggr.	17.7	16	14	22	9	16	14	40	20	6	16	47	33	20	6	28	8	12	24	4
<i>Pilosella officinarum</i>	12.9	9	3	13	17	9	3	31	11	6	26	27	35	11	7	10	1	44	8	
Alliance 3.1.1 (18 taxa, 18 exclusive)																				
<i>Cynosurus cristatus</i>	4.4	1	1	7	1	1	1	23	1	1	0	2	1	1	1	1	1	1	1	2
<i>Danthonia alpina</i>	9.3	1	1	12	8	1	1	35	1	5	13	52	18	1	13	1	1	7	18	
<i>Euphrasia stricta</i>	5.5	2	1	8	3	2	1	26	1	1	4	38	13	1	1	1	1	4	4	
<i>Polygala comosa</i>	3.4	7	1	6	0	19	1	19	1	1	1	29	8	1	1	1	1	1	1	
<i>Moenchia montica</i>	3.8	7	1	5	7	1	17	1	1	7	1	29	5	1	1	1	1	1	1	
<i>Prunella laciniata</i>	4.9	2	1	7	3	2	1	21	3	1	4	32	9	3	2	2	2	4	4	
<i>Trifolium incarnatum</i>	4.3	15	3	4	1	15	3	13	4	0	2	24	1	4	1	1	1	3	3	
<i>Campanula rapunculoides</i>	1.5	1	1	2	1	1	1	7	1	0	1	13	1	1	1	1	1	1	1	
<i>Centaurium erythraea</i>	3.4	2	1	4	4	2	1	11	3	1	6	20	1	3	1	2	1	3	8	
<i>Ornithogalum pyrenaicum</i>	1.0	1	2	2	1	5	1	5	1	1	1	10	1	1	1	1	1	1	1	
Alliance 3.1.2 (18 taxa, 15 exclusive)																				
<i>Ranunculus montanus</i> aggr.	3.5	5	2	5	2	15	1	15	1	1	4	5	25	1	1	2	1	3	4	
<i>Brachypodium pinnatum</i>	5.4	1	1	9	0	1	1	21	5	1	5	10	31	5	1	8	6	1	1	
<i>Rhinanthus minor</i>	3.1	1	5	1	1	16	1	16	1	0	2	9	22	1	1	1	1	1	2	
<i>Primula veris</i>	4.6	7	2	7	2	16	1	16	1	5	3	5	27	1	8	7	1	6	8	
<i>Polygala major</i>	4.4	1	6	3	1	16	1	16	1	4	4	5	26	1	1	4	6	1	1	
<i>Alchemilla hybrida</i> aggr.	1.6	2	2	1	1	8	0	8	0	2	2	1	14	1	1	1	1	3	3	
<i>Veronica chamaedrys</i>	3.3	1	5	2	1	14	3	14	3	0	4	7	21	3	1	1	1	5	2	
<i>Cruciata glabra</i>	1.8	1	3	0	1	9	1	9	1	0	1	3	15	1	1	1	1	1	1	
<i>Silene sendtneri</i>	1.4	2	2	7	7	7	1	7	1	1	1	1	13	1	1	2	1	2	1	

(Continues)

TABLE 2 (Continued)

	Classes			Orders			Alliances				
	All	1	2	6	1	2	1	11	1	1	3
<i>Avenella flexuosa</i>	1.4	2	1	6	1	2	1	11	1	1	3
Order 3.2 (12 taxa, 6 exclusive)											
<i>Medicago falcata</i>	12.3	4	18	14	27	5	14	15	27	20	5
<i>Festuca valesiaca</i>	30.3	27	36	27	42	2	27	49	48	15	2
<i>Agrimonia eupatoria</i>	3.6	3	5	3	21	0	3	11	21	1	5
<i>Poa pratensis</i> agg.	9.7	7	14	7	20	3	7	22	16	9	1
<i>Fragaria viridis</i>	4.0	1	6	11	17	2	1	9	17	6	1
<i>Daucus carota</i>	2.3	2	1	4	13	1	2	7	1	1	1
<i>Medicago lupulina</i>	4.6	3	7	2	9	2	3	11	7	4	1
Order 3.3 (51 taxa, 51 exclusive)											
<i>Achillea clypeolata</i>	8.4	3	10	10	4	11	3	10	4	28	5
<i>Tanacetum millefolium</i>	2.5	1	4	1	1	28	1	1	1	1	1
<i>Satureja coerulea</i>	3.0	2	5	2	1	30	1	2	30	1	1
<i>Agropyron cristatum</i>	11.3	1	13	13	5	21	1	13	5	13	1
<i>Iris pumila</i>	5.5	1	9	1	1	34	1	1	1	2	2
<i>Euphorbia nicaeensis</i>	4.8	1	8	1	1	35	1	1	17	1	1
<i>Salvia nutans</i>	2.0	1	3	1	1	21	1	1	21	1	1
<i>Galatella villosa</i>	1.8	3	3	1	1	19	0	1	1	1	1
<i>Cephalaria uraltensis</i>	2.3	1	4	1	1	21	1	1	1	3	1
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]
<i>Teucrium capitatum</i>	25.3	23	71	71	24	34	1	71	24	2	2
<i>Sideritis montana</i>	12.6	6	34	34	14	18	1	34	14	2	1
Order 3.4 (13 taxa, 13 exclusive)											
<i>Artemisia alba</i>	9.7	1	2	2	2	35	1	2	2	32	2
<i>Teucrium montanum</i>	16.8	1	3	2	4	45	24	3	4	8	1
<i>Leontodon crispus</i>	25.6	8	28	10	16	58	1	28	16	21	1
<i>Asperula purpurea</i>	12.3	1	17	4	5	34	7	11	5	6	6
<i>Melica ciliata</i>	13.9	10	16	16	7	39	1	16	7	14	2
<i>Vincetoxicum hirundinaria</i>	7.6	1	12	3	5	23	3	3	1	28	3
<i>Stipa pulcherrima</i>	6.6	3	4	1	2	21	1	4	1	11	1
<i>Minuartia verna</i>	16.4	5	4	7	3	37	5	4	3	5	5
<i>Anthyllus vulneraria</i>	15.5	1	5	20	3	32	19	5	3	21	1
<i>Scorzonera austriaca</i>	3.1	1	5	1	1	10	1	1	1	13	1
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]
<i>Potentilla incana</i> aggr.	10.3	3	15	3	5	24	1	3	1	27	1
Alliance 3.4.1 (45 taxa, 39 exclusive)											

TABLE 2 (Continued)

	All	Classes				Orders				Alliances				
<i>Odontarrhena markgrafii</i>	8.1	10	9	1	1	1	1	1	1	1	1	65	1	28
<i>Euphorbia glabriflora</i>	6.8	4	10	3	4	1	22	5	4	1	1	58	1	10
<i>Bromopsis riparia</i>	11.2	1	16	6	1	1	12	9	1	1	12	68	10	14
<i>Stachys scardica</i>	7.5	1	8	12	1	3	16	18	1	2	3	47	1	36
<i>Centaurea kosaninii</i>	1.8	3	3	1	1	7	7	1	1	1	1	20	1	
<i>Halacsya sendtneri</i>	1.8	3	3	1	1	7	7	1	1	1	1	20	1	
<i>Stachys recta</i>	10.8	2	3	15	7	2	11	18	2	3	4	51	17	2
<i>Fumana bonapartei</i>	1.3	1	2	1	1	5	5	1	1	1	1	15	1	1
<i>Alyssum montanum</i>	7.2	1	7	11	1	1	15	29	3	1	1	37	6	4
<i>Potentilla visianii</i>	1.1	2	2	4	4	4	4	13	13	13	13	13	13	
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]
<i>Gallium mollugo</i> aggr.	13.9	2	3	18	13	2	31	19	2	3	6	53	32	7
<i>Thymus longicaulis</i>	11.3	3	4	12	14	3	16	22	3	4	3	42	6	10
Alliance 3.4.2 (5 taxa, 3 exclusive)														
<i>Satureja montana</i> aggr.	7.8	1	10	11	1	1	20	2	1	10	1	46	14	2
<i>Carex humilis</i>	8.8	1	12	8	1	4	24	6	1	6	3	17	6	16
<i>Stipa efocaulis</i>	2.8	3	4	3	3	1	9	3	1	3	1	16	12	
<i>Cotoneaster pyrenaicus</i>	0.8	1	0	1	1	2	2	1	1	1	1	7	1	1
Alliance 3.4.3 (74 taxa, 72 exclusive)														
<i>Festuca hirtovaginata</i>	3.7	6	6	15	15	15	15	1	1	12	12	43	1	2
<i>Anthyllis aurea</i>	3.3	6	6	13	13	13	13	1	1	38	38	38	1	2
<i>Viola herzogii</i>	2.4	4	4	10	10	10	10	1	1	29	29	29	1	1
<i>Fumana procumbens</i>	9.1	1	15	12	3	1	23	8	1	15	3	58	8	1
<i>Dianthus haematocalyx</i>	2.5	1	4	4	1	1	10	1	1	1	1	29	1	1
<i>Carex liparocarpos</i>	2.9	1	5	5	1	1	11	1	1	1	1	31	1	1
<i>Matthiola fruticulosa</i>	2.5	4	4	9	9	9	9	1	1	28	28	28	1	1
<i>Juniperus oxycedrus</i>	6.2	3	2	9	1	3	21	2	3	2	1	45	3	2
<i>Achillea ageritifolia</i>	3.5	1	6	6	1	1	13	1	1	1	1	33	6	1
<i>Jurinea consanguinea</i>	4.9	1	6	7	1	6	15	1	6	1	1	38	6	1
[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]
<i>Euphorbia myrsinites</i>	10.5	10	25	13	1	10	21	2	10	25	1	7	8	3
<i>Hypericum rumeliacum</i>	14.4	21	34	17	1	21	30	1	21	34	2	4	29	2
<i>Scabiosa trinifolia</i>	10.8	10	12	13	5	10	20	8	10	12	7	44	16	16
Order 4.1 (24 taxa, 23 exclusive)														
<i>Festuca vaginata</i>	5.6	1	0	22	1	1	1	65	1	1	1	65	1	1

TABLE 2 (Continued)

	All	Classes					Orders					Alliances																												
		4.1	3.8	2.8	11.3	4.3	2.3	2.6	2.2	1.7	23.3	19.5	20.1	3.0	1.2	19.8	2.5	6.8	0.8	1.3	1.2	8.1	3.0	8.0	3.9	6.3	7.3	2.1	15.3	17.5	3.4	1.8	4.3							
<i>Centaurea arenaria</i>	4.1	1	0	16	1	1	1	1	1	1	46	1	1	1	1	1	1	1	1	1	46	1	1	1	1	1	1	1	1	1	1	1	1	1	46	1				
<i>Polygonum arenarium</i>	3.8	1	0	14	1	1	1	1	1	43	1	1	1	1	1	1	1	1	1	1	43	1	1	1	1	1	1	1	1	1	1	1	1	43	1					
<i>Koeleria glauca</i>	2.8	0	0	11	1	1	1	1	1	33	1	1	1	1	1	1	1	1	1	33	1	1	1	1	1	1	1	1	1	1	1	1	33	1	1					
<i>Euphorbia seguieriana</i>	11.3	4	6	8	23	4	6	3	16	18	6	2	4	6	3	2	16	18	11	6	65	2	4	6	3	2	16	18	11	6	65	2	4	6	65	2				
<i>Artemisia campestris</i>	4.3	2	4	1	13	2	4	1	2	1	1	1	2	4	1	2	4	1	2	1	38	1	2	4	1	2	4	1	2	1	38	1	2	4	38	1				
<i>Stipa borysthena</i>	2.3	0	0	9	1	1	1	1	1	27	1	1	1	1	1	1	1	1	1	27	1	1	1	1	1	1	1	1	1	1	1	1	27	1	27	1				
<i>Peucedanum arenarium</i>	2.6	1	0	9	1	1	1	1	1	28	1	1	1	1	1	1	1	1	1	28	1	1	1	1	1	1	1	1	1	1	1	1	28	1	28	1				
<i>Festuca wagneri</i>	2.2	0	0	8	2	2	2	2	2	24	2	2	2	2	2	2	2	2	2	24	2	2	2	2	2	2	2	2	2	2	2	2	24	2	24	2				
<i>Tragopogon floccosus</i>	1.7	0	0	7	2	2	2	2	2	20	2	2	2	2	2	2	2	2	2	20	2	2	2	2	2	2	2	2	2	2	2	2	20	2	20	2				
Order 4.2 (5 taxa, 3 exclusive)																																								
<i>Plantago subulata</i> aggr.	23.3	7	1	15	56	7	1	9	4	2	27	85	7	1	6	11	4	2	66	9	69	7	1	6	11	4	2	66	9	5	69	7	1	6	11	4	2	66	9	
<i>Scleranthus perennis</i>	19.5	28	5	9	45	28	5	15	7	10	68	28	5	9	20	7	20	9	1	65	70	28	5	9	20	7	20	9	1	65	70	28	5	9	20	7	20	9		
<i>Carex caryophylla</i>	20.1	8	6	17	35	8	6	33	17	1	53	8	6	24	42	17	1	18	14	5	55	8	6	24	42	17	1	18	14	5	55	8	6	24	42	17	1	18	14	
Alliance 4.2.1 (16 taxa, 15 exclusive)																																								
<i>Jasione heldreichii</i>	3.0	4	1	1	9	4	1	1	1	1	13	4	1	1	1	1	1	1	1	25	13	4	1	1	1	1	1	1	1	1	1	1	1	1	13	4	1	1		
<i>Lotus alpinus</i>	1.2	0	0	5	5	5	5	5	5	7	7	7	7	7	7	7	7	7	7	14	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	7	
<i>Rumex acetosella</i>	19.8	34	3	14	34	34	3	28	8	11	52	34	3	27	28	8	28	4	2	67	36	34	3	27	28	8	28	4	2	67	36	34	3	27	28	8	28	4		
<i>Agrostis canina</i> aggr.	2.5	2	1	1	7	2	1	3	1	10	2	10	2	1	1	5	1	1	1	20	20	10	2	1	1	5	1	1	1	20	20	10	2	1	1	5	1	20	20	
<i>Pilosella hoppedana</i>	6.8	5	3	6	12	5	3	12	6	1	18	5	3	9	14	6	1	3	5	33	2	18	5	3	9	14	6	1	3	33	2	18	5	3	9	14	6	1	3	
<i>Centaurea deustiformis</i>	0.8	0	0	3	3	3	3	3	3	5	5	5	5	5	5	5	5	5	5	9	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	
<i>Euphrasia liburnica</i>	1.3	0	0	4	4	4	4	4	4	6	6	6	6	6	6	6	6	6	6	12	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
<i>Daphne oleoides</i>	1.2	0	0	4	4	4	4	4	4	6	6	6	6	6	6	6	6	6	6	11	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6	6
<i>Euphrasia pectinata</i>	8.1	2	2	9	11	2	2	13	2	11	17	2	2	7	18	2	15	10	8	33	17	17	2	2	7	18	2	15	10	8	33	17	17	2	15	10	8	33	17	
<i>Juniperus communis</i>	3.0	1	1	2	6	1	1	3	1	3	9	1	1	1	5	1	3	5	1	18	9	9	1	1	1	5	1	3	5	1	18	9	9	1	3	5	1	18	9	
Alliance 4.2.2 (19 taxa, 16 exclusive)																																								
<i>Poa molineri</i>	8.0	2	2	27	1	1	1	1	1	4	41	2	2	1	1	1	1	1	6	11	70	2	2	1	1	1	1	6	1	1	70	2	2	1	1	6	1	1	70	2
<i>Minuartia montana</i>	3.9	0	0	15	1	1	1	1	1	0	22	0	0	1	1	1	1	1	1	44	22	22	0	0	1	1	1	1	1	1	44	22	22	0	0	1	1	44	22	
<i>Pontechium maculatum</i>	6.3	4	4	17	2	2	2	2	2	7	25	4	4	1	2	1	20	1	1	50	25	25	4	4	1	2	1	20	1	1	50	25	25	4	4	1	2	20	1	
<i>Potentilla heptaphylla</i>	7.3	5	5	16	6	6	6	6	6	9	25	5	5	1	11	1	25	1	3	46	25	25	5	5	1	11	1	25	1	3	46	25	25	5	5	1	11	3	46	
<i>Erysimum carniolicum</i>	2.1	0	0	7	1	1	1	1	1	0	11	0	0	1	1	1	1	1	1	22	11	11	0	0	1	1	1	1	1	22	11	11	0	0	1	1	22	11		
<i>Koeleria splendens</i> aggr.	15.3	9	15	14	19	9	15	2	4	26	29	9	15	2	1	4	26	9	9	50	29	29	9	15	2	1	4	26	9	9	50	29	29	9	15	2	1	4	26	
<i>Dorycnium pentaphyllum</i>	17.5	3	8	19	23	3	8	16	17	3	34	3	8	25	7	17	3	64	14	2	66	34	3	8	25	7	17	3	64	14	2	66	34	3	8	25	7	17	3	
<i>Nocca praecox</i>	3.4	1	1	2	9	1	1	3	1	2	13	1	1	1	1	5	1	1	4	26	13	13	1	1	1	1	1	1	1	26	13	13	1	1	1	1	26	13		
<i>Armeria maritima</i>	1.8	0	0	1	6	1	1	1	1	1	9	0	0	1	1	1	1	2	2	18	9	9	0	0	1	1	1	2	2	18	9	9	0	0	1	1	18	9		
<i>Ornithogalum collinum</i>	4.3	1	1	3	10	1	1	4	1	3	16	1	1	1	1	7	1	7	2	28	16	16	1	1	1	1	1	7	2	28	16	16	1	1	7	2	28	16		

TABLE 2 (Continued)

	Classes												Orders												Alliances																
	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]	[...]
<i>Scabiosa columbaria</i> aggr.	14.0	1	3	15	21	1	3	26	4	1	15	31	1	3	9	43	4	1	32	12	1	10	52																		
Companion taxa																																									
<i>Sanguisorba minor</i>	37.7	44	46	40	28	44	46	48	38	38	36	42	44	46	54	42	38	38	59	30	18	23	60																		
<i>Plantago lanceolata</i>	28.5	43	31	29	22	43	31	60	45	14	8	33	43	31	64	55	45	14	12	11	1	52	14																		
<i>Chrysopsis gryllus</i>	27.3	39	41	30	12	39	41	29	49	28	26	18	9	39	41	52	5	49	28	25	9	43	14	4																	
<i>Teucrium chamaedrys</i>	23.8	12	30	32	6	12	30	30	54	41	23	7	6	12	30	30	29	54	41	4	57	9	7	12																	
<i>Euphorbia cyparissias</i>	23.0	22	17	26	18	22	17	35	39	4	23	3	26	22	17	36	34	39	4	20	47	3	3	43	8																
<i>Asperula cynanchica</i>	21.8	13	21	25	17	13	21	24	38	25	22	11	21	13	21	12	36	38	25	20	37	8	11	31	10																
<i>Thymus pannonicus</i> aggr.	19.5	12	3	19	29	12	3	16	45	25	10	39	24	12	3	21	11	45	25	13	17	39	6	42																	
<i>Arenaria serpyllifolia</i> aggr.	18.8	37	36	16	14	37	36	7	14	20	21	19	12	37	36	6	8	14	20	5	27	30	19	18	6																
<i>Centaurea stoebe</i>	18.8	25	15	18	19	25	15	18	34	17	14	28	25	15	14	21	34	17	22	18	3	42	14																		
<i>Astragalus onobrychis</i>	18.5	39	40	17	8	39	40	4	21	7	28	8	8	39	40	2	5	21	7	50	24	10	8	8																	
<i>Potentilla argentea</i>	16.9	27	8	17	16	27	8	33	36	2	6	24	27	8	41	25	36	2	7	9	1	43	4																		
<i>Bromus squarrosus</i>	16.3	45	35	12	10	45	35	4	21	21	12	25	3	45	35	4	3	21	21	4	15	17	25	6																	
<i>Convolvulus cantabrica</i>	14.3	25	34	16	0	25	34	1	16	44	17	1	25	34	1	16	44	25	15	11	1	1	1	1																	
<i>Hypericum perforatum</i>	13.7	13	6	15	14	13	6	25	19	5	10	8	17	13	6	24	25	19	5	15	14	1	8	34																	
<i>Erysimum diffusum</i>	13.5	28	22	13	8	28	22	1	9	27	17	18	3	28	22	1	9	27	22	10	19	18	3	2																	
<i>Climopodium alpinum</i>	12.8	14	8	14	11	14	8	5	4	25	8	16	14	8	3	13	5	4	20	21	33	16	16																		
<i>Potentilla recta</i>	12.5	35	26	10	6	35	26	10	11	16	8	10	35	26	9	11	11	16	9	7	7	11	8																		
<i>Koeleria nitidula</i>	11.8	16	29	12	5	16	29	8	12	18	12	8	16	29	7	8	12	18	1	29	6	16	16																		
<i>Koeleria macrantha</i>	11.4	4	2	15	10	4	2	18	22	17	9	16	7	4	2	18	17	22	17	20	7	1	16	13																	
Bryophytes and lichens																																									
Number of plots with records	1039	118	181	720	20	118	181	552	120	10	38	0	20	118	181	505	47	120	10	1	28	9	0	19	1																
Mean non-vascular species richness	2.5	2.8	2.7	2.2	3.8	2.8	2.7	2.0	2.9	2.0	2.2	?	3.8	2.8	2.7	1.9	2.1	2.9	2.0	?	1.3	3.0	?	3.8	?																
Diagnostic taxa																																									
<i>Dicranum scoparium</i>	1.0	1	1	1	1	1	4	1	1	1	1	?	?	1	0	8	1	?	?	?	?	?	?	?																	
<i>Syntrichia ruralis</i> aggr.	27.7	22	24	30	21	22	24	29	28	60	18	?	21	22	24	28	30	28	60	?	14	22	?	21	?																
<i>Ceratodon purpureus</i>	22.0	19	20	20	37	19	20	12	25	50	11	?	37	19	20	14	11	25	50	?	11	11	?	37	?																
<i>Xanthoparmelia pulla</i>	5.7	6	6	6	5	6	6	2	8	11	11	?	5	6	6	2	2	8	?	?	22	?	5	?																	
<i>Polytrichum piliferum</i>	6.2	8	6	2	26	8	6	4	7	?	?	?	26	8	6	3	4	7	?	?	?	?	?	?																	
<i>Dicranella heteromalla</i>	1.3	1	?	?	11	1	?	?	?	?	?	?	11	1	?	?	?	?	?	?	?	?	?	?																	
<i>Racomitrium canescens</i> aggr.	4.7	3	8	2	21	3	8	2	7	?	?	?	21	3	8	2	2	7	?	?	?	?	?	?																	
Companion taxa																																									
<i>Gladonia foliacea</i>	23.4	16	23	21	47	16	23	20	34	10	20	?	47	16	23	18	21	34	10	?	7	33	?	47	?																
<i>Tortella tortuosa</i>	13.2	21	14	13	5	21	14	16	9	?	18	?	5	21	14	18	15	9	?	?	14	22	?	5	?																

(Continues)

TABLE 2 (Continued)

	Classes										Orders										Alliances									
	All	5	12	7	26	5	12	8	16	16	6	?	26	5	12	7	9	16	?	11	?	26	?							
<i>Cladonia rangiformis</i>	9.5	8	12	7	26	5	12	8	16	16	6	?	26	5	12	7	9	16	?	11	?	26	?							
<i>Cladonia furcata</i>	8.8	8	12	7	16	8	12	4	11	13	?	?	16	8	12	3	4	11	?	4	22	?	16	?						
<i>Pleurochaete squarrosa</i>	7.6	8	15	6	11	8	15	5	15	10	?	?	11	8	15	8	2	15	?	10	?	11	?							
<i>Hypnum cupressiforme</i>	7.6	22	13	5	5	22	13	8	9	2	?	?	5	22	13	7	9	9	?	4	?	5	?							
<i>Cetraria aculeata</i>	7.0	12	11	3	21	12	11	4	12	?	?	?	21	12	11	5	2	12	?	?	?	21	?							
<i>Abietinella abietina</i>	6.8	12	10	6	5	12	10	10	8	4	?	?	5	12	10	10	9	8	?	7	?	5	?							
<i>Grimmia pulvinata</i>	6.8	8	13	6	5	8	13	6	8	7	?	?	5	8	13	4	9	8	?	4	11	?	5	?						
<i>Homalothecium lutescens</i>	6.7	10	6	7	5	10	6	8	7	10	4	?	5	10	6	5	11	7	10	?	7	?	5	?						
<i>Bryum caespiticium</i>	5.1	8	7	4	5	8	7	5	9	4	?	?	5	8	7	3	6	9	?	7	?	5	?							

Note: The full table is available in Appendix S21 and S22. For each order and alliance, the 10 diagnostic species with the highest phi-values are shown (or if there are fewer, all of them). Additionally, the diagnostic species of lower rank are displayed after [...] if their overall constancy is above 10%. At the bottom of the table the companion species among the vascular plants with at least 10% overall constancy are displayed, followed by diagnostic and companion species among bryophytes and lichens. The columns of the syntaxa are labelled with their number according to Table 1. The values displayed are percentage constancy values in the case of alliances and means of these of the included alliances in the case of superior syntaxa. For phi-values ≥ 0.4 , constancy values are bold. Constancies of bryophytes and lichens have been calculated based on those plots in which these taxa were surveyed ('?' if no such plots were available); here all companion species with at least 5% overall constancy are displayed. Diagnostic species of orders are highlighted with dark grey boxes, those of alliances with light grey boxes.

The final synoptic table (Table 2), excluding only 5% of plots that could not be assigned to an alliance by our ES, demonstrates that our orders and classes are positively characterised very well. Our orders possess between four (4.2: *Trifolio-Festucetalia*) and 54 (3.3) diagnostic species (including some shared with one or several other orders), many of which would also qualify as character species. Even the two least positively characterised orders, *Trifolio-Festucetalia* (4.2: three unique diagnostic species within our table) and *Festucetalia valesiaca* (3.2: six unique diagnostic species), could still be characterised positively through the rather high frequencies of their unique diagnostic species. The alliances within the non-monotypic orders were also positively characterised, with between five and 43 taxa qualifying as diagnostic species at the alliance level in the overall table (and more in the partial tables within the orders). While we planned to allow central (i.e., negatively characterised) alliances within orders, this option was not needed in the current data set. Our rules allowed species to be diagnostic for more than one unit of a certain hierarchical level, but a large majority of species were diagnostic for only one order or alliance.

4.4 | Description of the alliances

In the following, we briefly describe each of the 12 distinguished alliances arranged within the four classes. Further information on the alliances is given in the synoptic table (Table 2, Appendices S21–S22). An overview of diagnostic, constant and dominant species of each alliance can be found in Appendix S27, and a photo guide showing typical stands from throughout the study region in Appendix S28.

The alliances showed clear patterns in geographic distribution, some being widespread throughout most of the study area, others more narrowly distributed (Figure 3). Regarding elevation, alliance 4.1.1 is a lowland unit and the orders 3.4, 4.2 and the alliance 3.1.2 montane units, while the others are intermediate (Figure 4a). Most alliances occurred on relatively flat terrain, except those of order 3.3 and 3.4 (rocky grasslands of the *Festuco-Brometea*) and 4.2.2 (Figure 4b). The total vegetation cover (including the moss layer) was generally high and often close to 100%, except the five alliances that occupied steeper slopes (Figure 4c). Species richness of vascular plants was generally lower in the three *Koelerio-Coryneporetea* alliances than in those of the three other classes (Figure 4d).

Regarding soil moisture (mean EIVEM values), all alliances occurred in the drier parts of the landscape, but within the classes *Festuco-Brometea* and *Koelerio-Coryneporetea*, respectively, the orders 3.1 and 4.2 were less xerophytic than the other orders. Also soil nitrogen (EIVEN) was generally in the lower part of the gradient, with the order 3.4 of the *Festuco-Brometea* and all *Koelerio-Coryneporetea* alliances indicating even lower nitrogen availability than the others. Regarding soil reaction (EIVER), based on the species composition, none of the alliances seems to be associated with very low pH. However, among the sub-Mediterranean syntaxa, the *Stipo-Brachypodieta distachyae* were clearly associated with higher pH than the *Tuberarietea guttatae*, while among the temperate units the order 3.1 and particularly alliance 4.2.1 had below-average mean EIVER values. The mean light

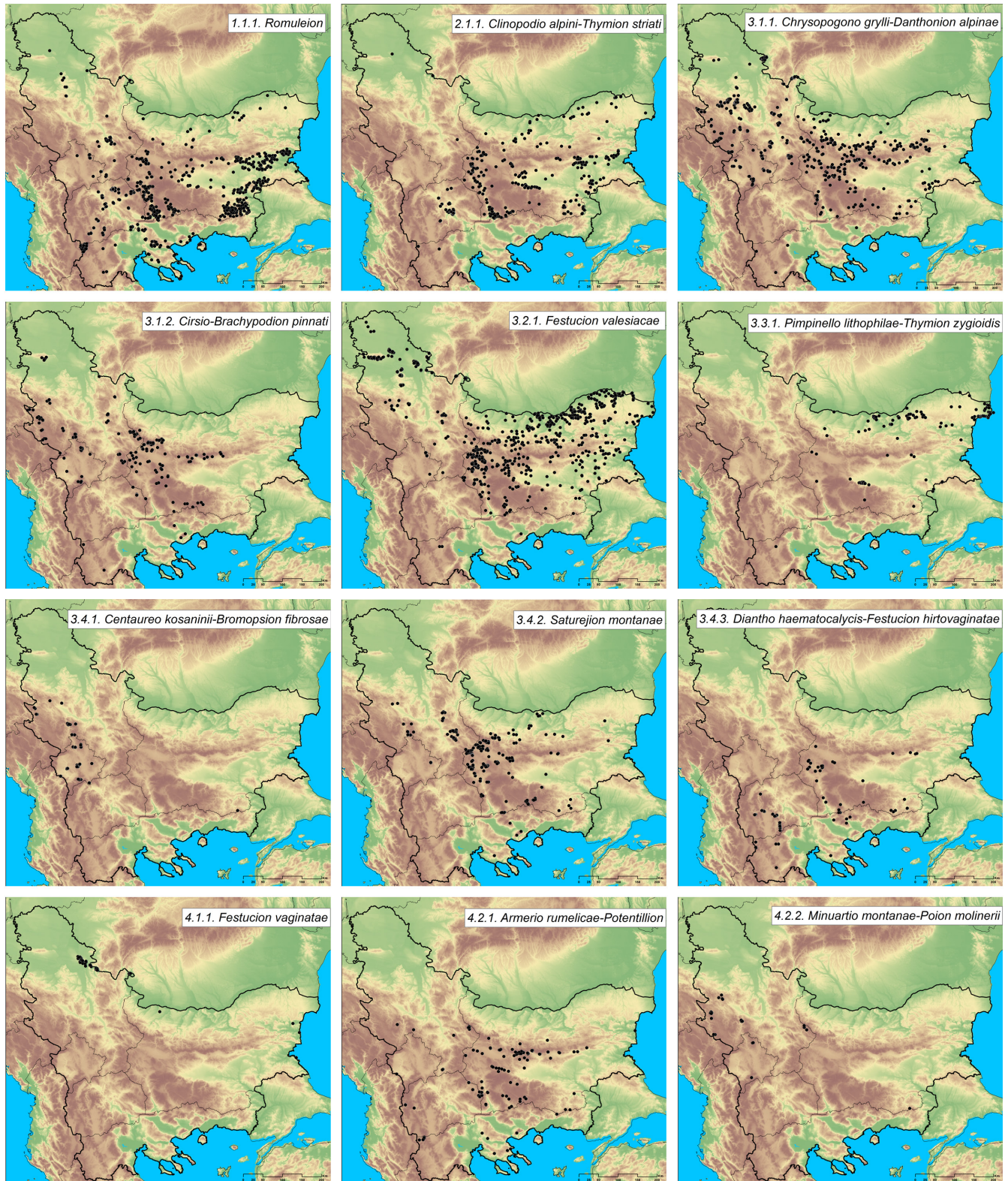


FIGURE 3 Distribution maps of the 12 distinguished alliances.

values (EIVE L) were generally high, but slightly lower for the two alliances of order 3.1. Mean temperature values (EIVE T) only partly mirrored the elevations, with the two sub-Mediterranean alliances as well as alliance 3.3.1 indicating particularly warm conditions, while the alliances of the two mesoxeric orders (3.1 and 4.2) showed cooler microclimate than the average of their classes.

4.4.1 | Submediterranean therophyte-rich acidophilous grasslands

Alliance 1.1.1 – Romuleion

This alliance is widely distributed throughout southern Bulgaria, northern Greece and North Macedonia on siliceous substrates

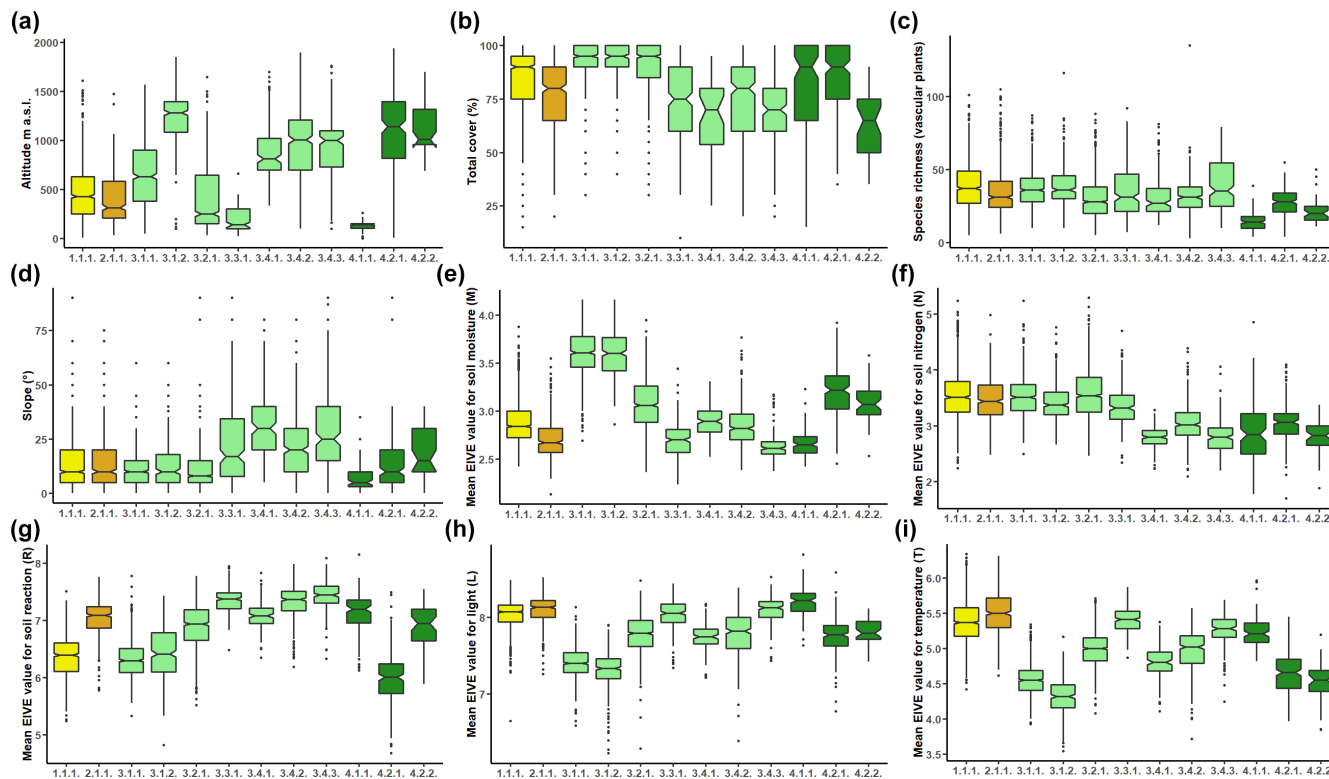


FIGURE 4 Boxplots of selected topographic, structural and biodiversity characteristics as well as mean Ecological Indicator Values for Europe (EIVE) of the 12 distinguished alliances: (a) altitude (m a.s.l.), (b) slope ($^{\circ}$), (c) total vegetation cover (%) and (d) vascular plant species richness (in plots of 15–100 m², mean: 53 m²) and (e–i) mean unweighted EIVE for five niche dimensions. The EIVE are all on a continuous scale from 0 to 10, with the endpoints representing the realised minima and maxima in Europe, respectively (Dengler et al., 2023). The boxes represent the interquartile ranges, the lines and points the ranges of the values and the notches the confidence interval around the median.

and rarely on sandy soils in the northern part of the study area. It occurs on flat to moderately inclined terrain in the lowlands and submontane regions. Soils are shallow to moderately deep, and rich in skeleton. These grasslands are mainly used as pastures. The stands are rich in therophytes such as *Bromus squarrosus*, *Galium divaricatum*, *Psilurus incurvus*, *Taeniatherum caput-medusae*, *Trifolium arvense*, *T. cherleri*, *T. hirtum*, *Vulpia ciliata*, but also also have a relatively high cover of perennial grasses like *Bothriochloa ischaemum*, *Chrysopogon gryllus* and *Festuca valesiaca*. The herb layer is moderately dense, while the cryptogam layer is usually well developed. Frequently, this alliance form mosaics with stands of the *Festucion valesiaca*, leading to varying proportions of hemicryptophytes and annual species.

4.4.2 | Submediterranean therophyte-rich basiphilous grasslands

Alliance 2.1.1 – Clinopodio alpini-Thymion striati

This alliance occurs on calcareous bedrock, predominantly in the southern part of the study area (south Bulgaria, North Macedonia, Greece), but rarely also north of the Balkan Range. It grows at low altitudes on gentle slopes. Soils are shallow to moderately deep. The herb layer is moderately dense, allowing the development

of a cryptogam layer. Diagnostic and constant species include many therophytes (such as *Aegilops comosa* subsp. *heldreichii*, *Brachypodium distachyon*, *Bombacillaena erecta*, *Medicago minima*, *Neotostema apulum* and *Ziziphora capitata*) and chamaephytes such as *Teucrium capitatum* and *Thymus striatus*. The *Clinopodio alpini-Thymion striati* and the *Romuleion* share some diagnostic species, such as *Aegilops neglecta*, *Dasyphyrum villosum*, *Eryngium campestre* and *Medicago rigidula*, and sometimes grow next to each other.

4.4.3 | Temperate mesoxerophilous grasslands on loamy soils

Alliance 3.1.1 – Chrysopogono grylli-Danthonion alpinae

This alliance includes mesoxerophilous grasslands of Bulgaria, Serbia, Kosovo and northern Greece. It grows mainly on siliceous and less frequently on calcareous bedrock in the submontane and montane belts. The stands mainly occur on slightly inclined terrain of different aspect, with shallow to moderately deep soils. The herb layer is usually dense and relatively tall. Among the diagnostic species of the alliance are mesoxerophilous taxa, such as *Danthonia alpina*, *Euphrasia stricta*, *Hypochaeris radicata*, *Moenchia mantica* and *Polygala comosa*. Like the following alliance, *Cirsio-Brachypodium*, the

stands are differentiated by various mesophilous grasses, typical of the order *Arrhenatheretalia*, such as *Agrostis capillaris*, *Alopecurus pratensis*, *Anthoxanthum odoratum* and *Festuca rubra* aggr.

Alliance 3.1.2 – *Cirsio-Brachypodium pinnati*

This vegetation type includes mesoxerophilous grasslands on shallow to moderately deep soils over calcareous substrate. It occurs throughout most of the study region in mountainous areas. These species-rich grasslands are used as pastures and hay meadows. They are dominated by grasses such as *Agrostis capillaris*, *Brachypodium pinnatum*, *Festuca dalmatica* aggr. and *Koeleria pyramidata*. This alliance shares some common constant species with the *Chrysopogono-Danthonion*, such as *Anthoxanthum odoratum*, *Briza media*, *Galium verum*, *Genista sagittalis*, *Leucanthemum vulgare* aggr. and *Lotus corniculatus*.

4.4.4 | Continental steppes on loamy soils

Alliance 3.2.1 – *Festucion valesiaca*

This alliance is the most frequent and widespread dry-grassland type in the study area, found from the lowlands to the montane belt in all countries covered. It occurs on different types of shallow to moderately deep soil. It is dominated by perennial grasses such as *Bothriochloa ischaemum*, *Chrysopogon gryllus*, *Festuca stricta*, *F. valesiaca*, *Poa pratensis* aggr. and *Stipa capillata*. Among the *Festuco-Brometea* alliances of the region, it has the smallest group of positive diagnostic species including *Agrimonia eupatoria*, *Daucus carota*, *Medicago falcata*, *M. lupulina* and *F. valesiaca*, several of which are also widespread in mesoxeric grasslands or ruderal communities, indicating that from the Balkan perspective this alliance (respectively its order) is a 'central' unit. The grasslands are mainly secondary, formed under relatively strong human impact, often replacing natural *Quercus* forests. Predominantly, they are used as pastures.

4.4.5 | Rocky grasslands of the lowlands of the steppe zone

Alliance 3.3.1 – *Pimpinello lithophilae-Thymion zygioidis*

This alliance comprises the calcareous rocky grasslands of north-eastern Bulgaria (Danube Plain) and occasionally the Thracian Lowland. It occurs at low elevation on flat to slightly inclined terrain, mostly on south- and east-facing slopes. The distribution of this alliance is related to regions where steppe vegetation has persisted during the Holocene. Several of the diagnostic species are steppe species in a narrow sense, such as *Artemisia lerchiana*, *Aster oleifolius*, *Astragalus glaucus*, *Iris pumila*, *Koeleria brevis*, *Tanacetum millefolium*, *Paeonia tenuifolia*, *Potentilla bornmuelleri* and *Thymus zygioides*. This vegetation is transitional between the Pontic steppes and the sub-Mediterranean grasslands of the Balkan Peninsula.

4.4.6 | Rocky grasslands of the mountains of the Balkan Peninsula

Alliance 3.4.1 – *Centaureo kosaninii-Bromopsion fibrosae*

This vegetation includes rocky grasslands on shallow soils over ultramafic bedrock, found in submontane and montane regions of Serbia and rarely in Greece and Bulgaria. It occurs predominantly on gentle slopes of varying aspect, but also on rock outcrops. It hosts serpentine specialists such as *Centaurea kosaninii*, *Euphorbia glabriflora*, *Fumana bonapartei*, *Halacsya sendtneri* and *Odontarrhena markgrafii*. This alliance is well developed in the sub-Mediterranean zone and is rich in Balkan endemic taxa such as *Centaurea kosaninii*, *Genista hasertiana*, *Polygala doerfleri* and *Stipa mayeri*.

Alliance 3.4.2 – *Saturejion montanae*

This alliance groups semi-closed perennial plant communities dominated by hemicryptophytes and dwarf shrubs on calcareous soils in the lowlands, submontane and montane regions of the sub-Mediterranean zone in Bulgaria, Serbia and northern Greece. It occurs both on steep and slightly inclined terrain with varying aspect. Soils are shallow to moderately deep, usually with rocky outcrops. The group of constant and diagnostic species includes *Carex humilis*, *Potentilla incana* aggr., *Satureja montana* aggr. and *Stipa eriocalis*. At lower elevations in the northeast of the study area, this vegetation transitions into rocky grasslands of the *Pimpinello-Thymion zygioidis* and in the south, under warmer conditions, into the *Clinopodio alpini-Thymion striati*.

Alliance 3.4.3 – *Diantho haematocalycis-Festucion hirtovaginatae*

This vegetation includes semiclosed dry grasslands on calcareous substrates in North Macedonia, northern Greece and southern Bulgaria. It occurs on steep to gentle slopes of varying aspect. Soils are shallow to moderately deep and rich in skeleton. Communities are rich in perennial steppe species such as *Festuca valesiaca* and *Stipa epilosa*, but many Mediterranean and sub-Mediterranean species also occur. It is rich in endemic species such as *Achillea clypeolata*, *Astragalus mariovoensis*, *Centaurea grbavacensis*, *Scorzonera mariovoensis*, *Stachys iva* and *Viola herzogii*. These grasslands are of secondary origin, forming after the destruction and degradation of various zonal forest communities dominated by *Carpinus orientalis* and *Quercus* spp.

4.4.7 | Subcontinental and continental sand steppes

Alliance 4.1.1 – *Festucion vaginatae*

This vegetation type includes sandy dry grasslands found along the Danube River and the Black Sea coast on fluvial and coastal dunes. Within the study area it is thus the most geographically restricted dry-grassland type, only found in small parts of Serbia and Bulgaria. From all studied community types, the alliance has the lowest elevational range, indicating a preference for a warm and dry climate. Plants are adapted to well-drained soils and disturbances due to sand movement. Constant and dominant species include psammophytic species such as *Corispermum nitidum*, *Festuca vaginata*, *F.*

wagneri, and *Peucedanum arenarium*. On average, the stands have the lowest plant species richness among all studied types, but they often have a large cover of certain bryophytes.

4.4.8 | Mesoxeric grasslands on siliceous and serpentine bedrock

Alliance 4.2.1 – *Armerio rumelicae*-*Potentillion*

This alliance is found on siliceous substrates in the submontane and montane belts of Bulgaria, Serbia, Kosovo, North Macedonia and northern Greece. It occurs on steep to slightly inclined terrain with varying aspect and high proportions of stones. Soils are shallow to moderately deep, sometimes with rock outcrops. The stands are moderately species-rich, characterised by high proportions of bryophytes and lichens, such as *Ceratodon purpureus*, *Cetraria aculeata*, *Cladonia foliacea*, *Cladonia furcata* aggr. *Polytrichum piliferum*, *Racomitrium canescens* aggr. and *Syntrichia ruralis* aggr. The herb layer is moderately dense to open and is formed of species such as *Agrostis castellana*, *Carex caryophylla*, *Festuca valesiaca*, *Plantago subulata* aggr. and *Poa bulbosa*.

Alliance 4.3.2 – *Minuartia montanae*-*Poa molinerii*

This alliance represents serpentine pioneer grasslands in the mountain regions of Serbia, Kosovo and Bulgaria. It occurs on gentle slopes of varying aspect. Soils are shallow, eroded and rich in skeleton. Diagnostic and constant species include xerophytic hemicryptophytes such as *Dorycnium pentaphyllum*, *Minuartia montana*, *Poa molinerii*, *Potentilla heptaphylla* and *Thymus pannonicus* aggr. The open structure of the vegetation also favours the distribution of rocky grassland species such as *Iris reichenbachii*, *Koeleria mitrushi* and *Festuca panciana*.

5 | DISCUSSION

5.1 | Balkan dry grasslands: New propositions and open issues

While our study in many aspects found support for previous syntaxonomic concepts, it also revealed new insights. Our approach was semisupervised (De Cáceres et al., 2015) as it started with information from existing classification systems (e.g. Mucina et al., 2016) and it aimed to improve certain parts of this European classification system while limiting the effects on classes and regions not covered. That way, we could suggest different solutions compared to the current mainstream and identify some open questions that could not be resolved with confidence due to regional data deficiencies. In the following, we highlight some of these critical and controversial issues.

5.1.1 | Mediterranean grassland classes

According to the recent syntaxonomic overview of Europe (Mucina et al., 2016), six classes of 'Mediterranean' dry grasslands could

have been expected to occur in the sub-Mediterranean areas of the region, particularly at or near the Aegean and the Black Sea coasts: *Tuberarietea guttatae*, *Helichryso-Crucianelletea maritima*, *Lygeo sparti-Stipetea tenacissimae*, *Poetea bulbosae*, *Stipo giganteae-Agrostietea castellanae* and *Stipo-Trachynietea distachyae*. Despite the reasonably good spatial and ecological coverage of our plots, the EuroVegChecklist ES (Mucina et al., 2016) did not assign any plots to the classes *Lygeo-Stipetea* and *Stipo-Agrostietea*, and only three and four plots to the *Helichryso-Crucianelletea* and *Poetea bulbosae*, respectively. This indicates that these classes either (i) are rare or do not occur in the study region, (ii) have been neglected in vegetation sampling in the study area, (iii) are generally poorly supported, or (iv) the species given in the EuroVegChecklist ES are not appropriate for their delimitation. It might turn out that the vegetation of the *Helichryso-Crucianelletea* should better be included fully into the *Koelerio-Corynephoretea* (Dengler, 2003) or split between this class and the *Ammophiletea* (Marcenó et al., 2018).

By contrast, the *Tuberarietea guttatae* and the *Stipo-Trachynietea distachyae* were well-represented in our data set. However, despite the large numbers of plots that we had, applying the same criteria as for all other syntaxa, we could distinguish only one order with one alliance each. This considerably contrasts with the number of alliances of (sub-)Mediterranean alliances that have been described from the region. According to Mucina et al. (2016) there should be three acidophytic alliances (*Romuleion*, *Scabioso-Trifolion dalmatici*, *Trifolion cherleri*), placed in three different classes (*Poetea bulbosae*, *Sedo-Scleranthetea*, *Tuberarietea guttatae*), while also three basiphytic alliances (*Cymbopogono-Brachypodion ramosi*, *Saturejo-Thymion*, *Xeranthemion annui*) from three different classes are listed (*Lygeo sparti-Stipetea tenacissimae*, *Festuco-Brometea*, *Stipo-Trachynietea distachyae*). In our classification and ES, they were merged in only two alliances (see Table S19.2 in Appendix S19). We cannot exclude that some of the other alliances were represented only marginally and thus not detected with our methodology. However, it appears that in the Mediterranean grassland classes, a considerable consolidation based on broad-scale analyses of extensive plot data sets including the whole Mediterranean Basin or at least both sub-Mediterranean and eu-Mediterranean regions will be needed to achieve a better-founded classification system with well-defined and meaningful syntaxa as well as a consistent differentiation from the 'temperate' classes. Possibly this would lead to a reduction of high-rank syntaxa compared to Mucina et al. (2016).

5.1.2 | *Brachypodietalia pinnati*

The two alliances separated match the concepts of Pedashenko et al. (2013), Ačić et al. (2015), Mucina et al. (2016) and Willner et al. (2019). However, since on the western Balkan Peninsula another mesoxeric alliance is generally accepted, namely the *Scorzonerion villosae* (Terzi, 2015, and Mucina et al., 2016, within the

order *Scorzonetalia villosae*; Willner et al., 2017, 2019, Dengler & Willner, 2023, within the order *Brachypodietalia pinnati*), we tested whether this alliance might be the better 'home' for the Central and Eastern Balkan 'Cirsio-Brachypodion' stands than the Central European *Cirsio-Brachypodion* s.str. As expected from the geographic location, our stands were intermediate transitional between both units, but overall, we found the arguments for inclusion into the *Cirsio-Brachypodion* more convincing (Appendix S29).

5.1.3 | *Festucetalia valesiaca*

Consistent with Pedashenko et al. (2013) and Mucina et al. (2016), we accepted within this order only one alliance, the *Festucion valesiaca*, placing the *Pimpinello-Thymion* in another order (see below). A split of the *Festucion valesiaca* into *Festucion valesiaca* s.str., *Festucion rupicolae* and the *Artemisio-Kochion* as suggested by Aćić et al. (2015) was not supported by our larger data set (similar to Willner et al., 2017).

5.1.4 | *Pimpinello-Thymion zygoidis*

This alliance has long been recognised as a very distinct unit, endemic to NE Bulgaria and the adjacent Dobruja region of Romania, where it grows on a lowland limestone plateau close to the Black Sea (Dihoru & Donița, 1970; Dihoru, 1999; Tzonev et al., 2006). It has been considered natural steppe vegetation (Bohn et al., 2004). However, there has been a dispute whether this alliance belongs to the *Festucetalia valesiaca* (Dihoru, 1999; Tzonev et al., 2006) or the *Stipo pulcherrimae-Festucetalia pallentis* (Tzonev et al., 2009; Mucina et al., 2016). Both solutions seem to be ecologically and chorologically meaningful. Thus, we tried both alternatives in our optimisation procedure for the orders. However, due to the high fraction of (mostly annual) species of Mediterranean origin, in both attempts most of the *Pimpinello-Thymion* plots were transferred to the order of the Mediterranean basiphilous grasslands after a few iterations, which would not make sense biogeographically. Thus, we decided to place the *Pimpinello-Thymion* into an order of its own, which remained stable in the iterations and even slightly increased beyond the traditional content of the alliances. It now also includes some floristically similar, therophyte-rich stands on eroded slopes of the Danubian Plain and the Thracian Lowland. To decide whether and which other alliances from outside the Balkan Peninsula should be joined with the *Pimpinello-Thymion* in this order would require an analysis on a broader geographic scale. One option would be to widen the concept of the *Tanacetum achilleifolii-Stipetalia lessingiana* (Mucina et al., 2016) to encompass the steppes of the southern steppe zone, as opposed to a narrower *Festucetalia valesiaca* restricted to the steppes of the more northern part of the steppe biome and steppe-like grasslands in the nemoral biome. Another option could be to include the alliance in the order *Thymo cretaeci-Hyssopietalia cretaeci* (Mucina et al., 2016) occupying chalk outcrops of the Central

Russian Upland. Moreover, two further orders of rocky grasslands in Ukraine, Crimea and the Caucasus are currently in preparation by D. Vynokurov (pers. comm.). What is lacking for any of these orders are broad-scale synoptic tables. Therefore, while the *Pimpinello-Thymion zygoidis* should not be included in the *Festucetalia valesiaca*, the *Stipo-Festucetalia* or the *Koelerietalia splendidis* based on our data, we leave its order affiliation open until there are sufficient published data of the *Festuco-Brometea* communities of the adjacent territories to the east.

5.1.5 | Rocky calcareous and serpentine grasslands in the mountains of the Balkan Peninsula

We found strong support for two floristically related (*Saturejion montanae*, *Diantho haematocalycis-Festucion hirtovaginatae*), but well separated alliances of rocky grasslands on limestone bedrock in the mountainous areas of the region. The alliance *Saturejion montanae*, dominated by dwarf shrubs and hemicryptophytes, occurs in the sub-Mediterranean zone of Bulgaria, Serbia and northern Greece. The *Diantho haematocalycis-Festucion hirtovaginatae*, which is found in the southern parts of the sub-Mediterranean zone in North Macedonia, SW Bulgaria and N Greece, is also dominated by hemicryptophytes and characterised by a higher abundance of thermophilous annual species.

Regarding the Balkan rocky grasslands on serpentinites, which are traditionally placed in a separate order *Halacsyetalia sendtneri* (Ritter-Studnička, 1970; Aćić et al., 2015; Kuzmanović et al., 2016; Mucina et al., 2016), our data suggest two clearly separated units in the study region: one belonging to the *Festuco-Brometea* and the other to the *Koelerio-Corynephoretea* (see below). The floristic composition of those in the *Festuco-Brometea* suggests that they belong to a common order of rocky grasslands instead of forming a separate order (see the long list of diagnostic species of this joint order 3.4 in Table 2). Species such as *Artemisia alba*, *Teucrium montanum* and *Leontodon crispus* are frequent in both calcareous and serpentine rocky grasslands of the Balkans. If both types were split into two orders, the order of non-serpentine grasslands would essentially be void of unique diagnostic species. Within the serpentine grasslands of the study region, two alliances have occasionally been recognised (e.g. Kuzmanović et al., 2016). Like Aćić et al. (2015), we could not find convincing support for such a subdivision in our data set, but this might partly be because the second alliance, *Potentillion visianii*, mainly occurs in Bosnia and Herzegovina, which was not included in our study.

Finally, the question remains which order the rocky grasslands of the Central and Eastern Balkan Peninsula should be assigned to. Basically, there are three options: (i) the order of peri-Alpine and peri-Carpathian rocky grasslands (*Stipo pulcherrimae-Festucetalia pallentis*; as in Pedashenko et al., 2013 and partly in Mucina et al., 2016), (ii) the Western Balkanic (Illyric) rocky grasslands (*Scorzonetalia villosae* excluding the mesoxeric type alliance *Scorzonion villosae*; the name of the remaining xerophytic order would be *Koelerietalia*

splendens; see Terzi, 2015) or (iii) a separate Central and Eastern Balkanic order (combining the *Halacsyetalia sendtneri* with alliances hitherto placed in other orders). We compared the species composition of our order 3.4 with the well-documented species compositions of the *Stipo-Festucetalia* from Central and Eastern Europe (Willner et al., 2017) and that of the *Koelerietalia splendens* in the western Balkans (Terzi, 2015) (Appendix S29). There are high similarities to both orders, thus we see no justification for a separate order of the Central and Eastern Balkan Peninsula. Overall, the relationship to the communities of the latter order was closer, so we decided to join our three alliances to the western Balkan alliances of the suborder *Koelerienalia splendens* (Terzi, 2015) under a conserved name *Koelerietalia splendens*. In consequence, both orders of mountainous rocky grasslands in the eastern half of Europe would be clearly separated geographically: *Stipo-Festucetalia* in the Alps and the Carpathians and their northern forelands, and *Koelerietalia splendens* in the sub-Mediterranean parts of the Balkan and Apennine Peninsulas.

5.1.6 | *Koelerio-Corynephoretea*

The class *Koelerio-Corynephoretea* s.l. has rarely been recognised in phytosociological works of the Central and Eastern Balkans (but see Tzonev et al., 2009; Pedashenko et al., 2013). By contrast, we found two well separated syntaxonomic groups that could be equated to orders in the European classification system of the class *Koelerio-Corynephoretea* by Dengler (2003: table 30).

The alliance *Festucion vaginatae* (order 4.1 in Table 2) is floristically quite distinct from all other units of the study area. Its placement in the syntaxonomic system is controversial: Ačić et al. (2015) assigned it to the *Festucetalia valesiaca* (*Festuco-Brometea*), while Mucina et al. (2016) placed it in a separate order *Festucetalia vaginatae* (*Koelerio-Corynephoretea*). Here we adopted the solution developed by Dengler (2003) based on the numerical analysis of hundreds of frequency tables from all over Europe, that is, joining it to an order of subcontinental and continental xeric calcareous sand grasslands (*Sedo acris-Festucetalia*; with *Koelerion glaucae*, *Festucion beckeri* and *Sileno conicae-Cerastion semidecandri* as further alliances from outside the study region). As seen in Table 2, the *Festucion vaginatae* includes the stands from the dunes of the Black Sea coast because their differences from the stands along the Danube justify, from our point of view, a separation at association, but not at alliance level. By contrast, some recent overviews place the Black Sea stands in a separate alliance *Scabiosion ucranicae*, either in the same order as the *Festucion vaginatae* (Tzonev et al., 2009) or even in a separate class (Mucina et al., 2016: *Helichryso-Crucianelletea*; Marcenò et al., 2018: *Ammophiletea*).

Mesoxeric, closed grasslands of siliceous soils in the mountainous areas of the Balkans (order 4.2 in Table 2) found little attention in the past and, if recorded, were assigned to varying syntaxa. The Eurasian Dry Grassland Group (EDGG) Research Expedition in Bulgaria involving several Central European specialists (Pedashenko

et al., 2013) recognised that such stands are ecologically and structurally very similar to, for example, the alliance *Armerion elongatae* from the subcontinental lowlands of Central Europe, sharing many identical or closely related species. These authors thus proposed to assign this alliance to the order *Trifolio arvensis-Festucetalia ovinae*, an order comprising mesoxeric siliceous grasslands widespread in Europe from the sub-Mediterranean to the hemiboreal zone (Dengler, 2001, 2003). There is an alliance described from Macedonia (*Armerio rumelicae-Potentillion*) whose type at least matches this concept and thus has to be adopted here, despite the fact that it was placed in the *Astragalo-Potentilletalia* (*Festuco-Brometea*) in the original description (Micevski, 1978) and even transferred to the Mediterranean to sub-Mediterranean class *Stipo giganteae-Agrostieta castellanae* by Mucina et al. (2016).

Our analyses further revealed among the serpentine grasslands a group floristically similar to the *Armerio-Potentillion*, which thus should be included in the same order. This alliance 4.2.2 corresponds to the '*Thymion jankae*' *nom. inval.* recognised in the synthetic study of the serpentine vegetation of the Balkans by Kuzmanović et al. (2016). These authors already suggested that it is clearly separated from the other serpentine vegetation types, thus likely warranting an alliance of its own. Based on its floristic composition, they indicated that this alliance would rather fit into the *Koelerio-Corynephoretea* than the *Festuco-Brometea*. Since we are now presenting the second broad-scale study to support the establishment of a new alliance, we formally describe it as *Minuartio montanae-Poion molinerii* (Appendix 1).

While both *Koelerio-Corynephoretea* orders were well supported by our analyses, based on the Balkan data alone there would have been no compelling argument to join them into one class. This was one of the reasons why our attempt first to classify classes and then orders failed. Based on a continent-wide analysis of a large data set (Dengler, 2003: table 30), their placement in this class appears to be well substantiated. There are two main reasons for the discrepancy between regional and European analyses: in our regional data set, only two of the various European orders of the class were present, that is, many of the syntaxa that in other regions form the floristic connection between the two orders were missing – either because the *Koelerio-Corynephoretea* actually have a lower diversity on the Balkans or because they were undersampled. Even more important might be that we lack enough plots with reliable recording of bryophytes and lichens, both of which are crucial for the syntaxonomic assignment of most *Koelerio-Corynephoretea* communities (see also Pedashenko et al., 2013; Kuzmanović et al., 2016). The undersampling of *Koelerio-Corynephoretea* plots in general and of bryophytes and lichens from these also calls for caution regarding the comprehensiveness of our syntaxonomic system.

The geological situation, distribution ranges of diagnostic species, as well as occasional reports, suggest that two additional orders of the class s.l., that is, including the *Sedo-Scleranthetea* (compare the system of Dengler, 2003), are likely present, the *Sedo-Scleranthetalia* (see Pedashenko et al., 2013) and *Alyso alyssoidis-Sedetalia* (see

Bergmeier et al., 2009). However, the available number of plots of these units was very low so that they did not appear as separate clusters in our analyses.

5.2 | The new classification approach in perspective

Recent developments in vegetation classification, mainly inspired by the *Vegetation of the Czech Republic* (see Chytrý, 2007), have elevated two essential aspects of transparent, data-driven vegetation classification (see De Cáceres et al., 2015) to new standards, and thus are followed by many researchers worldwide. First, *formal definitions of membership in syntaxa* in the form of an expert system (ES) that contains *intensive class definitions = consistent assignment rules* (see De Cáceres et al., 2015) make classification on the same or other data sets reproducible. While Chytrý (2007) used a modified variant of the Cocktail method (Bruehlheide, 1995, 1997), other implementations of intensive class definitions have meanwhile been developed in JUICE (Tichý, 2002) and were applied in recent works (e.g. Landucci et al., 2015; Schaminée et al., 2016; Chytrý et al., 2020). Second, *numerical-(statistical) fidelity measures* are now widely applied to decide on the diagnostic value of species more objectively than was possible in the past. Among these measures, the phi coefficient (Chytrý et al., 2002; Tichý & Chytrý, 2006; Chytrý, 2007; Willner et al., 2017) is most widely used and also here. However, there are also other options such as the total cover ratio (TCR; Willner, 2011; Willner et al., 2017) or the constancy ratio (Dengler, 2003; Dengler et al., 2005; Willner et al., 2019). While both procedural elements increased the reproducibility and transparency of vegetation classification and, thus, contributed to a renewed strong interest in this discipline, they left five other aspects unresolved, which we addressed by proposing the iterative cluster optimisation for hierarchical expert systems (ICO-HES):

1. Most importantly, the species of the intensive class definitions (used to create these units) and the diagnostic species (calculated based on the created units) are not identical in most of the published ES's. Although both groups of species are shown in many publications, they have not been directly linked so far. With ICO, we could *derive both diagnostic species and the definition of the units in the ES from the same unified workflow*, which in our examples converged to a quasi-stable solution after a few rounds. This procedure is a formal implementation of methods conducted in a similar way, but manually, by Luther-Mosebach et al. (2012), and in a simplified version with only one iteration by García-Mijangos et al. (2021). Another method that also iteratively optimises species groups in an ES, called GRIMP (Tichý et al., 2019), uses an alternative approach. In GRIMP, the best classification results are achieved if only a reduced subset of the best discriminating species is used in the ES (for a detailed comparison of both approaches, see Appendix S30).

2. The large majority of ES's so far were constructed to classify vegetation at only one syntaxonomic level. For example, Chytrý (2007) used Cocktail definitions to define the associations, while the placement of the associations into higher syntaxa was done outside the ES. By contrast, the fundamental idea of the phytosociological classification and the core of its high utility is its hierarchical nature (Dengler et al., 2008; Theurillat et al., 2021). Only recently hierarchical expert systems have been developed that implement this idea. Chytrý et al. (2020) created a system for habitat types of Europe with three levels, but here the set of criteria at different levels varies. Here we follow the idea of a *hierarchical expert system (HES) with identical criteria across the hierarchical levels* as recently suggested by García-Mijangos et al. (2021) for the grasslands of Navarre, Spain, and by Kaçki et al. (2021) for the mesic and wet grasslands of Poland.
3. Most recent studies using the ES approach relied largely on 'mimicking' established syntaxa from the literature (e.g. Chytrý, 2007; Schaminée et al., 2016; Chytrý et al., 2020). In contrast, our approach *can be implemented both in an unsupervised and in a semisupervised manner* (see Figure 2); thus, it can serve both for de novo classifications in hitherto completely unstudied systems and for expanding/improving existing classification systems.
4. So far, the phi coefficient was mostly used for the determination of diagnostic species by setting a certain threshold for phi, e.g. 0.25, and considering the species in all those units diagnostic in which the phi-values exceeded this value (e.g. Chytrý, 2007). This approach is based on a comparison of the target vegetation type with all other plots in the study. In consequence, a species would be considered as diagnostic in a syntaxon where it has $\phi=0.25$, but not in a similar syntaxon with $\phi=0.24$, even though this difference in phi normally does not reflect a statistically significant difference in the frequency of occurrence between those two units. Therefore, Bergmeier et al. (1990), Dengler (2003), Tsiripidis et al. (2009), De Cáceres et al. (2010) and Luther-Mosebach et al. (2012), among others, proposed methodological frameworks that do not only consider the absolute value of a measure of fidelity, but also its difference to the next similar syntaxon or between different combinations of vegetation groups in multiple comparisons. Based on these ideas, we implemented the *usage of phi-values meeting the double condition of a minimum absolute value and a minimum difference* to the syntaxon in which the species reaches its next higher frequency.
5. Cocktail-based ES's typically leave many plots unclassified, while some others are assigned to more than one unit. Chytrý (2007), for example, reports that 50%–70% of all plots remained unclassified by the Cocktail-based ES for the associations of the Czech Republic. Likewise, Kaçki et al. (2021) in their hierarchical Cocktail-based ES for the *Molinio-Arrhenatheretea* in Poland had 64% unassigned plots at the association level, 43% at the alliance level and 15% at the order level. The non-classification of such a large proportion of plots is partly a logical consequence of the fact that the number of transitional or untypical plots naturally increases when the vegetation continuum is divided into many finely

divided types such as associations. Partly, the reasons are technical, e.g. that the Cocktail method uses absolute numbers of occurring species, thus it has problems with species-poor subtypes as well as plots of smaller size than the average. As previously proposed for high-rank classifications (Michl et al., 2010; Chytrý et al., 2020; García-Mijangos et al., 2021), we applied a *procedure which, at each syntaxonomic level, assigns a plot to the vegetation type that fits best among all vegetation types within the next higher rank* (i.e., has the highest sum of square-root-transformed cover values of its diagnostic species). This led to no double-classified plots and only 5.1% plots of the initial data set remaining unassigned to one of the 12 alliances. The rates were even higher at the order and class level, reflecting that for more coarsely divided high-rank units the number of unequivocally classified plots is generally higher. Checking the classified plots revealed that their assignment was nearly always plausible, while checking the few unclassified plots indicated that often they likely did not have a complete species list—as their mean species richness was only about half of that of the classified plots.

As our approach is new, we documented the individual steps and settings as transparently as possible to allow other researchers to transfer them to their study systems, test and optimise them further. However, as in any classification, we are aware that many settings and decisions remain subjective, particularly in semisupervised classifications. For example, after trying several different thresholds of phi-values and phi-value differences, we found for our data set that 0.20 and 0.15, respectively, worked particularly well in the sense that they produced ecologically and chorologically meaningful units. In addition, our resulting classification system is largely comparable to previous systems, while modifying them in a limited number of cases. Our threshold of 0.20 corresponds well with previous studies that typically lowered thresholds with increasing ecological and chorological range of the investigations. For example, for the associations within a single country, Chytrý et al. (2016) proposed a threshold of 0.25, while Chytrý et al. (2020) used 0.15 when characterising the habitat types across Europe.

6 | CONCLUSIONS AND OUTLOOK

The classification approach presented here is the first to unite the determination of diagnostic species and of species groups used in an electronic ES in an iterative optimisation procedure, including the option to be employed in a hierarchical manner. With the documented settings, the approach turned out to deliver well-differentiated, ecologically and chorologically meaningful units. This approach is highly versatile, as it can work with any initial partitioning of the overall set of plot data, including the raw division resulting from a TWINSpan or other cluster analysis, the expert-interpreted/refined outcomes of such an analysis, selected typical plots for the units or plots defined by any other type of ES (such as Cocktail definitions). Thus, the approach is useful both when only the classification of a certain

syntaxonomic group from a certain geographic region should be improved within an existing classification system and when a new classification system in a hitherto unstudied region is to be developed.

Our study makes a major contribution towards the harmonisation of grassland classification in Europe, an important but challenging task (Dengler et al., 2013; Janišová et al., 2016). We thus advance some relatively comprehensive recent studies from the region (Ačić et al., 2015; Kuzmanović et al., 2016; Marcenò et al., 2018) based on a much larger data set and complement the broad-scale classification of the Pannonian-Pontic *Festuco-Brometea* communities by Willner et al. (2017, 2019) for the directly adjacent region to the south. Our results would allow further refinement of the new EUNIS grassland classifications, which are intended to largely match phytosociological orders (Janssen et al., 2016; Schaminée et al., 2016; Chytrý et al., 2020). While our classification results remove many inconsistencies among the classifications used in different Balkan countries and allow a much better integration of the studied dry grasslands into the European syntaxonomic classification scheme (Mucina et al., 2016; and updates by the European Vegetation Classification Committee [EVCC], see <http://euroveg.org/evc-committee>), they remain inconclusive in other regards. Thus, we call for extensions of this study with the same method to larger geographic areas, which would be much facilitated by the good spatial coverage of data meanwhile available in EVA (Chytrý et al., 2016). Moreover, our study, while being the most comprehensive for the region to date, highlights some important data gaps and limitations in data quality (e.g. recording of bryophytes and lichens, treatment of critical taxa) that should be addressed in the future. Finally, this article deals with the class, order and alliance levels, while initial trials (not included here) indicate that the approach is also able to divide alliances into well-defined associations (see also García-Mijangos et al., 2021).

AUTHOR CONTRIBUTIONS

Jürgen Dengler and Kiril Vassilev jointly conceived of the idea for this paper while Kiril Vassilev led the collection and digitisation of the underlying data. The novel classification approach (ICO-HES) is based on ideas of Jürgen Dengler and was refined and implemented jointly by him and Kiril Vassilev, while Lubomír Tichý helped with a partial implementation in JUICE. The paper was planned and mainly written by Kiril Vassilev and Jürgen Dengler, while Hristo Pedashenko prepared the maps and Beloslava Genova the boxplots. All other authors contributed data, checked/revised and approved the manuscript.

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DATA AVAILABILITY STATEMENT

The vegetation-plot data used in this study stem from the multicontributor Balkan Dry Grassland Vegetation Database (BDGD; <http://www.givd.info/ID/EU-00-013>). A TURBOVEG version of BDGD from the day of data extraction (prior to filtering and with the original taxon names) and a JUICE file (after filtering and with the harmonised taxon names) are stored in an internal repository and can be requested for re-analyses from the first author according to the rules of the BDGD Bylaws.

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- Appendix S9.** Expert system classes (*.hea).
- Appendix S10.** Expert system classes (*.txt).
- Appendix S11.** Expert system orders (*.hea).
- Appendix S12.** Expert system orders (*.txt).
- Appendix S13.** Expert system alliances of the *Brachypodietalia pinnati* (*.hea).
- Appendix S14.** Expert system alliances of the *Brachypodietalia pinnati* (*.txt).
- Appendix S15.** Expert system alliances of the *Trifolio arvensis-Festucetalia ovinae* (*.hea).
- Appendix S16.** Expert system alliances of the *Trifolio arvensis-Festucetalia ovinae* (*.txt).
- Appendix S17.** Expert system alliances of the *Koelerietalia splendidis* (*.hea).
- Appendix S18.** Expert system alliances of the *Koelerietalia splendidis* (*.txt).
- Appendix S19.** Nomenclatural types of dry-grassland syntaxa described from the study region and close surroundings (*.pdf).
- Appendix S20.** Confusion matrix of the final phytosociological alliances vs the in initial TWINSpan clusters (*.pdf).
- Appendix S21.** Complete synoptic table (*.pdf).
- Appendix S22.** Complete synoptic tables (hierarchical and non-hierarchical) (*.xlsx).
- Appendix S23.** Planned nomenclatural application to the Committee for Change and Conservation of Names (CCCN) (*.pdf).
- Appendix S24.** Planned applications to the European Vegetation Classification Committee (EVCC) of changes of syntaxon names (*.pdf).
- Appendix S25.** Planned applications to the European Vegetation Classification Committee (EVCC) of changes of the syntaxomic hierarchy (*.pdf).
- Appendix S26.** Demonstration of the convergence of our iterative approach exemplified by the expert system for orders (*.pdf).
- Appendix S27.** Diagnostic, constant and dominant species of the 12 distinguished alliances (*.pdf).
- Appendix S28.** Photo guide of the distinguished alliances (*.pdf).
- Appendix S29.** Similarity analyses of syntaxa from the study region with those in surrounding regions (*.pdf).
- Appendix S30.** Comparison of iterative cluster optimisation for hierarchical expert systems (ICO-HES) with GRIMP (*.pdf).

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

- Appendix S1.** List of original data sources used (*.xlsx).
- Appendix S2.** Distribution of plot sizes in the original data set per country (*.pdf).
- Appendix S3.** Taxonomic documentation of additional species and aggregates in comparison to the checklists used in general (*.pdf).
- Appendix S4.** European Expert System of classes used in this paper in comparison to Mucina et al. (2016) (*.xlsx).
- Appendix S5.** Changes of the class assignment between the expert system of Mucina et al. (2016) and the initial class assignment of this paper (*.pdf).
- Appendix S6.** Classification of the whole dry-grassland data set into 32 clusters and their initial syntaxonomic interpretation (*.pdf).
- Appendix S7.** Interpretation of the initial 32 clusters and their successive translation into an electronic expert system for the higher syntaxa (*.pdf).
- Appendix S8.** Instructions how to use the hierarchical expert system for the Balkan dry grasslands in JUICE (*.pdf).

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APPENDIX 1: FORMAL DESCRIPTION OF A NEW SYNTAXON

***Minuartio montanae-poion molinerii* all. nov. hoc loco.**

Type: *Poa molinerii*-*Plantagnetum carinatae* Pavlović 1951 (*holotypus hoc loco*).

Diagnostic species (in decreasing order of specificity; see Appendix S22): *Poa molinerii*, *Minuartia montana*, *Pontechium maculatum*, *Potentilla heptaphylla*, *Erysimum carniolicum*, *Koeleria splendens* aggr., *Dorycnium pentaphyllum*, *Noccaea praecox*, *Armeria maritima*, *Ornithogalum collinum*, *Thymus praecox*, *Scabiosa columbaria* aggr., *Poa alpina*, *Bromopsis pannonica*, *Euphorbia serpentini*, *Oenanthe silaifolia*, *Rorippa thracica*.

Note 1: The approximate concept of this alliance was already proposed by Kojić et al. (1992) under the invalid name '*Thymion jankae*' and later confirmed but not validated by Kuzmanović et al. (2016).

Note 2: The type association was lectotypified by Ačić et al. (2014).

APPENDIX 2: ALTERATIONS OF SYNTAXON NAMES

***Stipo-Brachypodietea distachyi* S. Brullo in S. Brullo et al. 2001 nom. mut. nov.**

(≡) *Stipo-Trachynietea distachyae* S. Brullo in S. Brullo et al. 2001.

Original diagnosis: Brullo et al. (2001).

Taxonomic sources: Tison and de Foucault (2014), Euro+Med (2019).

***Tuberarietea guttatae* Rivas Goday et Rivas-Martinez 1963 nom. mut. nov.**

(≡) *Helianthemetea guttati* Rivas Goday et Rivas-Martinez 1963.

Original diagnosis: Rivas Goday and Rivas-Martinez (1963).

Taxonomic sources: Pignatti et al. (2017–2019), Euro+Med (2019).

***Tuberarietalia guttatae* Br.-Bl. in Br.-Bl. et al. 1940 nom. mut. nov.**

(≡) *Helianthemetalia guttati* Br.-Bl. in Br.-Bl. et al. 1940.

Original diagnosis: Braun-Blanquet et al. (1940).

Taxonomic sources: Pignatti et al. (2017–2019), Euro+Med (2019).

***Chrysopogono grylli-Danthonion alpinae* Kojić 1959 nom. mut. nov.**

(≡) *Chrysopogono-Danthonion calycinae* Kojić 1959.

Original diagnosis: Kojić (1959).

Taxonomic sources: Pignatti et al. (2017–2019), Euro+Med (2019).

***Centaureo kosaninii-Bromopsis fibrosae* Blečić et al. 1969 nom. mut. nov.**

(≡) *Centaureo-Bromion fibrosi* Blečić et al. 1969.

Original diagnosis: Blečić et al. (1969).

Taxonomic sources: Fedorov (1974), Euro+Med (2019), Stupar et al. (2021).

***Clinopodio alpini-Thymion striati* Micevski 1971 nom. mut. nov.**

(≡) *Saturejo-Thymion* Micevski 1971.

Original diagnosis: Micevski (1971b).

Taxonomic sources: Fischer et al. (2008), Euro+Med (2019).

APPENDIX 3: TYPIFICATIONS OF SYNTAXA

***Pimpinello lithophilae-Thymion zygioidis* Dihoru & Donița 1970.**

Original form of the name: *Pimpinello-Thymion zygioidi*.

Original diagnosis: Dihoru and Donița (1970).

Type: *Agropyro brandzae-Thymetum zygioidis* Dihoru & Donița, 1970 (*lectotypus hoc loco*).

Note: The type association was neotypified by Dihoru (1999).

***Scabioso-Trifolion dalmatici* Horvatić et N. Randelović in N. Randelović 1977.**

Original diagnosis: Randelović (1977).

Type: *Hordeo-Xeranthemetum annui* Randelović 1977 (*lectotypus hoc loco*).

Note: The type association was lectotypified by Ačić et al. (2014).

***Brachypodio-Onobrychidetum pindicolae* Micevski 1978.**

Original form of the name: *Brachypodio-Onobrychietum pindicolae*.

Original diagnosis: Micevski (1971b).

Type: Micevski (1971b: table 3, relevé 1) (*lectotypus hoc loco*).

***Genisto carinalis-Agrostietum byzantinae* Micevski 1978.**

Original form of the name: *Genisto-Agrostidetum byzantinae*.

Original diagnosis: Micevski (1978).

Type: Micevski (1978: table 3, relevé 11) (*lectotypus hoc loco*).