Grasslands of Navarre (Spain), focusing on the *Festuco-Brometea*: classification, hierarchical expert system and characterisation

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Abstract

Aims: To clarify the syntaxonomic position of the grasslands in Navarre, with special focus on the dry grasslands, and to characterise the resulting syntaxonomic units in terms of diagnostic species and ecological conditions. **Study area:** Navarre (northern Spain). **Methods:** We sampled 119 plots of 10 m² following the standardised EDGG methodology and analysed them together with 839 plots of similar size recorded in the 1990. For the classification, we used the modified TWINSPAN algorithm, complemented by the determination of diagnostic species with phi coefficients of association, which led to the creation of an expert system. We conducted these steps in a hierarchical manner for each syntaxonomic rank. We visualised the position of the syntaxa along environmental gradients by means of NMDS. Species richness, and structural and ecological characteristics of the syntaxa were compared by ANOVAs. **Results:** We could clearly identify five phytosociological classes: *Lygeo-Stipetea, Festuco-Brometea, Molinio-Arrhenatheretea, Nardetea strictae,* and *Elyno-Seslerietea*. Within the *Festuco-Brometea* a xeric and a meso-xeric order could be distinguished, with two alliances each, and eight associations in total: *Thymelaeo-Aphyllanthetum, Jurineo-Festucetum, Helianthemo-Koelerietum, Prunello-Plantaginetum, Carduncello-Brachypodietum, Helictotricho-Seslerietum, Calamintho-Seselietum* and *Carici-Teucrietum*. **Conclusions:** The combination of numerical methods allowed a consistent and more objective classification of grassland types in Navarre than previous approaches. At the association level, we could largely reproduce the units previously described with traditional phytosociological methods. By contrast, at higher syntaxonomic level, our analyses suggest significant modifications. Most importantly, a major part of the units traditionally included in the *Festuco-Ononidetea* seem to fall within the *Festuco-Brometea*. We could show that bryophytes and lichens are core elements of these grasslands and particularly the Mediterranean ones of *Lygeo-Stipetea*, both in terms of biodiversity and

of diagnostic species. We conclude that the combination of our different numerical methods is promising for deriving more objective and reproducible delimitations of syntaxa in a hierarchical manner.

Keywords

Introduction

Grasslands represent one of the most extensive and diverse formations of the world, yet undervalued and under-researched. Grasslands are spontaneously occurring herbaceous vegetation types that are mostly dominated by grasses (*Poaceae*) or other graminoids (*Cyperaceae, Juncaceae*) and have a relatively high herb-layer cover (usually > 10%), while woody species (dwarf shrubs, shrubs and trees), if present at all, have a significantly lower cover than the herbs (Dengler et al. 2020a). Extending in all continents except Antarctica, grasslands host thousands of habitat specialist species, support agricultural production, people's livelihoods based on traditional and indigenous lifestyles, and several other ecosystem services such as pollination for crops and water regulation (Bengtsson et al. 2019). Palaearctic grasslands represent the richest habitats for vascular plants at small spatial scales (Dengler et al. 2020a). Temperate grasslands are, however, among the most threatened biomes of the world with the highest proportion of habitat conversion but lowest protection (Hoekstra et al. 2005).

Since the second half of the 20th century, European grasslands have experienced two extremes of the land-use gradient, and both resulted in the loss of grassland biodiversity (Török and Dengler 2018), which is specifically important in Western Europe, were grasslands are mostly secondary, originating from human land use (Boch et al. 2020): (i) intensification of land use or conversion to croplands in productive areas, and (ii) abandonment of marginal lands resulted in the regeneration of forest and shrublands, both processes leading to the loss of grassland-specific biodiversity (Dengler and Tischew 2018). It is necessary to understand biodiversity patterns of grasslands and how they relate to land use to be able to design conservation and management actions. This understanding requires the harmonisation and standardisation of grassland classification that leads to a consistent syntax-

onomy at the European level and therefore, then will increase the usefulness of vegetation typologies for conservation and management (Willner et al. 2017).

During the last decades, a great effort on grassland classification has been made, based on large vegetation-plot databases and numerical analysis in several countries or regions across Europe to delimit and define the different syntaxonomic units. Several studies have been developed at a regional, up to continental scale on dry-grasslands (Illyés et al. 2007; Vassilev et al. 2012; Aćić et al. 2015) or mesic and wet grasslands (Kuzemko 2016; Rodríguez-Rojo et al. 2017; Škvorc et al. 2020). The broadest studies regarding syntaxonomic scope and geographic extent are focused on dry and semi-dry grasslands (Willner et al. 2017, 2019). As a result, great advances to define the classes *Festuco-Brometea, Molinio-Arrhenatheretea, Nardetea strictae* and *Koelerio-Corynephoretea* in temperate Europe have been made. However, grasslands of Southern Europe are still not well-known and the distinction of the Mediterranean grasslands from those of temperate Europe is not clear, especially along the submediterranean areas that, although broadly classified as temperate, still exhibit the "Mediterranean" sharp drop in summer precipitation levels (Apostolova et al. 2014; Aćić et al. 2015).

Phytosociological studies in the Iberian Peninsula have been broadly developed in the last century and were synthesized in the syntaxonomic checklist of Spain (Rivas-Martínez 2011). More recently, some reviews based on large vegetation databases aimed to obtain a consistent grassland classification (Rodríguez-Rojo and Fernández-González 2014; Rodríguez-Rojo et al. 2014; García-Madrid et al. 2016; Gavilán et al. 2017). Nevertheless, there is a lack of studies on the typical Mediterranean grassland and low scrub classes *Festuco hystricis-Ononidetea striatae, Ononido-Rosmarinetea* and *Lygeo sparti-Stipetea tenacissimae* (but see Marcenò et al. 2019). Moreover, in the submediterranean areas, these Mediterranean grasslands are in touch (across elevational or edaphic

gradients) with temperate grasslands placed in the class *Festuco-Brometea*, but their boundaries are not clearly defined (Cancellieri et al. 2020). Studies of such transitional areas are necessary to discriminate between different grassland types and define the diagnostic species that differentiate these classes.

Navarre region, located in northern Iberian Peninsula, is a bioclimatically diverse region where Alpine, Atlantic and Mediterranean biogeographical areas converge. The long history of grazing and management throughout the area has resulted in the broad spread of grasslands. The region has an important elevational and precipitation gradient that allows the coexistence of dry and mesic grasslands as well as alpine and Mediterranean semi-arid communities (Berastegi 2013). This makes this region very suitable for studying the diversity of grassland communities that are driven by ecological and management gradients. Navarre is also an interesting area for the challenge of drawing the boundaries between the temperate and Mediterranean grasslands and establishing their valid classification. Many phytosociological studies have been carried out in Navarran grasslands (Darquistade et al. 2004; Berastegi et al. 2005; Berastegi et al. 2010; Berastegi 2013). Nevertheless, only a few of these studies have applied numerical methods (Peralta and Olano 2001), and none of them included bryophytes and lichens, although these taxonomic groups may become an important component of several grassland types (Biurrun et al. 2021).

According to Berastegi (2013), 69 grassland associations or communities can be recognised in Navarre, grouped in 32 alliances and 11 phytosociological classes. In the high-elevation areas of Pyrenees, communities of *Carici rupestris-Kobresietea bellardii, Juncetea trifidi,* and *Elyno-Seslerietea* coexist; in the temperate zone, grasslands of *Nardetea strictae, Sedo-Scleranthetea, Molinio-Arrhenetheretea* and *Festuco-Brometea,* and in Mediterranean areas communities of *Festuco-Ononidetea, Lygeo-Stipetea, Poetea bulbosae* and *Stipo-Trachynietea* (Berastegi 2013). Although some of these classes are well defined floristically and biogeographically, those occurring in submediterranean areas need clarification as many species of different floristic origin coexist in the same area. In these cases, the occurrence of temperate or Mediterranean grasslands is driven by edaphic and microclimatic conditions. There are also some interpretation issues, such as the inclusion of some Mediterranean communities in *Festuco-Ononidetea* or *Ononido-Rosmarinetea* (Berastegi et al. 2005; Berastegi 2013). All this led to the organisation of the 7th Field Workshop (Biurrun et al. 2014) to sample by means of biodiversity plots (Dengler et al. 2016a) all types of grasslands along latitudinal and elevational gradients. The expedition ran from subalpine areas in Pyrenees to semi-arid Mediterranean ones where information on bryophytes and lichens as well as vascular plants was recorded.

The high grassland diversity in Navarre reflects the richness of grassland habitats of interest for European Community (European Commission 2013). Regarding the habitat types included in the Annex I of the Habitat Directive, nine of those belonging to natural and semi-natural grassland formations are present in Navarre (Peralta et al. 2018). Phytosociological classifications of formally defined syntaxa were also used to interpret the types in the Habitats Directive, so determining diagnostic species for different types of grassland is necessary to interpret the habitats and to assess their conservation status (Tsiripidis et al. 2018). However, the definition of these habitats is sometimes ambiguous and there are still some inconsistent interpretations between countries and regions, which impede effective conservation of grasslands habitats (Evans 2013). Rodriguez-Rojo et al. (2020) aimed to develop an expert system for semi-natural grassland habitat identification through the analysis of their characteristic species, but Mediterranean grasslands were not included in the analysis. The delimitation and definition of diagnostic species of the Mediterranean grassland classes would help to properly interpret the habitat types that would lead to their adequate management and protection.

The large amount of data available related to grassland in the region of Navarre and its strategic geographical position where different climatic conditions converge provide a unique opportunity to clarify grassland syntaxonomy, especially those from submediterranean areas. More specifically, we aim to 1) Identify the main grassland types in Navarre using numerical and reproducible methods, 2) Compare our results with existing traditional classifications at the level of alliance or association 3) Define the diagnostic species of syntaxa including bryophytes and lichens. 4) Characterise and differentiate associations with regard to topographic, edaphic and climatic variables.

Study area

Navarre is a territory of 10,391 km² located in the north-central part of the Iberian Peninsula. There is a wide elevational range in the region, from 25 m a.s.l. in Endarlatsa, 15 km from the Cantabrian Sea in the north, to 2,466 m a.s.l. in the Mesa de los Tres Reyes in the western Pyrenees. The bioclimate is temperate in the northern part of the region, and Mediterranean in the south, with large submediterranean areas in the central part (Loidi and Báscones 2006; Peralta et al. 2018). As regards the thermic and humidity types proposed in the bioclimatic classification of Rivas-Martínez (Rivas-Martínez 1996), mesotemperate (colline), supratemperate (montane), orotemperate (subalpine) and cryorotemperate (alpine) thermotypes can be distinguished in the temperate zone, while in the Mediterranean areas only the mesomediterranean and the supramediterranean occur. There is a high ombrotype diversity, from the semiarid in the Ebro valley to the ultrahyperhumid in the northern mountains (Peralta et al. 2018). The temperate-climate area is included in the Atlantic and Alpine regions. The western part has

a stronger Atlantic influence (Atlantic region) while the eastern area is more influenced by the Pyrenees (Alpine region). The Mediterrranean-climate area is included in the Mediterranean region.

Several types of deciduous forests prevail in the temperate zone, where secondary grasslands, mainly mesic and meso-xeric grasslands, are an important component of the landscape. Sclerophyllous woodlands dominate in the Mediterranean areas of southern Navarre, with Mediterranean grasslands and garrigues as secondary vegetation. In the Pyrenees, alpine grasslands and scrubs occur above 1,700 m a.s.l., in the subalpine belt mostly as secondary vegetation replacing *Pinus uncinata* woodlands, and as potential natural vegetation in the alpine belt, above ca. 2,100 m a.s.l. (Loidi and Báscones 2006).

Geological diversity also has a great influence on the vegetation. Shales, quartzites or granites from the Palaeozoic are common in the northern area of Navarre, mostly in the Atlantic region. Red sandstones and conglomerates from the Triassic surround these Palaeozoic rocks. Limestones, marls and dolomites from the Jurassic and Cretaceous period, and also limestones, marls, flysch substrates, but also calcarenites from the continental Tertiary are dominant in all of the central area of Navarre. From the continental Tertiary, sandstones, clays, slimes, but also limestones and gypsum are dominant in the south of Navarre, mostly in the Mediterranean region (Del Valle Lersundi et al. 1997).

Methods

Vegetation data

We took 119 10-m² plots sampled following the standard EDGG methodology (Dengler et al. 2016a) during the EDGG Field Workshop in Navarre, between 16th and 23rd of June 2014 (Biurrun et al. 2014). The sampling focused on dry and semi-dry grasslands but covered the full climatic/elevation gradient in the region. All vascular plants as well and terricolous bryophytes and lichens, and their percentage cover were recorded. Additionally, an extensive set of structural and site variables were recorded (for all available variables and the underlying methodology, see Suppl. material 1).

Furthermore, we included those 839 vegetation plots from Berastegi (2013), recorded between 1996 and 1999, that had a plot size between 5 and 25 m². We excluded smaller and larger plots because otherwise serious distortion of species constancies and fidelities would be expected (Dengler et al. 2009). In these plots, only vascular plants were recorded, with a 7-step variant of the Braun-Blanquet scale (Braun-Blanquet 1932). Apart from coordinates and elevation, no other structural or site variables are available for these data.

Although these plots from the additional dataset were evenly distributed across the region and all grassland types, we wish to highlight that four of the 11 classes represented in Berastegi (2013) were only documented by fewer than 10 relevés. Two of them normally occur as small patches in mosaics with grasslands of other classes (*Stipo-Trachynietea* and *Poetea bulbosae)* and the other two are very rare in Navarre (*Carici-Kobresietea* and *Caricetea curvulae)*. Another important aspect of this dataset is that the classes *Festuco-Ononidetea* and *Ononido-Rosmarinetea* have been only partially included. The former one encompasses oro- and supramediterranean grasslands and shrublands (Mucina et al. 2016), but Berastegi (2013) only considered the dry grasslands of the associations *Carici-Teucrietum pyrenaici, Helianthemo-Koelerietum vallesianae* and *Helictotricho-Seslerietum hispanicae* from the order *Ononidetalia striatae* (and thus excluded dwarf-shrub communities), and those belonging to the order *Festuco-Poetalia*. The *Ononido-Rosmarinetea*, and specifically the order *Rosmarinetalia*, are defined as Mediterranean scrub (tomillar, espleguer, romeral, garrigue) on base-rich substrates (Mucina et al. 2016). In this study we only considered the association *Thymelaeo-Aphyllanthetum monspeliensis,* described from the central part of Navarre (Braun-Blanquet 1966) and characterised by dwarf chamaephytes of the genera *Thymus*, *Helianthemum, Fumana* and *Teucrium* among others. Berastegi (2013) only sampled stands of the subassociation *brachypodietosum retusi,* dominated by hard-leaved grasses (*Brachypodium retusum, Helictochloa bromoides*) and other hemicryptophytes such as *Bromopsis erecta* subsp. *erecta, Carex humilis, Helictochloa pratensis* subsp. *iberica, Sanguisorba minor* aggr. and *Carex flacca* subsp. *flacca*.

The combination of both datasets resulted in a total of 958 vegetation plots. The data from EDGG expedition are stored in and available from the GrassPlot database (Dengler et al. 2018a; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot) as dataset ES_A. The data from Berastegi (2013) are stored in the Vegetation-Plot Database of the University of the Basque Country (BIOVEG) (Biurrun et al. 2012), which is available in the European Vegetation Archive (Chytrý et al. 2016) and the Global Vegetation Database sPlot (Bruelheide et al. 2019) as dataset EU-00-011. All plots are provided in Suppl. materials 1 (header data) and 2 (composition data).

Soil analyses

Soil samples were collected in each EDGG plot. Samples were taken with a hand shovel from the uppermost 5–10 cm at five random points within the plot, merged in a mixed sample and air-dried. The coarse fragment of the samples was determined by dry screening (Ø > 2 mm) and soil texture was determined by the Bouyoucos hydrometer method (Gee and Bauder 1986). The acidity and electrical conductivity (EC) were determined in air-dried soil samples dissolved in pure water using pH meter and EC meter (Thomas 1996). Lime content was determined by a Scheibler calcimeter. Soil organic matter content was determined by Walkley-Black wet combustion.

Climatic data

We retrieved climatic data from CHELSA dataset version 1.2 (Karger et al. 2017) at 30 arc sec resolution. As climatic parameters, we selected mean annual temperature, annual precipitation and Mediterranity Index: Med = Eva / Prec, where Eva is mean potential evapotranspiration during summer months, and Prec is sum of precipitation during the summer months (Rivas-Martínez 1996).

Data preparation for classification analyses

Before numerical analysis, we unified species taxonomy and nomenclature. Vascular plants were named according to Euro+Med PlantBase (Euro+Med 2006–2021), bryophytes according to Hodges et al. (2020) and lichens according to The British Lichen Society (2021), with the exception of those taxa not included there: *Endocarpon loscosii*, *Heppia lutosa*, *Psora saviczii* and *P. vallesiaca* follow Nimis and Martellos (2021), while *Buellia zoharyi*, *Fulgensia poeltii*, *Lichenochora clauzadei* and *Toninia massata* follow Llimona et al. (2001). We merged several groups of closely related species that cannot always be determined to species level into aggregates (aggr.), whose definitions are provided in Suppl. material 3. Species recognised only at the genus level were deleted, and subspecies that were not always recognised by the authors were combined into species. Bryophytes and lichens were removed for the initial unsupervised classification, but re-integrated later (see below) since they were only recorded in a subset of relevés.

Numerical classification and expert system development

For the initial unsupervised classifications, we used the modified version of TWINSPAN (Roleček et al. 2009) implemented in JUICE (Tichý 2002) with the three pseudospecies cut levels at 0%, 5% and 15%, and average Sørensen dissimilarity as a measure of cluster heterogeneity. Species with only one occurrence were excluded. TWINSPAN analysis resulted in ten groups as the best solution that corresponded very closely to the phytosociological classes of grasslands represented in the study area according to a previous study (Berastegi 2013).

In the case of very large datasets, classification is highly dependent on the selection of attributes (species) used. The more attributes used, the data become more scattered (Visa et al. 2011). In this context, the selection of diagnostic species that can be used in the classification of vegetation is one of the challenges to be addressed. Here we used confusion matrices to select relevés that matched both supervised and unsupervised classifications for subsequent selection of diagnostic species. These species were used for further classification (expert system) of the entire dataset, so that misclassified relevés were reorganised appropriately.

We created the confusion matrix comparing the original (expert-based) and new numerical (unsupervised) classifications (see Suppl. material 4). We selected those relevés that were consistently classified in both approaches as a sort of consensus core of the respective vegetation units. Based on these plots ($n = 639$), we determined the diagnostic species for the classes (see below). The list of diagnostic species was then translated into an expert system implemented in JUICE (Tichý 2002), with the principle that each plot is assigned to the class whose diagnostic species prevail, based on the sum of square root transformed cover values (as for example widely implemented in Chytrý et al. (2020)). This approach in its current implementation in JUICE leaves a few plots unassigned if they have exactly the same score of diagnostic species for two classes. After applying the so-developed expert system to the whole dataset, we then determined the diagnostic species of the resulting classes again.

In the case of the classes, we found that three of the traditional classes shared a significant number of frequent species and therefore, we decided to merge them and re-run the previous steps to achieve the final expert system and the final set of diagnostic species of classes. We continued then, with the same approach, with our main target class *Festuco-Brometea* to search for the most plausible division into orders. Criteria were based on how well the resulting units were floristically and ecologically characterised and how closely they matched the general syntaxonomic system of Europe. Next, we continued in each of the resulting orders to find an appropriate division into alliances and finally for each of the alliances we analysed the appropriate subdivision into associations separately. For each syntaxonomic level and cluster we therefore followed the procedure of: (1) running modified TWINSPAN, (2) identifying a reasonable number of syntaxa of the next lower level and (3) determining their diagnostic species. In the case of order and alliance we selected the relevés that matched both the expert and TWINSPAN classification, but for associations we used only the TWINSPAN results, (4) translating these into an expert system, (5) appling this expert system to the data including the type relevés of all associations included in *Festuco-Brometea* (details provided in Suppl. material 5) and (6) re-determining the diagnostic species based on the group assignment resulting from the expert system. Accordingly, we can then present a hierarchical expert system in JUICE syntax that allows the standardised reproduction of our classification and its application on new relevés (Suppl. material 6–12).

We followed the fourth edition of the International Code of Phytosociological Nomenclature (ICPN; Theurillat et al. 2021) for the nomenclature of plant communities.

We determined diagnostic species using the phi coefficient of association (Chytrý et al. 2002) standardised to equal plot number per cluster (Tichý and Chytrý 2006). We also determined the diagnostic species in a hierarchical fashion, corresponding to the hierarchical nature of syntaxonomy (Dengler et al. 2008; Theurillat et al. 2021) and to our hierarchical expert system. Since this approach

is not implemented in JUICE (Tichý 2002) thus far, we carried out all calculations in Microsoft Excel, which also allowed the production of formatted tables. We acknowledge that this approach has the potential shortcoming of not being able to filter for statistical significance with Fisher's exact test as is possible in JUICE. However, given the relatively large number of plots per unit and the relatively high thresholds for phi that we applied, the number of non-significant diagnostic species should be negligible. We considered species as diagnostic when phi ≥ 0.25 and as highly diagnostic when phi ≥ 0.5. While phi-values refer to the concentration of a species in one syntaxon compared to the rest of the dataset as a whole, in fact the syntaxonomically relevant aspect is the comparison to the syntaxon of the same rank where the species reaches the next-higher constancy/fidelity (see Dengler 2003; Dengler et al. 2005, 2018b; Tsiripidis et al. 2009). Therefore, for species to be considered diagnostic, we also required that their phi-value was at least 0.25 higher than in the syntaxon of the same rank with the next-higher phi-value. If all syntaxa of a certain rank were ordered by decreasing phi-values of a certain species, the species was considered diagnostic for the first syntaxa prior to a decrease in phi-values ≥ 0.25. If no such decrease occurred or if the maximum phi-value was below 0.25, the species was not considered diagnostic anywhere. We applied these calculations for all four syntaxonomic levels and identified a species as diagnostic to the level where it reached its maximum phi-value, provided all aforementioned criteria were fulfilled. Last but not least, we also determined diagnostic species for the bryophytes and lichens, which had not been used in the set-up of the system, by adding their data again post-hoc. Importantly, here the constancy values were calculated based on the smaller sample of plots from the EDGG Field Workshop only, but otherwise in the same way.

NMDS ordination

To visualize the gradient of vascular plant species composition across the vegetation types, we used non-metric multidimensional scaling (NMDS; McCune and Grace 2002) calculated in the Canoco 5 software (ter Braak and Šmilauer 2012). Prior to the calculation, the Braun-Blanquet scale was transformed to mean percentage cover values. Bray-Curtis dissimilarity was calculated on the log-transformed cover of each vascular plant species in each plot. The sample configuration from non-metric multidimensional scaling (NMDS) was centred and rotated by principal component analysis. Elevation and three bioclimatic variables (mean annual temperature, annual precipitation and Mediterraneity Index) were used as supplementary variables. The whole data set (containing 958 samples) as well as the data subset of relevés included in the *Festuco-Brometea* (containing 339 samples) were analysed.

Analyses of differences between syntaxa

Differences among classes regarding structural, topographic, bioclimatic and soil variables, as well as regarding richness values, were analysed by means of analyses of variance (ANOVAs) in the R programming language (R Core Team 2021). The same was done with the *Festuco-Brometea* subset to compare associations and alliances. Tukey's post-hoc test was applied following a significant ANOVA ($p < 0.05$). We checked whether the assumptions of linear models (homoscedasticity and normality of residuals) were severely violated by visual inspection of the boxplots, and since this was not the case, we stuck to the linear model (ANOVA) (see Quinn and Keough 2002).

Results

Subdivision of all grasslands into classes

At the level of ten groups, the TWINSPAN analysis resulted in a division of the data where the classification into seven classes proposed by Berastegi (2013) can be recognised to a large extent (Figure 1). We then reduced the hierarchy of these groups into eight clusters. Clusters 1 and 2 were related to *Elyno-Seslerietea* and *Festuco-Ononidetea* classes, respectively. Cluster 3 grouped relevés from *Lygeo-Stipetea* and *Stipo-Trachynietea* classes. Cluster 4 was composed mostly of the relevés of the association *Elytrigio campestris-Brachypodietum phoenicoidis,* traditionally assigned to the order *Brachypodietalia phoenicoidis* in *Festuco-Brometea*. Clusters 5 and 6 were related to *Ononido-Rosmarinetea* and *Festuco-Brometea*, respectively. Groups 7, 8 and 9 corresponded to three orders of *Molinio-Arrhenatheretea* (*Holoschoenetalia, Molinietalia* and *Arrhenatheretalia*), so we grouped them in Cluster 7. Cluster 8 grouped relevés belonging to the classes *Nardetea strictae* and *Sedo-Scleranthetea*.

The synoptic table with the diagnostic species for each cluster of the modified TWINSPAN analysis is presented in Suppl. material 13 (cluster 4 was not considered as it was related only to one association). In this table, we can see that the relevés in clusters 2 and 5 related to the classes *Festuco-Ononidetea* and *Ononido-Rosmarinetea* presented many diagnostic species considered characteristic of *Festuco-Brometea* (*Bromopsis erecta* subsp. *erecta, Carex humilis, Carthamus mitissimus, Potentilla tabernaemontani*). Therefore, these two groups were joined to cluster 6, related to the *Festuco-Brometea,* for subsequent analyses. We finally recognised five groups corresponding to the following classes of grasslands in Navarre: LYG (*Lygeo-Stipetea*), FES (*Festuco-Brometea*), MOL (*Molinio-Arrhenatheretea*), NAR (*Nardetea strictae*) and SES (*Elyno-Seslerietea*).

The relationship between the previous expert-based classification (Berastegi 2013) and our classification of five classes based on the expert system analysis is displayed in
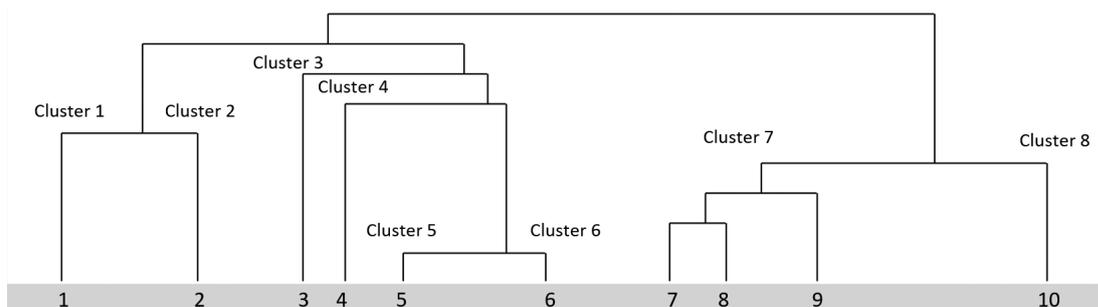
Figure 1. Dendogram of the modified TWINSPAN classification of the 958 grassland relevés from Navarre into ten groups gathered in eight clusters.

Table 1. Relationship between the original classification and the expert system classification. In each column the number of relevés and the proportion related to the total of relevés belonging to the original classification (in brackets) that match the expert system are shown.

Syntaxonomic classes (original classification)	Expert System classification						Nº rel. per class
	LYG (%)	FES (%)	MOL (%)	NAR (%)	SES (%)	Non-classified	
Lygeo–Stipetea	25 (96)	1 (4)					26
Stipo–Trachynietea	10 (100)						10
Ononido–Rosmarineta	5 (13)	33 (87)					38
Festuco–Brometea	8 (4)	131 (61)	34 (16)	40 (19)		2	215
Festuco–Ononidetea		158 (75)	1 (< 1)	2 (1)	48 (23)	1	210
Molinio–Arrhenatheretea		13 (6)	185 (86)	17 (8)		1	216
Nardetea strictae				149 (96)	5 (3)	1	155
Sedo–Scleranthetea				11 (85)	1 (8)	1	13
Elyno–Seslerietea		1 (2)		3 (5)	58 (93)	2	64
Carici–Kobresietea					2		2
Cariceta curvulae				1			1
Poetea bulbosae	6	2					8
Nº relevés per group	54	339	220	223	114	8	958

Table 1. The proportion of relevés matching in both classifications (in brackets) ranged between 60 and 100%. In FES the expert system gathered most of the relevés previously classified in *Festuco-Brometea*, *Festuco-Ononidetea* and *Ononido-Rosmarineta*. However, 35% of relevés previously classified in *Festuco-Brometea* were distributed among MOL and NAR. From the class *Festuco-Ononidetea* 23% relevés were classified in SES and 13% relevés from *Ononido-Rosmarineta* were included into LYG. Only eight relevés (0,8%) remained unclassified.

LYG – *Lygeo-Stipetea* (Figure 2D)

The expert system analysis included in this group LYG most relevés that were originally classified in the class *Lygeo-Stipetea*. Communities dominated by therophytes of *Stipo-Trachynietea* and those from *Poetea bulbosae* were also classified in this group, as they shared many annual species: *Bombycilaena erecta, Catapodium rigidum, Linum strictum, Trachynia distachya,* etc. LYG also includes some relevés from the subassociation *Thymelaeo-Aphyllanthetum brachypodietosum retusi* of the class *Ononido-Rosmarineta* and from the association *Elytrigio campestris-Brachypodietum phoenicoidis* of *Festuco-Brometea*.

These communities are characterised by the presence of hard-leaved grasses such as *Brachypodium retusum, Helictochloa bromoides, Lygeum spartum* and *Stipa parviflora* and dwarf chamaephytes as well as many therophytes (Table 2). They are distributed throughout the southern part of Navarre, with a typical Mediterranean climate, although they also occur in the lower elevations of the central area, always in the mesomediterranean thermotype (Figure 3).

FES – *Festuco-Brometea*

After applying the expert system most relevés of *Festuca-Brometea*, *Festuco-Ononidetea* and *Ononido-Rosmarineta* were classified in the FES group (Table 1). The diagnostic species for this group with highest fidelity index were *Bromopsis erecta* subsp. *erecta, Carthamus mitissimus, Carex humilis, Potentilla tabernaemontani, Coronilla minima, Festuca rectifolia* and *Seseli montanum* subsp. *montanum* (Table 2).

This group (FES) occupies the transition areas between the Pyrenees and Cantabrian mountains and the Mediterranean region (Figure 3). These communities grow at moderate elevations, mostly in the upper colline and montane belts, and with average precipitation and temperatures of 1,230 mm and 10 °C, respectively (Table 3).

Table 2. Abridged constancy table of the five grassland classes considered in this study. Values are percentage constancies, and species are ordered by decreasing phi-values in the respective syntaxon, respectively by decreasing overall constancy for non-diagnostic species. In the upper part vascular plants are given, in the lower part bryophytes and lichens, whose constancies and fidelities have been calculated based only on the plots of the EDGG Field Workshop. In the table, the 15 vascular plant taxa and the eight non-vascular plant taxa with the highest fidelity in a class are shown, plus all taxa that are diagnostic for multiple classes and all taxa with at least 10% overall constancy. Diagnostic species (phi ≥ 0.25) are highlighted in grey, highly diagnostic species (phi ≥ 0.5) in dark grey. The complete constancy table combined with the table of the underlying 958 vegetation plots is given in Suppl. material 2.

Class	All	LYG	FES	MOL	NAR	SES
# plots	958	54	339	220	223	114
# plots with bryophyte/lichen treatment	119	19	64	8	11	17
Class LYG (47 taxa)						
Linum strictum	3.9	52	2	1	.	.
Brachypodium retusum	8.4	52	14	1	.	.
Catapodium rigidum	4.3	43	5	1	.	.
Lygeum spartum	2.0	33	<1	.	.	.
Asterolinon linum-stellatum	2.2	33	1	<1	.	.
Artemisia herba-alba	1.8	31	.	.	.	.
Thymus vulgaris subsp. vulgaris	9.9	50	20	.	.	.
Polygala monspeliaca	2.4	33	1	.	.	.
Trachynia distachya	3.0	35	2	<1	.	1
Teucrium capitatum subsp. capitatum	4.3	35	6	.	.	.
Bombycilaena erecta	2.8	31	3	.	.	.
Euphorbia exigua	3.9	33	5	<1	.	.
Plantago lagopus subsp. lagopus	1.5	26	.	.	.	.
Plantago albicans	1.5	26	.	.	.	.
Atractylis humilis	1.8	24	1	.	.	.
[…]						
Class FES (21 taxa)						
Bromopsis erecta subsp. erecta	27.1	2	65	6	5	11
Carthamus mitissimus	19.4	7	51	1	3	2
Carex humilis	14.5	4	40	.	.	1
Potentilla tabernaemontani	19.5	6	48	1	4	10
Coronilla minima	14.2	7	38	<1	.	1
Festuca rectifolia	17.7	4	42	.	2	15
Seseli montanum subsp. montanum	14.1	2	33	1	6	4
Helictochloa pratensis subsp. iberica	20.9	2	46	<1	4	30
Geum sylvaticum	6.8	.	18	.	1	1
Scabiosa columbaria subsp. columbaria	11.1	.	25	4	3	5
Medicago lupulina	20.1	6	39	18	3	8
Onobrychis conferta subsp. hispanica	6.3	2	17	1	.	.
Sanguisorba minor aggr.	16.0	17	34	6	6	1
Teucrium chamaedrys	6.8	4	18	.	.	2
Trifolium montanum subsp. montanum	6.2	.	15	2	1	.
[…]						
Class MOL (33 taxa)						
Holcus lanatus	11.6	.	3	44	1	.
Ranunculus acris subsp. friesianus	7.8	.	1	32	<1	.
Agrostis stolonifera subsp. stolonifera	9.1	2	3	34	<1	.
Trifolium fragiferum	6.6	.	.	28	1	.
Ranunculus repens	6.5	.	.	26	2	.
Poa trivialis subsp. trivialis	8.9	.	6	30	.	.
Lolium perenne	11.1	2	4	35	7	.
Schedonorus arundinaceus subsp. arundinaceus	6.4	.	2	25	.	.
Juncus articulatus	4.9	.	.	21	<1	.
Juncus inflexus	4.3	.	.	19	.	.
Centaurea debeauxii	6.8	.	4	23	1	.
Anthoxanthum odoratum	10.5	.	4	30	9	2
Rumex acetosa subsp. acetosa	4.8	.	<1	19	.	3
Potentilla reptans	6.7	6	2	24	1	.
Veronica chamaedrys subsp. chamaedrys	5.0	.	<1	18	3	.
[…]						
Class NAR (17 taxa)						
Potentilla erecta	16.7	.	1	5	63	4
Galium saxatile	11.5	.	<1	<1	48	1
Agrostis capillaris	35.4	.	18	27	86	23
Festuca microphylla	40.2	.	22	19	94	48
Polygala serpyllifolia	8.6	.	2	<1	33	.
Nardus stricta	8.5	.	.	.	34	5
Danthonia decumbens	17.1	.	10	9	47	4

Class	All	LYG	FES	MOL	NAR	SES
# plots	958	54	339	220	223	114
# plots with bryophyte/lichen treatment	119	19	64	8	11	17
Agrostis curtisii	5.7	.	.	.	25	.
Jasione laevis subsp. *laevis*	5.8	.	.	.	25	1
Carex pilulifera subsp. *pilulifera*	5.5	.	.	<1	23	.
Calluna vulgaris	7.4	.	.	.	27	8
Veronica officinalis	5.0	.	.	<1	21	1
Helictochloa marginata subsp. *marginata*	6.7	.	3	.	24	2
Trifolium alpinum	3.7	.	.	.	16	.
Vaccinium myrtillus	2.7	.	.	.	11	1
[...]						
Class SES (46 taxa)						
Helictotrichon sedenense subsp. *sedenense*	5.6	.	.	.	<1	46
Carex sempervirens subsp. *sempervirens*	5.4	.	1	.	<1	43
Alchemilla plicatula aggr.	13.5	.	4	.	19	61
Festuca gautieri subsp. *scoparia*	4.7	.	<1	.	<1	38
Poa alpina	10.4	.	5	.	12	50
Androsace villosa subsp. *villosa*	4.4	.	1	.	.	32
Paronychia kapela subsp. *serpyllifolia*	4.6	.	1	.	2	32
Agrostis schleicheri	3.9	.	1	.	.	29
Carex ornithopoda	4.8	.	2	.	2	32
Ranunculus carinthiacus	4.1	.	1	.	2	29
Sesleria caerulea subsp. *caerulea*	4.3	.	2	.	<1	29
Trifolium thalii	7.9	.	<1	.	13	38
Silene acaulis	3.4	.	.	.	1	26
Aster alpinus	3.5	.	1	.	<1	25
Saxifraga paniculata	2.9	.	<1	.	.	24
[...]						
Anthyllis vulneraria	13.6	4	22	1	1	43
Diagnostic for multiple classes (13 taxa)						
Eryngium campestre	16.1	37	32	9	1	.
Genista scorpius	7.0	30	15	.	.	.
Koeleria vallesiana	25.1	37	53	.	.	34
Dactylis glomerata	21.0	52	20	43	3	2
Carex flacca subsp. *flacca*	25.3	.	45	35	4	3
Pilosella officinarum	29.6	13	41	5	48	13
Thymus praecox	42.5	.	63	1	43	82
Carex caryophyllea	27.9	4	31	4	51	30
Helianthemum canum subsp. *canum*	14.6	2	27	.	1	39
Teucrium pyrenaicum	11.0	.	24	<1	<1	18
Trifolium repens	30.0	.	17	47	52	8
Campanula scheuchzeri	7.0	.	1	<1	15	25
Plantago alpina	6.5	.	1	.	20	13
Companion species						
Lotus corniculatus	44.3	4	53	32	54	43
Plantago lanceolata	37.5	7	50	47	29	11
Trifolium pratense	32.0	4	29	46	37	20
Bellis perennis	31.1	7	26	43	41	15
Achillea millefolium	25.6	2	24	24	41	12
Hypochaeris radicata	24.8	15	19	30	40	9
Plantago media	24.7	.	31	24	30	9
Galium pumilum	23.7	2	40	8	15	34
Briza media subsp. *media*	22.2	.	38	25	9	9
Brachypodium rupestre	21.5	.	32	19	18	10
Ranunculus bulbosus subsp. *bulbosus*	21.5	2	28	20	24	11
Cerastium fontanum subsp. *vulgare*	17.7	.	11	22	35	6
Daucus carota	16.1	19	22	32	.	.
Linum catharticum subsp. *catharticum*	15.7	.	28	3	13	18
Galium verum subsp. *verum*	14.3	13	20	12	15	2
Potentilla montana	13.6	.	17	1	26	10
Cynosurus cristatus	13.0	.	13	27	10	.
Prunella vulgaris	11.5	.	7	26	12	3
Helianthemum nummularium	11.3	.	21	<1	8	15
Blackstonia perfoliata	11.0	17	25	5	.	.
Hippocrepis comosa	10.9	2	20	<1	5	18
Leontodon saxatilis subsp. *saxatilis*	10.9	19	12	15	9	.
Colchicum montanum	10.8	.	20	1	11	5
Trifolium campestre	10.8	13	19	12	3	.
Phleum pratense	10.5	11	17	15	1	.
Erica vagans	10.4	.	17	.	17	4
[...]						

Class	All	LYG	FES	MOL	NAR	SES
# plots	958	54	339	220	223	114
# plots with bryophyte/lichen treatment	119	19	64	8	11	17
Bryophytes and lichens (based on plots from the Field Workshop)						
Class LYG (12 taxa)						
Seirophora lacunosa	5.9	37	.	.	.	.
Gyalolechia fulgens	5.9	37	.	.	.	.
Didymodon acutus	23.5	58	25	.	.	6
Squamarina cartilaginea	6.7	37	.	.	.	6
Weissia condensa	7.6	32	3	.	.	6
Fulgensia poeltii	4.2	21	2	.	.	.
Lathagrium cristatum	4.2	21	2	.	.	.
Enchylium tenax	10.1	32	8	.	.	6
[...]						
Class FES (5 taxa)						
Cladonia rangiformis	14.3	.	27	.	.	.
Cladonia convoluta	8.4	.	16	.	.	.
Eurhynchiastrum pulchellum	5.9	.	11	.	.	.
Campyliadelphus chrysophyllus	12.6	.	20	.	.	12
Cladonia foliacea	4.2	.	8	.	.	.
Class MOL (2 taxa)						
Brachythecium laetum	4.2	.	.	50	9	.
Rhytidiadelphus squarrosus	2.5	.	3	13	.	.
Class NAR (3 taxa)						
Tortula acaulon	1.7	.	.	.	18	.
Lophocolea minor	0.8	.	.	.	9	.
Tortula inermis	0.8	.	.	.	9	.
Class SES (20 taxa)						
Cladonia pocillum	5.9	.	3	.	.	29
Tortella tortuosa	20.2	.	23	.	9	47
Fissidens dubius	15.1	.	19	.	.	35
Mnium marginatum	2.5	.	.	.	.	18
Polytrichum juniperinum	2.5	.	.	.	.	18
Scapania calcicola	2.5	.	.	.	.	18
Tortella inclinata	10.9	5	8	.	9	35
Ptychostomum capillare aggr.	11.8	5	13	.	.	29
[...]						
Ditrichum pusillum	10.1	11	6	.	9	29
Diagnostic for multiple classes						
Tortella squarrosa	31.1	32	41	.	.	29
Abietinella abietina	10.9	.	19	13	.	.
Ctenidium molluscum	31.1	.	44	13	.	47
Flexitrichum gracile	21.0	.	33	.	.	24
Companion species						
Homalothecium lutescens	34.5	16	42	50	9	35
Weissia controversa	23.5	42	23	13	9	18
Hypnum cupressiforme	22.7	5	28	.	36	24
Pseudoscleropodium purum	13.4	.	20	13	9	6
Calliergonella cuspidata	12.6	.	20	13	9	.

MOL – *Molinio-Arrhenatheretea* (Figure 2C)

86% of the relevés previously assigned to the *Molinio-Arrhenetheretea* were included in the group MOL, together with 16% of the relevés of *Festuco-Brometea*. This group is characterized by several diagnostic species of the class *Molinio-Arrhenatheretea*, such as *Agrostis stolonifera* subsp. *stolonifera, Anthoxanthum odoratum, Holcus lanatus, Juncus articulatus, J. inflexus, Lolium perenne, Poa trivialis* subsp. *trivialis, Ranunculus acris* subsp. *friesianus, R. repens* and *Trifolium fragiferum* subsp. *fragiferum,* among other species (Table 2).

The relevés from *Festuco-Brometea* class classified in the group MOL had been originally assigned to the associations *Seseli-Brachypodietum* and *Elytrigio-Brachypodietum phoenicoidis* from *Festuco-Brometea*. The presence of *Agrimonia eupatoria, Agrostis stolonifera* subsp. *stolonifera, Bromus hordeaceus* subsp. *hordeaceus, Poa trivialis* subsp. *trivialis, Potentilla reptans, Ranunculus acris* subsp. *friesianus* and *Schedonorus arundinaceus* subsp. *arundinaceus* relates these relevés to this group (MOL).

This group is widely distributed throughout the study area (Figure 3), although it does not reach high elevations. In the temperate zone it can be found in the meso- and supratemperate, and in the Mediterranean zone it is restricted to wet soils, both in the meso- and the supramediterranean. These grasslands and pastures grow on flat areas with a proportion of 100% fine soil, which results in an almost total vegetation cover (Table 3).

NAR – *Nardetea strictae* (Figure 2B)

Table 1 shows that almost all the relevés originally classified in the class *Nardetea strictae* have been classified in group NAR by the expert system. Most relevés of the
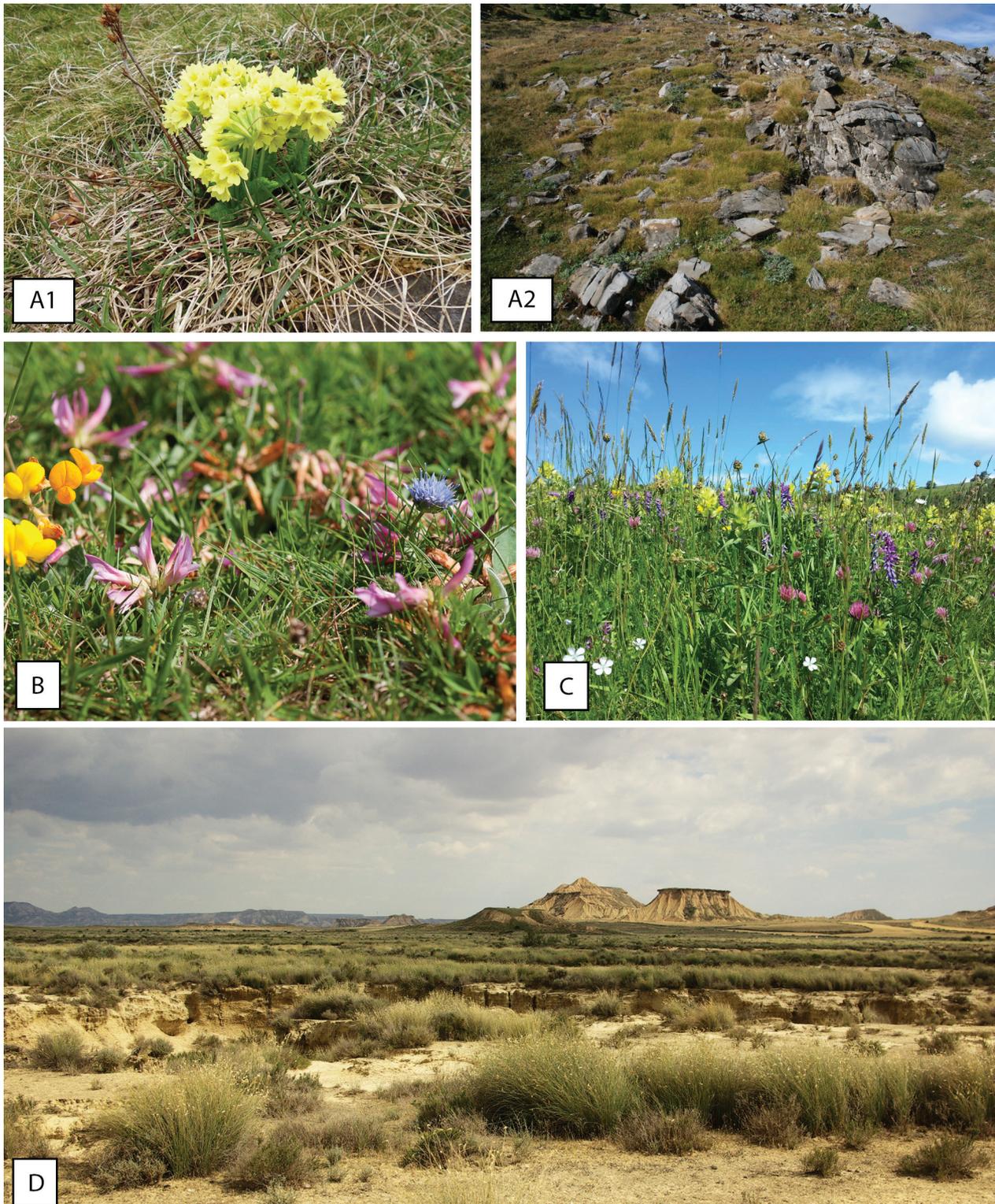
Figure 2. Photo plate showing typical stands of four of the five distinguished vegetation classes (for *Festuco-Brometea*, see Figures 13–14). A *Elyno-Seslerietea*, A1 *Primula intricata*, A2 *Festuca gautieri* subsp. *scoparia*; B *Nardetea strictae* (*Nardus stricta, Trifolium alpinum, Lotus alpinus, Jasione laevis* subsp. *laevis*); C *Molinio-Arrhenatheretea*; D *Lygeo-Stipetea* (*Lygeum spartum*). Photos: J. Dengler (A1, A2, B); A. Berastegi (C); Renaud Jaunatre (D).

class *Sedo-Scleranthetea* were also classified in this group, as well as some relevés of *Festuco-Brometea* (19%) and *Molinio-Arrhenateretea* (8%). The diagnostic species include acidophilous taxa such as *Agrostis capillaris, Carex pilulifera* subsp. *pilulifera, Danthonia decumbens, Galium saxatile, Jasione laevis* subsp. *laevis* or *Potentilla erecta* (Table 2).

Relevés from *Festuco-Brometea* included in this group correspond to communities of the association *Cala-mintho-Seselietum montani* that grow in places with a

very humid ombroclimate, which causes acidification of the soil leading to the presence of acidophilous species diagnostic of *Nardetea*. As regards *Molinio-Arrhenatheretea*, relevés originally assigned to the association *Merendero-Cynosuretum* were classified in this group. In both cases, the species shared with *Nardetea* were *Agrostis capillaris, Carex pilulifera* subsp. *pilulifera, Danthonia decumbens, Festuca microphylla, Galium saxatile, Helictochloa marginata* subsp. *marginata, Luzula campestris, Jasione laevis* subsp. *laevis, Polygala serpyllifolia, Potentilla erecta,* among others.

The relevés of this group are widely distributed in the montane and subalpine belts of the Pyrenees and Basque-Cantabrian mountains under temperate climate (Figure 3).

SES – *Elyno-Seslerietea* (Figure 2A)

The expert system classification within the group SES included most of the relevés of the class *Elyno-Seslerietea* and 23% of relevés from *Festuco-Ononidetea*. *Agrostis schleicheri, Alchemilla plicatula* aggr., *Androsace villosa* subsp. *villosa, Carex ornithopoda* subsp. *ornithopoda, C. sempervirens* subsp. *sempervirens, Festuca gautieri* subsp. *scoparia, Helictotrichon sedenense* subsp. *sedenense, Paronychia kapela* subsp. *serpyllifolia, Poa alpina, Ranunculus carinthiacus, Sesleria caerulea* subsp. *caerulea, Silene acaulis* and *Trifolium thalii* are diagnostic species of this group (Table 2).

Relevés of *Festuco-Ononidetea* included in this group correspond to communities of the Pyrenean subalpine

alliance *Festucion scopariae*, which share most of the diagnostic species of the group, such as *Aster alpinus, Minuartia verna* subsp. *verna,* and *Saxifraga paniculata,* in addition to those aforementioned.

This group SES includes the plots at highest elevations in calcareous mountains, in the upper montane and subalpine belts. In these cases, they share territories with the previous group NAR, but in rocky calcareous places (Figure 3). However, the concentration of calcium carbonate in the soil is very low due to the decarbonation effect caused by high precipitation and snow accumulation (Table 3).

Ordination

The NMDS ordination diagram clearly differentiated between the five groups defined by our class expert system (Figure 4). Axis 1 distributes *Lygeo-Stipetea, Festuco-Brometea, Molinio-Arrhenatheretea, Nardetea strictae* and *Elyno-Seslerietea* along a decreasing mediterraneity and increasing precipitation gradient. Axis 2 separates classes *Molinio-Arrhenatheretea* and *Nardetea*, in the upper part, from the others. This axis could be related to soil moisture.

Site conditions and biodiversity of different classes

The differences between classes regarding elevation and climatic conditions can be seen in Table 3 and Figure 5. The class *Lygeo-Stipetea* (LYG) shows the highest Mediterraneity index and the highest mean annual temperature and is generally present at lower elevations with the lowest annual precipitation. On the other hand, the classes *Nardetea* (NAR) and *Elyno-Seslerietea* (SES) develop at the highest elevations, linked to the highest annual precipitation and lowest mean annual temperature and Mediterraneity Index.

Regarding soil, topographic and structural variables (Table 3, Figure 5), the class *Nardetea* represents the highest soil depth and is also the most acidophilous communi-
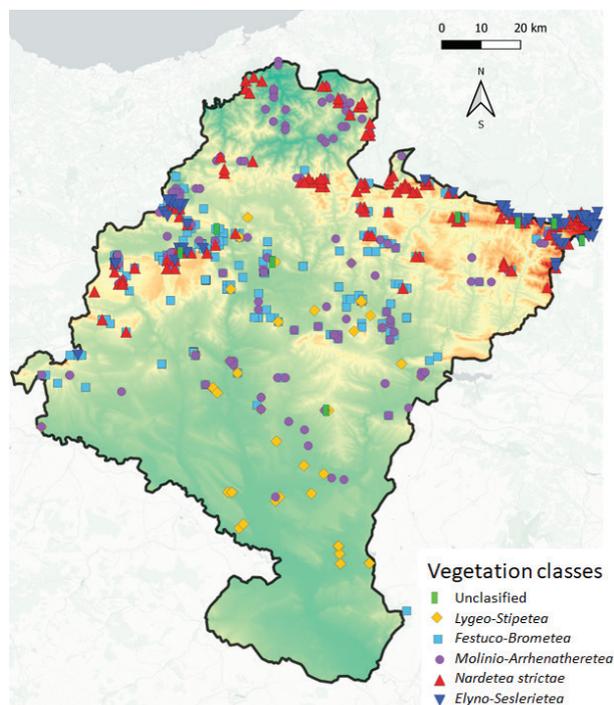

Figure 3. Study area (Navarre) and location of grassland relevés classified to classes according to expert system analysis.
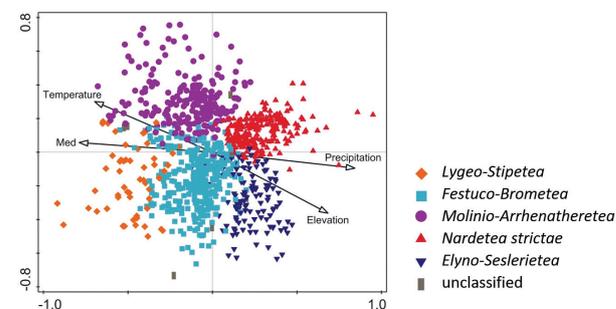

Figure 4. NMDS ordination of all grassland relevés. Eigenvalues: Axis 1 – 0.4434, Axis 2 – 0.4010, Axis 3 (not shown) – 0.1556. Med stands for Mediterraneity Index.

Table 3. Comparison of climatic, structural, ecological and diversity characteristics among the five classes. The *p*-values and significance levels refer to ANOVAs.

Parameter	LYG	FES	MOL	NAR	SES	*p*-value	Sig.
Total number of relevés	54	339	220	223	114		
Number of relevés from EDGG FW	19	64	8	11	17		
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD		
Parameters calculated for all relevés							
Geographical and climatic parameters							
Elevation [m a.s.l.]	439 ± 157	853 ± 286	577 ± 272	1265 ± 378	1752 ± 386	<0.001	***
Mediterranity index	1.36 ± 0.46	0.66 ± 0.19	0.77 ± 0.31	0.41 ± 0.1	0.36 ± 0.08	<0.001	***
Annual mean temperature [°C]	13.2 ± 1.3	10.5 ± 1.5	11.8 ± 1.6	8.0 ± 2.4	5.3 ± 2.7	<0.001	***
Mean annual precepitation [mm]	686 ± 260	1232 ± 283	1134 ± 331	1751 ± 271	1865 ± 232	<0.001	***
Parameters calculated for relevés from EDGG Field Workshop							
Vegetation structure							
Cover vegetation total [%]	67 ± 22	81 ± 19	98 ± 2	86 ± 9	55 ± 22	<0.001	***
Cover shrub layer [%]	1 ± 1	1 ± 3	0 ± 0	0 ± 0	0 ± 0	0.138	
Cover herb layer [%]	55 ± 25	76 ± 20	98 ± 2	77 ± 25	51 ± 22	<0.001	***
Cover cryptogam layer [%]	19 ± 21	16 ± 18	31 ± 32	1 ± 2	10 ± 10	0.005	**
Cover litter [%]	16 ± 17	9 ± 14	8 ± 12	6 ± 6	14 ± 25	0.365	n.s.
Herb layer maximum height [cm]	66 ± 26	65 ± 31	108 ± 32	31 ± 17	24 ± 19	<0.001	***
Species richness							
Species richness (total)	35.6 ± 6.8	55.3 ± 14.5	45.3 ± 14.7	40.5 ± 6.9	44.0 ± 11.7	<0.001	***
Species richness (vascular plants)	29.2 ± 7.5	48.0 ± 11.9	43.5 ± 14.0	37.5 ± 6.4	34.4 ± 7.7	<0.001	***
Species richness (cryptogams)	6.4 ± 4.2	7.3 ± 4.9	2.0 ± 1.7	2.9 ± 2.0	9.6 ± 6.2	<0.001	***
Species richness (bryophytes)	3.2 ± 2.0	6.3 ± 4.2	2.0 ± 1.7	2.5 ± 1.6	7.2 ± 5.6	<0.001	***
Species richness (lichens)	3.2 ± 3.2	1.0 ± 1.3	0.0 ± 0.0	0.4 ± 0.7	2.4 ± 2.3	<0.001	***
Topography							
Southing (cosine of aspect)	0.1 ± 0.6	-0.3 ± 0.68	-0.46 ± 0.65	0.24 ± 0.69	0.08 ± 0.89	0.019	*
Inclination [°]	8 ± 9	16 ± 13	6 ± 6	26 ± 9	32 ± 11	<0.001	***
Maximum microrelief [cm]	7 ± 7	9 ± 8	4 ± 3	9 ± 4	29 ± 26	<0.001	***
Soil parameters							
Soil depth mean [cm]	12 ± 6	16 ± 8	17 ± 5	36 ± 16	6 ± 5	<0.001	***
Soil depth CV	54 ± 32	50 ± 40	49 ± 34	30 ± 16	97 ± 51	0.001	***
Cover rocks and stones [%]	6 ± 13	7 ± 14	0 ± 0	2 ± 3	35 ± 23	<0.001	***
Cover gravel [%]	19 ± 29	6 ± 15	0 ± 0	1 ± 1	13 ± 16	0.011	*
Cover fine soil [%]	75 ± 35	88 ± 22	100 ± 0	97 ± 3	52 ± 32	<0.001	***
Coarse fragments [%]	16 ± 13	22 ± 17	15 ± 14	12 ± 8	24 ± 16	0.139	n.s.
Fine fragments < 2mm [%]	84 ± 13	78 ± 17	85 ± 14	88 ± 8	76 ± 16	0.139	n.s.
pH	7.69 ± 0.24	7.52 ± 0.42	7.66 ± 0.99	6.8 ± 0.29	7.46 ± 0.38	<0.001	***
Electrical conductivity [µS/cm]	283 ± 184	232 ± 86	168 ± 78	146 ± 80	310 ± 158	0.002	**
CaCO3 [%]	40.7 ± 10.5	26.7 ± 19.1	8.5 ± 8.5	4 ± 1.1	4.6 ± 1.8	<0.001	***
Organic matter [%]	0.6 ± 0.6	1.4 ± 0.8	1.2 ± 0.3	1.3 ± 0.2	2.2 ± 0.7	<0.001	***

ty. The class *Elyno-Seslerietea* is characterised by a higher cover of stones and rocks as well as higher soil organic matter content, and, together with *Nardetea* and *Molinio-Arrhenatheretea,* is the poorest in soil carbonate content. Conversely, *Lygeo-Stipetea* is signified by its high soil carbonate content and low soil organic matter. *Molinio-Arrhenatheretea* is distinghuished by its high cover of the herb layer and cryptogams.

The total species richness is highest in *Festuco-Brometea,* although differences with the second richer class *Molinio-Arrhenatheretea* are not significant (Figure 6). *Festuco-Brometea* is also rich in vascular plants and bryophytes, although for the former values do not significantly differ from those of *Molinio-Arrhenatheretea*, and for the latter from those of *Elyno-Seslerietea*. The latter class stands out because of its high cryptogam richness, both in bryophytes and lichens. On the other hand, *Molinio-Arrhenetheretea* and *Nardetea* are the poorest in cryptogams. Finally, *Lygeo-Stipetea* shares with *Elyno-Seslerietea* the high number of lichens, although its richness in bryophytes is lower.

Subdivision of the *Festuco-Brometea* into orders, alliances and associations

The TWISPAN analysis for the group FES related to the class *Festuco-Brometea* resulted in four main divisions that can be interpreted at order and alliance levels (Figure 7). Order 1 grouped relevés originally classified in the classes *Ononido-Rosmarinetea* (*Thymelaeo-Aphyllanthetum monspeliensis)* and *Festuco-Ononidetea* (*Ononidetalia striatae*: *Helianthemo-Koelerietum vallesianae*; *Festuco-Poetalia ligulatae*: *Jurineo-Festucetum hystricis*). The dry grasslands of the *Thymelaeo-Aphyllanthetum* association were included in alliance 1.1. The two associations from *Festuco-Ononidetea, Helianthemo-Koelerietum* and *Jurineo-Festucetum*, were merged in the alliance 1.2.

Diagnostic species for order 1 were *Carex humilis, Galium lucidum* subsp. *fruticescens, Helianthemum apenninum* subsp. *apenninum* and *Koeleria vallesiana* (Table 4). The alliance 1.1 was characterized by the presence of Mediterranean species such as *Aphyllanthes monspeliensis, Brachypodium retusum, Coris monspeliensi*s, *Helictochloa*
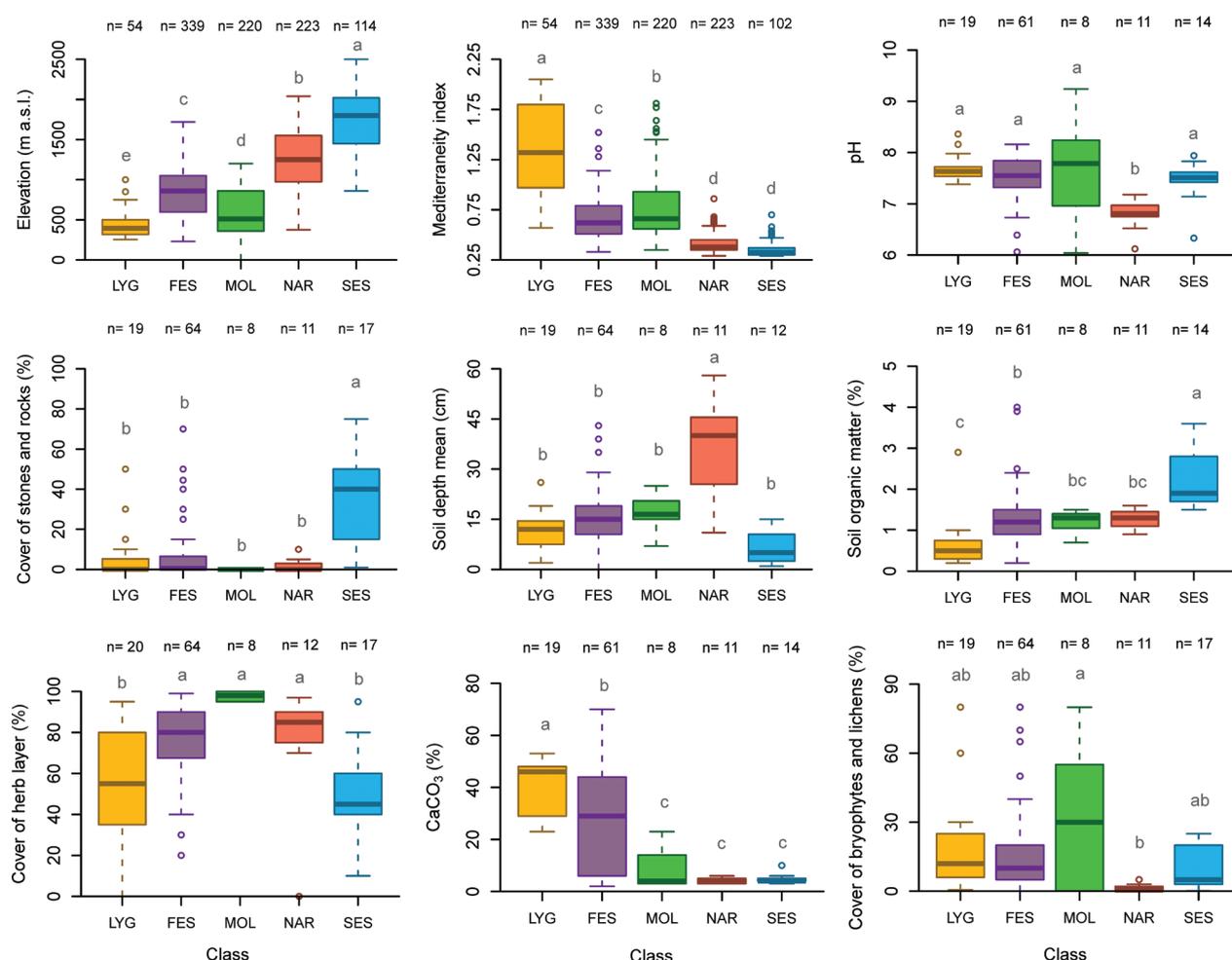
Figure 5. Comparison of nine ecological variables among the five classes. For elevation and Mediterraneity Index, all relevés were analysed, whereas for the rest of variables only relevés from EDGG Field Workshop were used. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.
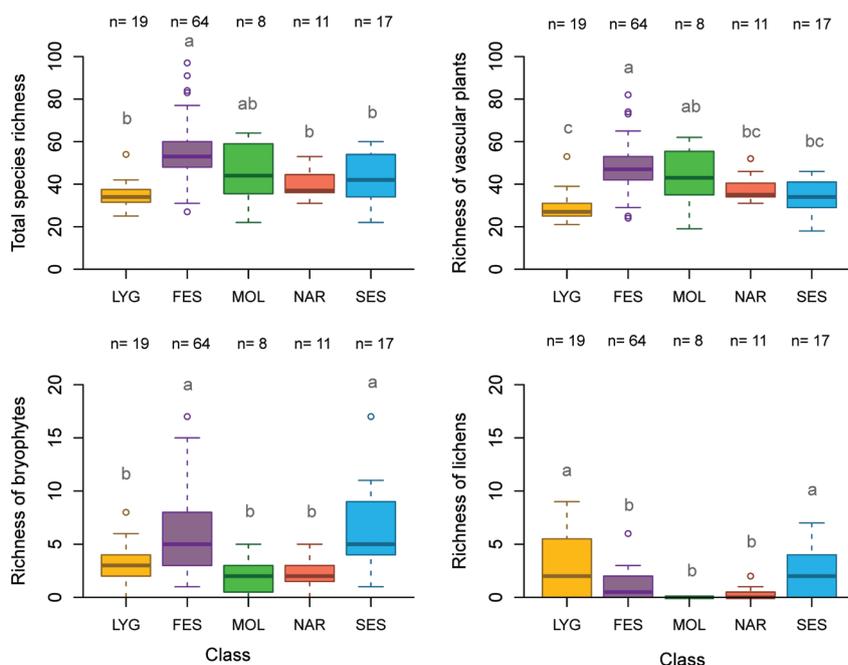
Figure 6. Comparison of species richness divided into four groups (total species, vascular plants, bryophytes and lichens) among the five classes using the relevés from EDGG Field Workshop. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

Table 4. Abridged constancy table of the class *Festuco-Brometea* and its subordinate syntaxa. Values are percentage constancies, and species are ordered by decreasing phi-values in the respective syntaxon, respectively by decreasing overall constancy for non-diagnostic species. In the upper part vascular plants are given, in the lower part bryophytes and lichens, whose constancies and fidelities have been calculated based on the plots of the EDGG Field Workshop only where they have been recorded (in italics if based on data from a single plot, with ? if no such data were available for any plot). In the table, the 15 vascular plant taxa and the eight non-vascular plant taxa with the highest fidelity in a syntaxon are shown, plus all taxa that are diagnostic for multiple syntaxa and all taxa with at least 10% overall constancy. Diagnostic species (phi ≥ 0.25) for higher syntaxa highlighted in light grey, diagnostic species for associations in dark grey, while differential species of associations within the respective alliance are given with a frame. The complete constancy table combined with the table of the underlying 339 vegetation plots is given in Suppl. material 14.

|	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance		1.1	2	1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association				1.1.1	1.2.1	1.2.2	2.1.1	1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Ord. 1 (4 taxa)															
Koeleria vallesiana	53.1	92	26	85	97	15	29	85	100	95	36	4	<1	27	36
Carex humilis	40.1	66	22	65	67	8	26	65	96	56	14	4	42	28	19
Helianthemum apenninum subsp. apenninum	13.6	29	3	19	34	3	3	19	32	36	<1	4	<1	3	4
Galium lucidum subsp. fruticescens	9.7	21	2	15	24	3	2	15	24	25	<1	4	17	<1	1
All. 1.1 (38 taxa + 1 multiple diagnostic taxon)															
Brachypodium retusum	14.5	29	5	75	1	18	1	75	<1	2	43	4	8	1	<1
Thymus vulgaris subsp. vulgaris	20.1	45	3	81	24	8	1	81	44	16	7	8	<1	1	1
Lavandula latifolia	7.1	17	1	42	1	3	<1	42	4	<1	<1	4	<1	<1	<1
Aphyllanthes monspeliensis	14.7	24	9	58	3	10	8	58	4	3	14	8	<1	13	4
Coris monspeliensis	6.8	14	2	38	<1	8	<1	38	<1	<1	14	4	<1	<1	<1
Teucrium chamaedrys	18.0	35	7	60	20	10	6	60	16	21	14	8	42	3	3
Helictochloa bromoides	6.2	13	2	35	<1	8	<1	35	<1	<1	14	4	<1	<1	<1
Bupleurum rigidum subsp. rigidum	4.7	11	1	29	<1	3	<1	29	<1	<1	7	<1	<1	4	<1
Linum appressum	9.7	17	5	40	2	8	4	40	4	2	21	27	8	4	4
Genista scorpius	15.0	23	10	58	2	35	3	58	4	2	50	15	8	5	1
Dorycnium pentaphyllum subsp. pentaphyllum	16.5	24	12	58	3	33	6	58	4	3	64	<1	33	<1	3
Santolina villosa	3.8	9	1	23	<1	<1	1	23	<1	<1	<1	<1	8	8	<1
Coronilla minima	38.3	60	23	79	49	25	23	79	72	41	36	19	8	29	17
Fumana ericifolia	3.5	8	1	21	<1	<1	1	21	<1	<1	<1	<1	<1	<1	1
Linum narbonense	6.2	12	3	29	1	5	2	29	<1	2	14	<1	8	3	<1
[...]															
Asperula cynanchica	17.7	22	15	44	9	8	16	44	4	11	14	4	17	18	14
Catananche caerulea	13.6	17	12	42	1	23	9	42	<1	2	21	23	<1	17	1
Festuca marginata subsp. andres-molinae	10.3	14	8	35	2	20	4	35	8	<1	29	15	<1	9	<1
Assoc. 1.1.1 (7 taxa)															
Rhamnus alaternus subsp. alaternus	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	1	<1
Odontites kaliformis	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	1	<1
Lithodora fruticosa	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Gladiolus illyricus	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Atractylis humilis	1.2	3	<1	8	<1	<1	<1	8	<1	<1	<1	<1	<1	<1	<1
Aster willkommii	1.2	3	<1	8	<1	<1	<1	8	<1	2	<1	<1	<1	<1	<1
Helichrysum stoechas subsp. stoechas	1.8	4	<1	10	1	<1	<1	10	<1	2	<1	<1	<1	<1	<1
All. 1.2 (8 taxa + 1 multiple diagnostic)															
Sedum album	14.2	27	6	2	41	<1	7	2	48	39	<1	<1	8	<1	14

	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order	1	1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Ononis striata	4.7	12	<1	2	17	<1	<1	2	20	16	<1	<1	<1	<1	<1
Asperula pyrenaica	12.7	19	8	4	29	3	9	4	28	30	<1	4	<1	4	17
Plantago atrata subsp. discolor	5.6	12	2	2	17	<1	2	2	12	20	<1	<1	<1	3	1
Anthyllis vulneraria	22.1	29	18	8	41	15	18	8	40	43	14	15	<1	15	23
Thymus praecox	62.8	60	65	33	76	23	76	33	80	74	21	23	42	67	91
Oreochloa confusa	3.8	7	2	<1	11	<1	2	<1	16	8	<1	<1	<1	<1	4
Dianthus pungens subsp. brachyanthus	3.2	6	1	<1	10	<1	1	<1	16	8	<1	<1	<1	<1	3
Brimeura amethystina	3.2	6	1	<1	10	<1	1	<1	4	13	<1	<1	<1	1	1
Assoc. 1.2.1 (13 taxa)															
Arenaria grandiflora subsp. grandiflora	13.0	29	2	4	44	<1	3	4	88	25	<1	<1	<1	<1	6
Festuca hystrix	5.9	14	<1	4	21	<1	<1	4	56	7	<1	<1	<1	<1	<1
Helianthemum canum subsp. canum	26.8	49	12	12	71	<1	14	12	100	59	<1	<1	<1	12	20
Klasea nudicaulis	6.5	15	1	4	22	<1	1	4	48	11	7	<1	<1	<1	1
Anthyllis montana	2.9	7	<1	<1	11	<1	<1	<1	32	3	<1	<1	<1	<1	1
Jurinea humilis	3.5	8	1	<1	13	<1	1	<1	28	7	<1	<1	<1	<1	1
Erucastrum nasturtiifolium subsp. sudrei	1.8	4	<1	<1	7	<1	<1	<1	20	2	<1	<1	<1	<1	<1
Trinia glauca	7.7	17	1	10	22	1	1	10	36	16	<1	<1	<1	3	<1
Festuca ovina aggr.	11.2	18	7	8	24	8	8	8	44	16	8	8	8	8	9
Aster alpinus	1.2	3	<1	<1	5	<1	<1	<1	16	<1	<1	<1	<1	<1	<1
Paronychia kapela subsp. kapela	0.9	2	<1	<1	3	<1	<1	<1	12	<1	<1	<1	<1	<1	<1
Arenaria erinacea	0.9	2	<1	<1	3	<1	<1	<1	12	<1	<1	<1	<1	<1	<1
Scilla verna	6.8	10	5	4	14	3	5	4	28	8	<1	4	<1	5	4
Assoc. 1.2.2 (5 taxa + 1 multiple diagnostic taxon + 1 differential taxon)															
Conopodium arvense	4.4	9	2	<1	14	2	2	<1	<1	20	<1	<1	<1	3	1
Sedum acre	2.9	6	1	<1	10	<1	1	<1	<1	15	<1	<1	<1	<1	1
Deschampsia media subsp. hispanica	3.2	7	1	3	11	3	<1	<1	<1	16	<1	4	33	<1	<1
Helianthemum salicifolium	1.5	4	<1	3	6	<1	<1	<1	<1	8	<1	<1	<1	<1	<1
Erodium glandulosum	1.5	4	<1	<1	6	<1	<1	<1	12	8	<1	<1	<1	<1	<1
Medicago lupulina	38.9	33	43	12	46	33	46	12	4	64	21	38	8	54	43
Ord. 2 (12 taxa)															
Lotus corniculatus	52.8	24	73	13	30	58	77	13	20	34	57	58	17	85	78
Trifolium pratense	28.6	4	46	2	6	45	46	2	<1	8	29	54	8	62	35
Briza media subsp. media	38.3	17	54	25	11	45	56	25	4	15	43	46	33	83	29
Trifolium ochroleucon	15.6	1	26	<1	2	20	27	<1	<1	3	7	27	<1	47	9
Trifolium repens	16.5	2	27	2	2	20	28	2	<1	3	<1	31	<1	27	35
Cynosurus cristatus	12.7	<1	22	<1	<1	28	20	<1	<1	<1	7	38	<1	35	7
Ranunculus bulbosus subsp. bulbosus	28.0	12	40	17	8	45	38	17	4	10	21	58	8	44	38
Plantago lanceolata	50.4	32	64	23	37	50	67	23	12	48	43	54	25	73	72
Endressia castellana	9.4	<1	16	<1	<1	10	18	<1	<1	<1	<1	15	<1	23	10
Ononis spinosa	13.0	2	21	2	2	28	19	2	<1	3	7	38	<1	35	4
Trisetum flavescens subsp. flavescens	11.8	2	19	4	1	20	18	4	<1	2	<1	31	<1	31	7
Festuca nigrescens	9.1	1	15	<1	1	13	16	<1	<1	2	<1	19	17	24	4
All. 2.1 (11 taxa + 1 multiple diagnostic taxon)															
Schedonorus arundinaceus subsp. fenas	5.9	<1	10	<1	<1	38	3	<1	<1	<1	36	38	<1	5	1

	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order	1	1	2	1	1	2	2	1	1	1	2	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.1	2.2	2.2	2.2
Association				1.1	1.2	2.1	2.2	1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.1.1	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	1	20	12
Centaurea jacea	17.1	6	25	13	2	55	17	13	<1	3	57	54	17	17	29	3
Arrhenatherum elatius	6.2	1	10	4	<1	33	4	4	<1	<1	29	35	33	33	3	<1
Convolvulus arvensis	4.4	1	7	2	<1	28	2	2	<1	3	21	31	<1	<1	3	1
Brachypodium phoenicoides	10.0	8	12	19	1	43	4	19	<1	2	43	42	<1	<1	4	4
Blackstonia perfoliata	24.8	23	26	58	2	68	16	58	<1	3	79	62	<1	<1	27	6
Daucus carota	21.8	10	30	17	6	53	24	17	4	8	36	62	17	17	44	4
Carex flacca subsp. flacca	45.1	26	59	58	7	80	53	58	4	8	86	77	58	58	81	22
Agrimonia eupatoria	4.1	1	7	2	<1	20	3	2	<1	<1	14	23	<1	<1	6	<1
Poa compressa	3.2	1	5	<1	1	18	2	<1	<1	2	7	23	<1	<1	4	<1
Dactylis glomerata	19.8	15	23	27	8	48	17	27	4	10	29	58	58	58	21	6
Medicago sativa subsp. sativa	1.2	<1	2	<1	<1	10	<1	<1	<1	<1	7	12	<1	<1	<1	<1
Assoc. 2.1.1 (7 taxa + 2 differential taxa)																
Plantago maritima subsp. serpentina	6.8	6	7	15	1	25	3	15	<1	2	57	8	<1	<1	3	3
Festuca capillifolia	5.3	4	7	6	2	28	1	6	4	2	50	15	<1	<1	3	<1
Jasonia tuberosa	6.2	9	4	21	2	15	1	21	<1	3	43	<1	<1	<1	1	1
Prunella hyssopifolia	11.5	8	14	19	1	35	9	19	<1	2	57	23	<1	<1	15	3
Agrostis stolonifera subsp. stolonifera	2.7	<1	5	<1	<1	18	1	<1	<1	<1	29	12	<1	<1	3	<1
Lotus tenuis	0.6	<1	1	<1	<1	5	<1	<1	<1	<1	14	<1	<1	<1	<1	<1
Lathyrus latifolius	0.6	<1	1	<1	<1	5	<1	<1	<1	<1	14	<1	<1	<1	<1	<1
Assoc. 2.1.2 (28 taxa + 3 differential taxa)																
Phleum pratense	17.1	4	26	10	1	53	19	10	<1	2	14	73	<1	<1	28	13
Poa trivialis subsp. trivialis	5.6	<1	10	<1	<1	28	5	<1	<1	<1	<1	42	<1	<1	8	3
Vicia parviflora	3.2	<1	6	<1	<1	23	1	<1	<1	<1	<1	35	<1	<1	1	1
Brachypodium phoenicoides x rupestre	9.4	2	15	6	<1	40	8	6	<1	<1	7	58	8	8	12	4
Xeranthemum cylindraceum	2.7	1	4	2	<1	18	1	2	<1	<1	<1	27	<1	<1	<1	1
Trifolium campestre	18.6	7	27	6	8	40	23	6	8	8	<1	62	8	8	24	26
Vicia sativa subsp. nigra	5.9	2	9	2	2	25	4	2	<1	3	<1	38	8	8	6	1
Iris spuria subsp. maritima	1.8	<1	3	<1	<1	13	1	<1	<1	<1	<1	19	<1	<1	1	<1
Gaudinia fragilis	2.1	<1	4	<1	<1	13	1	<1	<1	<1	<1	19	<1	<1	3	<1
Trifolium angustifolium	2.4	1	4	2	<1	13	1	2	<1	<1	<1	19	<1	<1	1	3
Lathyrus pratensis subsp. pratensis	1.5	<1	3	<1	<1	10	1	<1	<1	<1	<1	15	<1	<1	1	<1
Jacobaea vulgaris	3.2	<1	6	<1	<1	18	3	<1	<1	<1	7	23	<1	<1	5	<1
Allium oleraceum	1.8	<1	3	<1	<1	10	1	<1	<1	<1	<1	15	<1	<1	1	1
Cerastium fontanum subsp. vulgare	10.6	4	15	<1	7	23	13	<1	4	7	<1	35	<1	<1	14	14
Picris hieracioides	7.1	4	9	12	<1	23	6	12	<1	<1	7	31	<1	<1	10	1
[...]																
Eryngium campestre	32.4	29	35	58	13	58	29	58	8	15	29	73	25	25	31	28
Galium verum subsp. verum	19.8	9	27	6	11	38	24	6	<1	16	14	50	17	17	22	29
Anacamptis pyramidalis	10.6	7	13	19	<1	28	9	19	<1	<1	14	35	<1	<1	19	<1
All. 2.2 (10 taxa + 1 multiple diagnostic taxon)																
Brachypodium rupestre	32.4	12	47	12	11	3	58	12	4	15	7	<1	92	92	73	36
Festuca microphylla	22.4	4	35	2	6	3	43	2	<1	8	7	<1	25	25	46	43
Achillea millefolium	24.5	7	37	6	8	13	43	6	12	7	7	15	8	8	47	42
Agrostis capillaris	17.7	3	28	<1	5	5	34	<1	4	5	<1	8	8	8	37	35

	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Erica vagans	17.1	3	27	6	1	13	31	6	4	<1	<1	19	58	41	14
Potentilla montana	16.8	3	27	<1	5	8	31	<1	4	5	<1	12	25	24	39
Helianthemum nummularium	21.2	7	31	<1	11	<1	39	<1	<1	16	<1	<1	17	36	46
Danthonia decumbens	10.3	1	17	<1	1	3	21	<1	<1	2	<1	4	<1	29	14
Scabiosa columbaria subsp. columbaria	25.4	12	35	10	14	10	41	10	<1	20	7	12	42	56	23
Gentiana verna subsp. verna	5.6	1	9	<1	1	<1	11	<1	<1	2	<1	<1	<1	9	16
Assoc. 2.2.1 (21 taxa + 1 multiple diagnostic taxon + 2 differential taxa)															
Vincetoxicum hirundinaria subsp. intermedium	3.8	4	4	4	3	<1	5	4	4	3	<1	<1	58	1	<1
Sesleria autumnalis	2.7	1	4	<1	2	<1	4	<1	<1	3	<1	<1	50	1	<1
Tanacetum corymbosum subsp. corymbosum	2.9	1	4	2	1	<1	5	2	<1	2	<1	<1	33	5	<1
Genista hispanica subsp. occidentalis	15.9	7	22	10	6	10	25	10	8	5	7	12	67	32	9
Euphorbia characias	2.1	2	2	4	1	<1	3	4	<1	2	<1	<1	25	<1	1
Euphorbia amygdaloides	0.6	<1	1	<1	<1	<1	1	<1	<1	<1	<1	<1	17	<1	<1
Cruciata laevipes	0.6	<1	1	<1	<1	<1	1	<1	<1	<1	<1	<1	17	<1	<1
Teucrium pyrenaicum	23.9	22	25	10	30	3	31	10	28	30	7	67	67	29	26
Pimpinella major subsp. major	1.2	<1	2	<1	<1	<1	3	<1	<1	<1	<1	17	17	1	1
Helictotrichon cantabricum	6.8	6	8	12	2	13	6	12	4	2	21	8	42	5	1
Viola alba aggr.	3.5	4	3	12	<1	<1	4	12	<1	<1	<1	<1	25	4	<1
Dianthus hyssopifolius subsp. hyssopifolius	4.1	3	5	<1	5	<1	6	4	<1	7	<1	<1	25	3	7
Helleborus foetidus	0.9	<1	2	<1	<1	3	1	<1	<1	<1	<1	4	17	<1	<1
Senecio lagascanus	1.8	3	1	4	2	<1	1	4	<1	3	<1	<1	17	<1	<1
Echium vulgare subsp. vulgare	2.1	1	3	2	1	<1	3	2	<1	2	<1	<1	17	3	1
Assoc. 2.2.2 (4 taxa + 1 multiple diagnostic taxon + 2 differential taxa)															
Leontodon hispidus	9.1	1	15	2	1	<1	18	2	<1	2	<1	<1	<1	32	6
Plantago media	31.3	9	47	8	9	25	53	8	8	10	14	31	8	72	39
Linum catharticum subsp. catharticum	27.7	12	39	19	7	25	43	19	<1	10	29	23	<1	63	28
Polygala vulgaris subsp. vulgaris	7.1	1	12	2	<1	5	13	2	8	<1	<1	8	<1	24	1
Prunella vulgaris	6.8	1	11	2	1	5	12	2	<1	2	<1	8	<1	21	4
Holcus lanatus	2.9	<1	5	<1	<1	3	6	<1	<1	<1	<1	4	<1	12	<1
Assoc. 2.2.3 (10 taxa + 1 multiple diagnostic taxon)															
Carex caryophyllea	31.3	14	43	6	20	13	51	6	8	25	7	15	17	36	72
Festuca rectifolia	42.5	45	41	6	68	8	49	6	36	80	<1	12	17	26	81
Bellis perennis	25.7	12	35	6	16	18	39	6	<1	23	7	23	<1	31	57
Colchicum montanum	20.4	17	23	2	25	3	28	2	8	33	<1	4	<1	19	43
Alchemilla plicatula aggr.	3.5	1	6	<1	1	<1	7	<1	<1	2	<1	<1	<1	1	14
Aira caryophyllea subsp. caryophyllea	9.1	5	12	2	7	8	13	2	<1	10	2	12	<1	4	26
Vicia pyrenaica	2.9	1	4	<1	2	<1	5	<1	<1	2	<1	<1	<1	<1	12
Poa alpina	4.7	3	6	<1	5	<1	8	<1	<1	7	<1	<1	<1	1	16
Cerastium arvense	8.3	9	8	<1	14	<1	10	<1	8	15	<1	<1	<1	<1	23
Erinus alpinus	3.8	3	5	<1	5	<1	6	<1	<1	5	<1	<1	<1	<1	13
Euphrasia salisburgensis	2.1	<1	4	<1	<1	<1	4	<1	<1	<1	<1	<1	<1	1	9
Other species (class character species and companion species)															
Bromopsis erecta subsp. erecta	65.2	60	69	69	55	53	73	69	32	66	29	65	75	82	61
Carthamus mitissimus	50.7	56	47	58	55	23	53	58	44	61	14	27	33	63	45

	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order	Class	1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Potentilla tabernaemontani	48.1	56	43	52	59	20	48	52	36	69	21	19	8	36	68
Helictochloa pratensis subsp. *iberica*	45.7	48	44	52	46	18	51	52	36	51	7	23	42	51	51
Pilosella officinarum	41.3	31	49	40	25	23	55	40	8	33	29	19	<1	59	61
Galium pumilum	39.8	27	49	44	17	48	49	44	4	23	36	54	58	60	33
Sanguisorba minor aggr.	33.9	29	37	44	21	20	41	44	8	26	14	23	25	54	30
Seseli montanum subsp. *montanum*	32.7	32	34	23	37	35	33	23	32	39	21	42	8	32	38
Hippocrepis comosa	20.4	12	27	13	10	10	31	13	8	11	14	8	8	41	22
Hypochaeris radicata	18.9	10	25	15	7	25	25	15	<1	10	43	15	17	32	19
Geum sylvaticum	18.0	12	23	12	11	10	26	12	8	13	7	12	17	32	20
Onobrychis conferta subsp. *hispanica*	16.8	20	15	31	14	8	16	31	16	13	14	4	<1	28	6
Trifolium montanum subsp. *montanum*	15.3	6	22	2	9	15	23	2	8	10	7	19	<1	33	14
Clinopodium alpinum subsp. *pyrenaeum*	14.2	19	11	13	23	<1	13	13	8	30	<1	<1	17	10	19
Leucanthemum pallens	13.6	9	17	19	3	23	15	19	<1	5	14	27	33	26	3
Filipendula vulgaris	12.7	6	17	<1	10	13	18	<1	12	10	7	15	<1	13	20
Astragalus monspessulanus subsp. *monspessulanus*	12.4	19	8	15	21	5	9	15	28	18	7	4	8	10	9
Leontodon saxatilis subsp. *saxatilis*	12.1	8	15	8	8	25	13	8	<1	11	21	27	<1	12	14
Prunella laciniata	12.1	4	18	8	1	8	21	8	<1	2	<1	12	8	26	17
Thymelaea ruizii	11.5	12	12	21	6	10	12	21	4	7	14	8	8	17	7
Ononis pusilla	10.3	19	4	25	16	5	4	25	8	20	14	<1	<1	3	6
Bellis sylvestris	10.0	14	8	23	8	10	7	23	8	8	7	12	<1	10	4
[...]															

Bryophytes and lichens (based on plots from the Field Workshop)

Ord. 1 (1 taxon)

	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Tortella squarrosa	40.6	70	24	72	60	13	27	72	?	60	<1	14	<1	20	42

All. 1.1 (1 taxon)

Flexitrichum gracile	32.8	48	24	61	<1	<1	30	61	?	<1	<1	<1	<1	30	33

All. 1.2 (8 taxa)

Cladonia foliacea	7.8	13	5	<1	60	<1	6	<1	?	60	<1	<1	<1	<1	17
Didymodon acutus	25.0	30	22	22	60	<1	27	22	?	60	<1	<1	<1	40	8
Lathagrium cristatum	1.6	4	<1	<1	20	<1	<1	<1	?	20	<1	<1	<1	<1	<1
Pseudocrossidium hornschuchianum	1.6	4	<1	<1	20	<1	<1	<1	?	20	<1	<1	<1	<1	<1
Scytinium schraderi	1.6	4	<1	<1	20	<1	<1	<1	?	20	<1	<1	<1	<1	<1
Encalypta vulgaris	3.1	4	2	<1	20	<1	3	<1	?	20	<1	<1	<1	8	8
Didymodon vinealis	4.7	9	2	6	20	<1	3	6	?	20	<1	<1	<1	5	<1
Ditrichum pusillum	6.3	9	5	6	20	<1	6	6	?	20	<1	<1	<1	5	8

Ord. 2 (4 taxa)

Pseudoscleropodium purum	20.3	<1	32	<1	<1	25	33	<1	?	<1	<1	29	<1	40	25
Cladonia rangiformis	26.6	9	37	6	20	13	42	6	?	20	100	<1	<1	20	83
Eurhynchiastrum pulchellum	10.9	<1	17	<1	<1	25	15	<1	?	<1	<1	29	<1	20	8
Fissidens dubius	18.8	4	27	6	20	13	30	6	?	<1	100	<1	100	25	33

All. 2.1 (2 taxa)

Calliergonella cuspidata	20.3	<1	32	<1	<1	50	27	<1	?	<1	100	43	<1	35	17
Weissia controversa	23.4	17	27	17	20	50	21	17	?	20	100	43	100	25	8

Assoc. 2.1.2 (6 taxa)

	Class	Ord.	Ord.	All.	All.	All.	All.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.	Assoc.
Order		1	2	1	1	2	2	1	1	1	2	2	2	2	2
Alliance				1.1	1.2	2.1	2.2	1.1	1.2	1.2	2.1	2.1	2.2	2.2	2.2
Association								1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3
# plots	339	139	200	52	87	40	160	52	25	61	14	26	12	78	69
Field Workshop (with bryophytes + lichens)	64	23	41	18	5	8	33	18	<1	5	1	7	1	20	12
Oxyrrhynchium hians	6.3	4	7	6	<1	38	<1	6	<1	<1	<1	43	<1	<1	<1
Fissidens taxifolius	14.1	4	20	6	<1	38	15	6	?	<1	<1	43	<1	25	<1
Brachytheciastrum velutinum	1.6	<1	2	<1	<1	13	<1	<1	?	<1	<1	14	<1	<1	<1
Brachythecium rutabulum	1.6	<1	2	<1	<1	13	<1	<1	?	<1	<1	14	<1	<1	<1
Plagiomnium undulatum	1.6	<1	2	<1	<1	13	<1	<1	?	<1	<1	14	<1	<1	<1
Weissia condensa	3.1	4	2	6	<1	13	<1	6	?	<1	<1	14	<1	<1	<1
All. 2.2 (6 taxa)															
Entodon concinnus	12.5	<1	20	<1	<1	<1	24	<1	?	<1	<1	<1	<1	20	33
Abietinella abietina	18.8	9	24	11	<1	<1	30	11	?	<1	<1	<1	<1	30	33
Enchylium tenax	7.8	<1	12	<1	<1	<1	15	<1	?	<1	<1	<1	<1	20	8
Cladonia convoluta	15.6	9	20	11	<1	<1	24	11	?	<1	<1	<1	<1	20	33
Thuidium assimile	6.3	<1	10	<1	<1	<1	12	<1	?	<1	<1	<1	<1	10	17
Cladonia cariosa	4.7	<1	7	6	<1	<1	9	<1	?	<1	<1	<1	<1	10	8
Assoc. 2.2.2 (4 taxa)															
Barbula unguiculata	6.3	<1	10	<1	<1	<1	12	<1	?	<1	<1	<1	<1	20	<1
Campyliadelphus chrysophyllus	20.3	13	24	17	<1	13	27	17	?	<1	<1	14	<1	40	8
Rhytidiadelphus squarrosus	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	10	<1
Thuidium delicatulum	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	10	<1
Assoc. 2.2.3 (23 taxa)															
Exsertotheca crispa	14.1	<1	22	<1	<1	<1	27	<1	?	<1	<1	<1	<1	15	50
Ptychostomum capillare aggr.	12.5	4	17	<1	20	<1	21	<1	?	20	<1	<1	<1	5	50
- Ptychostomum capillare	7.8	4	10	<1	20	<1	12	<1	?	20	<1	<1	<1	5	25
- Ptychostomum elegans	6.3	<1	10	<1	<1	<1	12	<1	?	<1	<1	<1	<1	<1	33
Tortella tortuosa	23.4	17	27	17	20	<1	33	17	?	20	<1	14	<1	20	58
Hypnum cupressiforme	28.1	17	34	17	20	13	39	17	?	20	<1	14	<1	30	58
Cetraria islandica	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	<1	17
Lophocolea heterophylla	3.1	<1	5	<1	<1	<1	6	<1	?	<1	<1	<1	<1	<1	17
Tortella inclinata	7.8	9	7	11	<1	<1	9	11	?	<1	<1	<1	<1	<1	25
Bryum argenteum	4.7	<1	7	<1	20	<1	9	<1	?	20	<1	<1	<1	5	17
[...]															
Other species (class character species and companion species)															
Ctenidium molluscum	43.8	35	49	44	<1	38	52	44	?	<1	100	29	<1	55	50
Homalothecium lutescens	42.2	35	46	44	<1	63	42	44	?	<1	100	57	<1	40	50
Syntrichia ruralis aggr.	12.5	13	12	11	20	<1	15	11	?	20	<1	<1	<1	5	33
[...]															

Figure 7. Dendogram of the modified TWINSPAN classification of the 339 relevés from *Festuco-Brometea* into two orders and four alliances.

bromoides and *Thymus vulgaris* subsp. *vulgaris* (Table 4). Only one association was recognised in this alliance and corresponded to *Thymelaeo-Aphyllanthetum monspeliensis,* as both the type relevé of the association (Braun-Blanquet 1966) and the type of the subassociation *brachypodietum retusi* (Berastegi et al. 2005) were placed in this group by the expert system. Inside the alliance 1.2 the relevés were split into two groups. The types of the associations *Jurineo-Festucetum hystricis* and *Helianthemo-Koelerietum vallesianae*, both described by Berastegi (2013), were classified to the groups 1.2.1 and 1.2.2. respectively. The diagnostic species for this alliance were *Asperula pyrenaica, Ononis striata, Plantago atrata* subsp. *discolor* and *Sedum album,* among others.

The NMDS analysis in Figure 8 shows a clear separation of this order 1 in the upper left part of the diagram. There is also a clear segregation of the alliances. Alliance 1.1 is associated with mediterraneity and high temperatures and alliance 1.2 with elevation and precipitation.

The order 2 was defined by *Briza media* subsp. *media, Cynosurus cristatus*, *Lotus corniculatus*, *Trifolium ochroleucon* and *T. pratense* subsp. *pratense,* as diagnostic species (Table 4). It was divided into two alliances. Alliance 2.1 grouped relevés that develop in more Mediterranean areas with lower mean annual precipitation and some of its diagnostic species were *Arrhenatherum elatius, Blackstonia perfoliata, Brachypodium phoenicoides, Centaurea jacea* and *Schedonorus arundinaceus* subsp. *fenax*. Relevés from more humid areas were classified in alliance 2.2, that presented *Achillea millefolium* subsp. *millefolium, Agrostis capillaris, Brachypodium rupestre* and *Festuca microphylla* among its diagnostic species. These two alliances are also clearly separated in the ordination diagram along the mediterraneity and precipitation gradients (Figure 8).

Inside the alliance 2.1 two groups were distinguished. Each one was related to one association previously described according to the analysis of their types: group 2.1.1 to the association *Prunello-Plantaginetum serpentinae* and group 2.1.2 to the association *Carduncello-Brachypodietum phoenicoidis.*

Finally, alliance 2.2 was split into three groups corresponding to the associations *Helictotricho-Seslerietum hispanicae, Calamintho-Seselietum montani* and *Carici-Teucrietum pyrenaici* according to the position of their type relevés. The latter is mainly distributed in the calcareous Cantabrian and Pyrenean mountains (Figure 9) and was

correlated with the highest elevations and annual precipitation values (Figure 8).

Site conditions and biodiversity of the different vegetation units

The alliance 1.2 is distributed in the highest elevations but also shows by far the highest values of southing; alliance 2.2 is also found in high elevations, and both share lower mediterraneity values compared to alliances 1.1 and 2.1; the two latter alliances show similar values of high temperature and low precipitation but 2.1 occurs in the most thermic and less rainy areas (Table 5, Figure 10). Differences are not so clear in the case of soil carbonate content, although alliance 1.1 shows the highest mean. Regarding structural parameters, the biggest differences amongst alliances are in their shrub layer cover, with highest values for alliance 1.1 (Table 5). At association level, Figure 11 shows that 2.2.3 is found at higher elevations than the other two associations within the alliance, reaching similar elevations as the two associations in alliance 1.2, and shows the lowest mediterraneity values. Association 2.1.2 is found at the lowest elevations and shows the highest mediterraneity, although the lowest precipitation corresponds to its sister association 2.1.1 (Table 6).

The total species richness is similar among the different alliances, as well as richness of vascular plants and lichens (Figure 12). On the contrary, alliance 2.2 outstands by its high bryophyte richness (Figure 12).
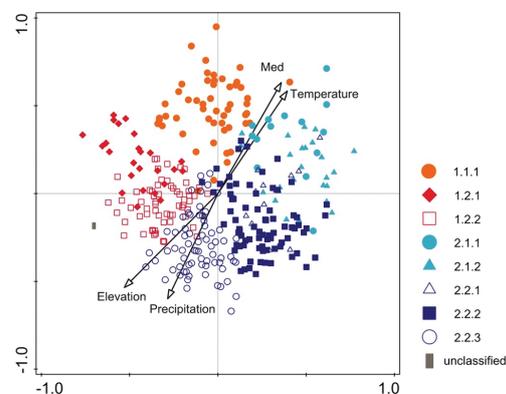
Figure 8. NMDS ordination of relevés from *Festuco-Brometea*. Eigenvalues: Axis 1 – 0.4308, Axis 2 – 0.3302, Axis 3 (not shown) – 0.2389. Med stands for Mediterraneity Index.
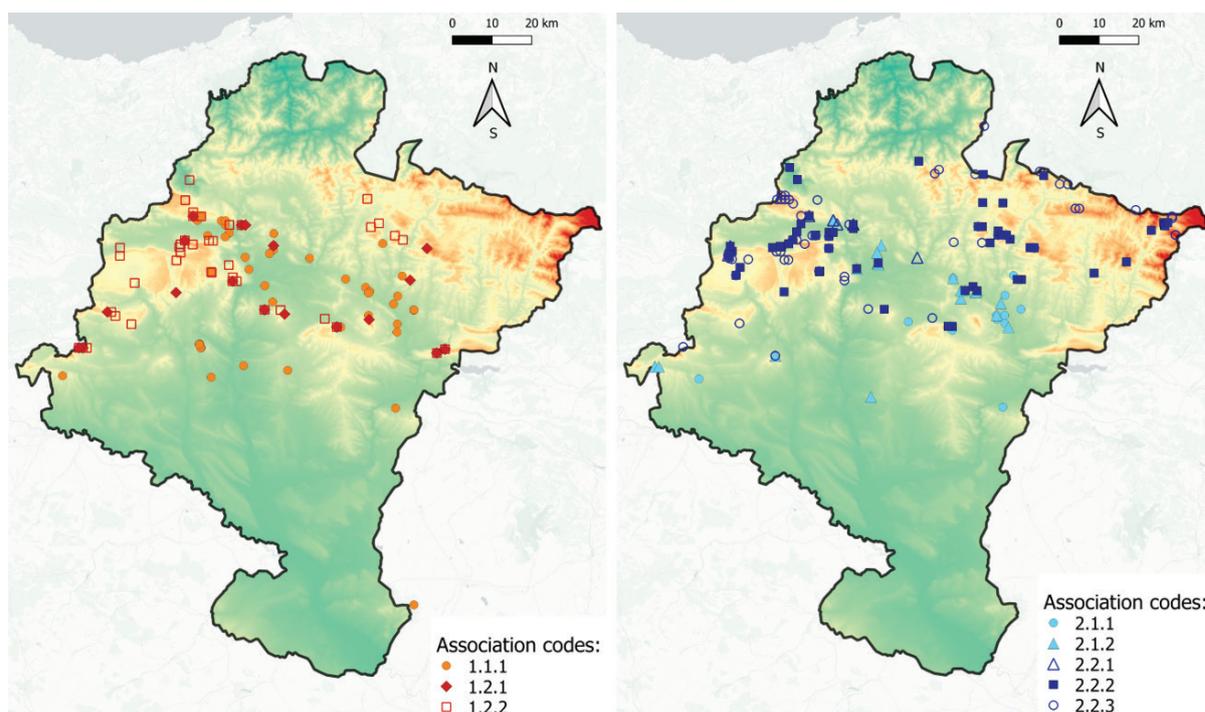
Figure 9. Location of the relevés from the class *Festuco-Brometea*: Order 1 (left) and Order 2 (right).

Table 5. Climatic structural, ecological and diversity characteristics of the orders and alliances within the *Festuco-Brometea*. The *p*-values and significance levels refer to ANOVAs.

Parameter	Alliances				*p*-value	Sig.
	1.1	1.2	2.1	2.2		
Total number of relevés	52	87	40	160		
Number of relevés from EDGG FW	18	5	8	33		
	Mean ± SD	Mean ± SD	Mean ± SD	Mean ± SD		
	Parameters calculated for all relevés					
Geographical and climatic parameters						
Elevation [m a.s.l.]	602±151	1030±215	561±139	912±273	<0.001	***
Mediterranity index	0.83±0.19	0.6±0.12	0.91±0.15	0.58±0.15	<0.001	***
Annual mean temperature [ºC]	11.9±1.0	9.9±1.0	12.1±0.7	10.0±1.5	<0.001	***
Mean annual precipitation [mm]	1025±205	1287±210	920±167	1346±27.0	<0.001	***
	Parameters calculated for relevés from EDGG Field Workshop					
Vegetation structure						
Cover vegetation total [%]	74±27	68±16	91±7	85±14	0.033	*
Cover shrub layer [%]	4±4	0±0	1±2	0±1	<0.001	***
Cover herb layer [%]	69±22	62±15	79±26	81±16	0.068	.
Cover cryptogam layer [%]	15±17	9±7	34±32	14±12	0.021	*
Cover litter [%]	11±13	3±4	26±27	5±7	0.001	**
Herb layer maximum height [cm]	77±32	38±15	86±33	58±27	0.005	**
Species richness						
Species richness (total)	48.2±10.1	50.6±1.5	55.3±17.9	59.8±15.4	0.041	*
Species richness (vascular plants)	42.9±8.9	46.0±3.8	50.6±16.8	50.5±12.2	0.151	n.s
Species richness (cryptogams)	5.3±2.7	4.6±2.6	4.6±3.0	9.4±5.7	0.004	**
Species richness (bryophytes)	4.7±2.4	3.4±2.1	4.5±2.9	8.0±4.8	0.007	**
Species richness (lichens)	0.6±0.8	1.2±0.8	0.1±0.4	1.4±1.5	0.029	*
Topography						
Southing (cosine of aspect)	-0.1±0.7	0.8±0.2	-0.5±0.6	-0.5±0.5	<0.001	***
Inclination [º]	19±11	14±5	11±7	16±15	0.563	n.s
Maximum microrelief [cm]	7±4	9±7	7±7	11±9	0.240	n.s
Soil parameters						
Soil depth mean [cm]	14±6	8±5	21±9	17±9	0.034	*
Soil depth CV	48±26	100±82	35±29	46±35	0.020	*
Cover rocks and stones [%]	6±11	9±13	1±4	8±16	0.600	n.s
Cover gravel [%]	10±21	15±17	0±0	3±10	0.112	n.s
Cover fine soil [%]	84±26	76±18	99±4	89±22	0.261	n.s
Coarse fragments [%]	17±15	30±25	30±19	22±16	0.278	n.s
Fine fragments < 2mm [%]	83±15	70±25	70±19	78±16	0.278	n.s
pH	7.65±0.37	7.31±0.86	7.32±0.36	7.52±0.38	0.229	n.s
Electrical conductivity [µS/cm]	188±60	213±141	225±103	261±80	0.031	*
CaCO3 [%]	42.9±9	27.3±23.2	17.9±11.6	19.5±19	<0.001	***
Organic matter [%]	0.8±0.3	1.8±1.5	1.3±0.4	1.6±0.8	0.001	**
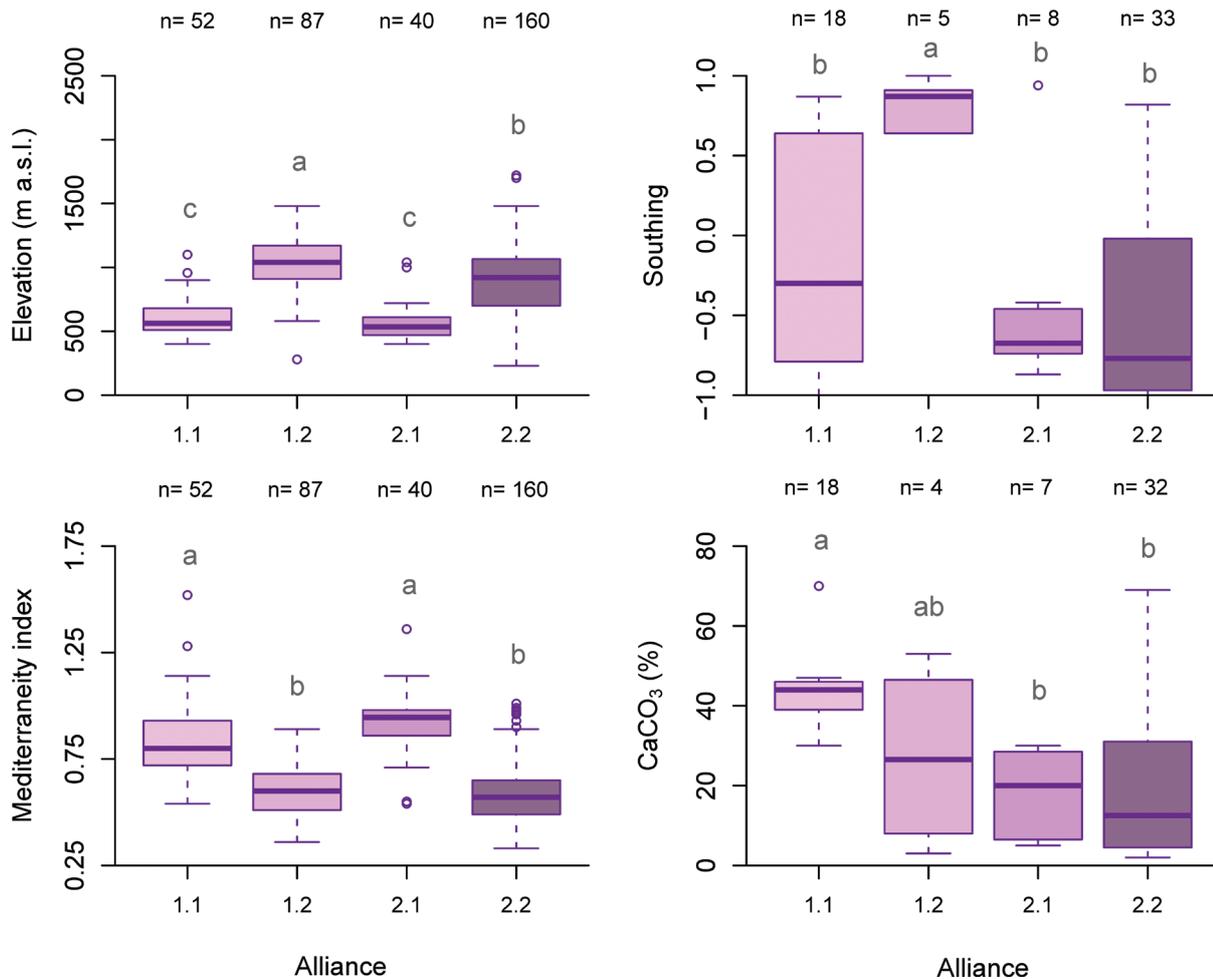
Figure 10. Comparison of four ecological variables among the four alliances. For elevation and Mediterraneity Index, all relevés were analysed, whereas for the rest of variables only relevés from EDGG Field Workshop were used. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

Table 6. Ecological characteristics of the associations within the *Festuco-Brometea*. The *p*-values and significance levels refer to ANOVAs.

Parameter	Association								*p*-values	Sig.
	1.1.1	1.2.1	1.2.2	2.1.1	2.1.2	2.2.1	2.2.2	2.2.3		
Total number of relevés	52	25	61	14	26	12	78	69		
Elevation [m a.s.l.]	602	1113	989	578	552	800	797	1060	<0.001	***
Mediterraneity index	0.83	0.61	0.59	0.89	0.91	0.57	0.64	0.51	<0.001	***
Annual mean temperature [°C]	11.8	9.8	9.9	12.1	12.1	10.5	10.5	9.4	<0.001	***
Mean annual precipitation [mm]	1025	1242	1302	905	928	1369	1258	1445	<0.001	***

Description of the *Festuco-Brometea* associations

Association 1.1.1 – *Thymelaeo ruizii-Aphyllanthetum monspeliensis*
(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 13)

Characterisation: Grasslands usually growing on the middle part of slopes, characterised by the dominance of *Brachypodium retusum* and *Bromopsis erecta* subsp. *erecta*. Typical Mediterranean grasses such as *Brachypodium retusum, B. phoenicoides, Dactylis glomerata* subsp. *hispanica, Festuca marginata* subsp. *andres-molinae* and *Helictochloa bromoides*, and chamaephytes as *Helianthemum apenni-*

num subsp. *apenninum, Lavandula latifolia* and *Thymus vulgaris* subsp. *vulgaris* are frequent in this association. In addition, typical species of submediterranean and temperate grasslands are also common: *Carex humilis, Koeleria vallesiana, Plantago lanceolata, Potentilla tabernaemontani, Sanguisorba minor*, and *Teucrium pyrenaicum*.

Ecology and distribution: These grasslands are typical of temperate submediterranean transitional areas, at elevations between 400 to 1,100 m a.s.l. The sampled stands are grazed or recently abandoned. They are distributed in the middle part of Navarre region, as serial stages of *Quercus faginea, Q. pubescens* and *Q. rotundifolia* forests, and main land use are the cereal crops. They are usually found in carbonate soils developed on marls, limestones, flysch,
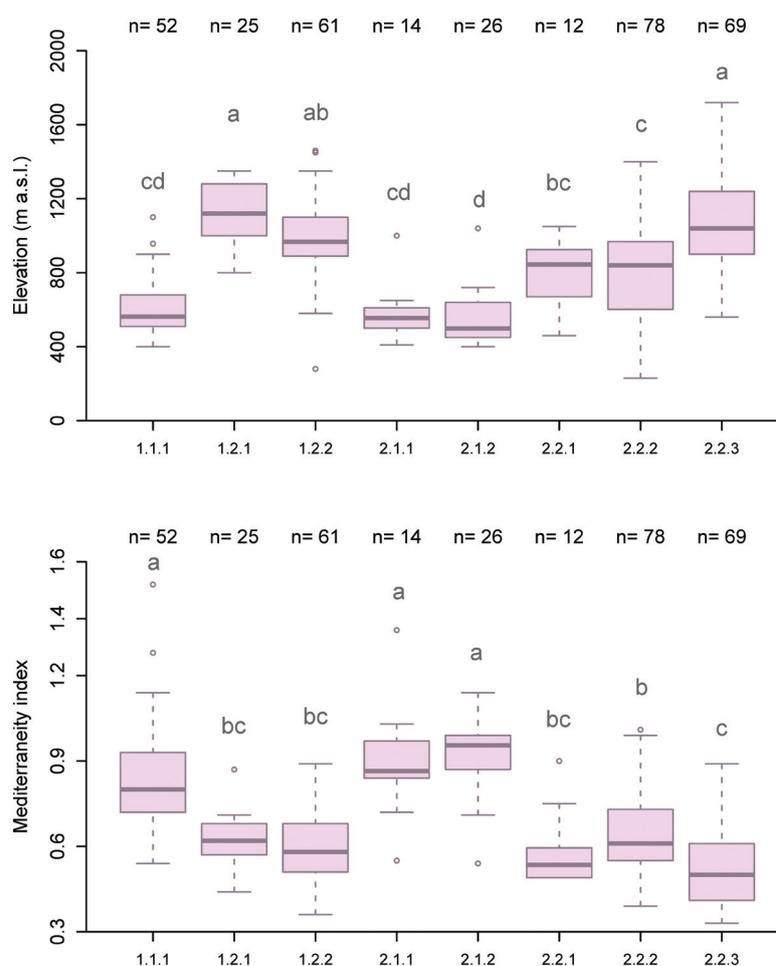
Figure 11. Comparison of elevation and Mediterraneity Index among the associations using all relevés from *Festu-co-Brometea*. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

conglomerates and sandstones, in the meso-supramed-iterranean and mesotemperate-supratemperate sub-humid to humid belts (Berastegi et al. 2005).

Syntaxonomy: This unit matches quite well with the association *Thymelaeo ruizii-Aphyllanthetum monspeliensis,* described from the submediterranean central areas in Navarre by Braun-Blanquet (1966) as a dwarf-shrub community. However, Berastegi (2013) did not sample communities of the typical stands rich in dwarf shrubs, and our dataset only includes relevés of the subassociation *brachypodietosum retusi*. Therefore, the identity of this unit is mostly based on this subassociation dominated by hard-leaved grasses (*Brachypodiun retusum, Helictochloa bromoides*) and other hemicryptophytes such as *Bromopsis erecta* subsp. *erecta, Carex flacca* subsp. *flacca, C. humilis, Helictochloa pratensis* subsp. *iberica* and *Sanguisorba minor* aggr. (Berastegi et al. 2005). Although the type relevé assigned by Braun-Blanquet was also placed by the expert system in the same cluster, we would like to acknowledge that it is only one relevé and thus that the identity of this unit with the whole *Thymelaeo-Aphyllanthetum* is only provisional. Chamaephyte-rich stands should be included in new analyses to draw a final conclusion.

Association 1.2.1 – *Jurineo humilis-Festucetum hystricis* (relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 13)

Characterisation: These grasslands grow on ridges and flat summit areas that are very windy, in mountain ranges usually above 900 m a.s.l. located in the transition between temperate and Mediterranean climates, in areas where cryoturbation phenomenon usually occurs. *Carex humilis, Helianthemum canum* subsp. *canum* and *Koeleria vallesiana* show a very high constancy in these open grasslands, but they are characterised by species like *Anthyllis montana, Arenaria grandiflora* subsp. *grandiflora, Festuca hystrix, Jurinea humilis* and *Klasea nudicaulis,* most of them typical of the high Mediterranean mountains.

Ecology and distribution: These communities can be found at elevations between 650 and 1,350 m a.s.l., although more commonly above 900 m, in the supramediterranean and supratemperate subhumid-humid belts (Berastegi 2013). They grow on different calcareous rocks such as limestones, calcarenites, marl limestones and conglomerates, on very windy ridges and flat summit areas. Due to the landforms and the elevation at which they are
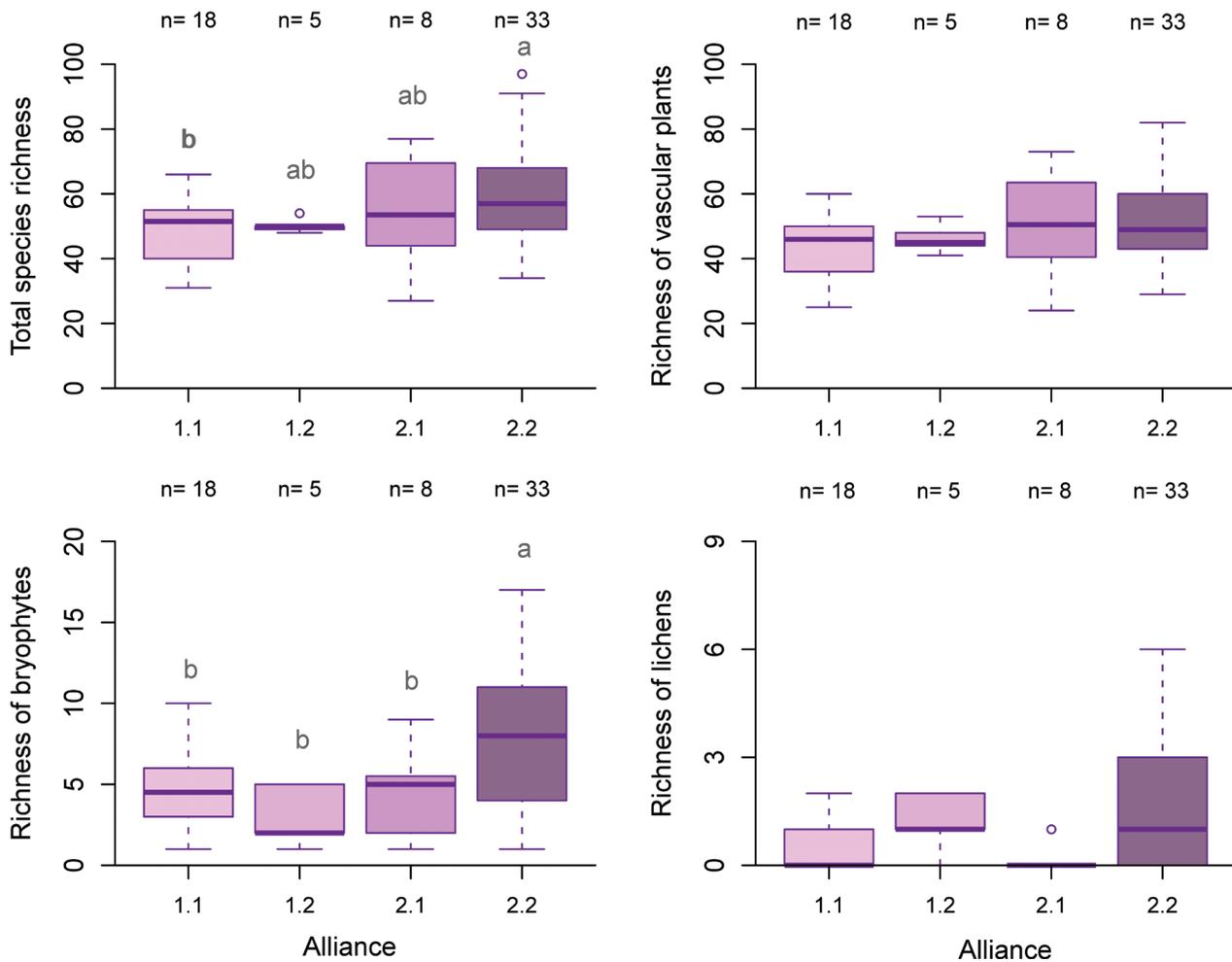
Figure 12. Comparison of species richness divided into four groups (total species, vascular plants, bryophytes and lichens) among the four alliances in *Festuco-Brometea* using the relevés from EDGG Field Workshop. Letters represent homogeneous groups (at α = 0.05) according to Tukey's post-hoc test following a significant ANOVA.

found, the soils are usually stony due to the disintegration processes of the parent rock. Although the ombrotype of this area, e.g., the humidity type, is subhumid to humid, water availability for plants is very low, due to the low water retention capacity of the soils. They are often permanent natural communities, but they may also represent an initial successional stage, colonizing eroded soils after the elimination of more mature stages of the vegetation series in which they are integrated: *Fagus sylvatica*, *Quercus pubescens* and *Q. rotundifolia* series.

Syntaxonomy: This unit fits quite well with the association *Jurineo humilis-Festucetum hystricis*. Berastegi (2013) included these rocky grasslands in the class *Festuco-Ononidetea*, order *Festuco-Poetalia ligulatae* and alliance *Plantagini-Thymion mastigophori*, due to their affinity to the communities of the associations *Koelerio vallesianae-Thymetum mastigophori* García-Mijangos et al. 1994 and *Festuco hystricis-Genistetum eliassennenii* García-Mijangos et al. 1994 from submediterranean territories west of Navarre, where they are widely represented in the landscape (Loidi et al. 1997). These communities reach the central-western area of Navarre, but in specific geographical and ecological conditions, interspersed among

other communities with which they share many species. For this reason, they do not achieve enough differential characteristics in the classification analysis to be considered in a different phytosociological class. It is therefore provisionally proposed that they should be included in the *Festuco-Brometea*, at least in Navarre context.

Association 1.2.2 – *Helianthemo incani-Koelerietum vallesianae*
(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 13)

Characterisation: These communities are dominated by dry grassland species such as *Carex humilis*, *Coronilla minima*, *Festuca rectifolia*, *Helianthemum canum* subsp. *canum*, *Helictochloa pratensis* subsp. *iberica*, *Koeleria vallesiana*, *Potentilla tabernaemontani,* or *Thymus praecox*. Typical species of meso-xeric grasslands such as *Bromopsis erecta* subsp. *erecta* or *Carthamus mitissimus* are also common. From a physiognomic point of view, they are characterised by being short grasslands, with a cover of around 70-90%, in which some creeping chamaephytes can be important.
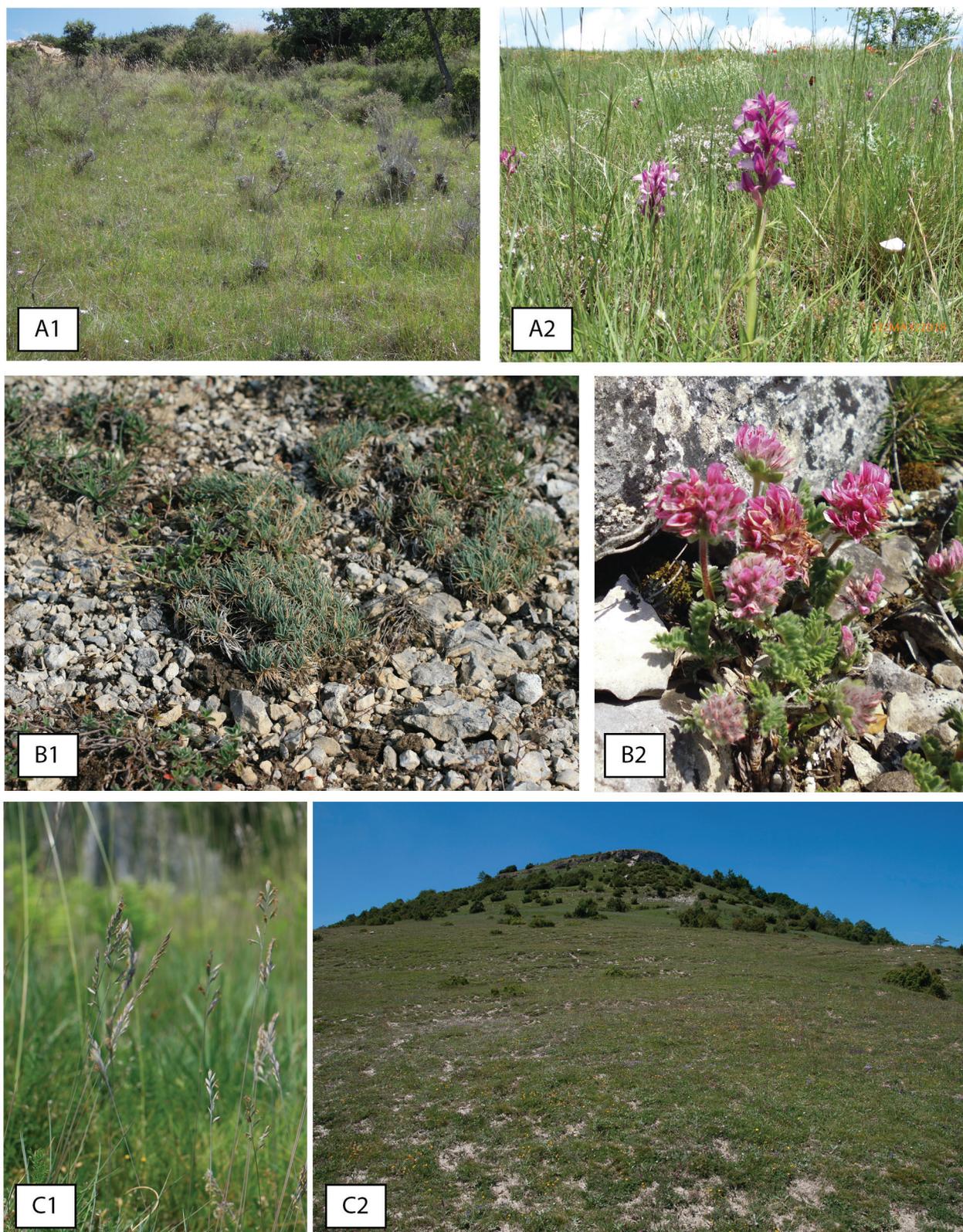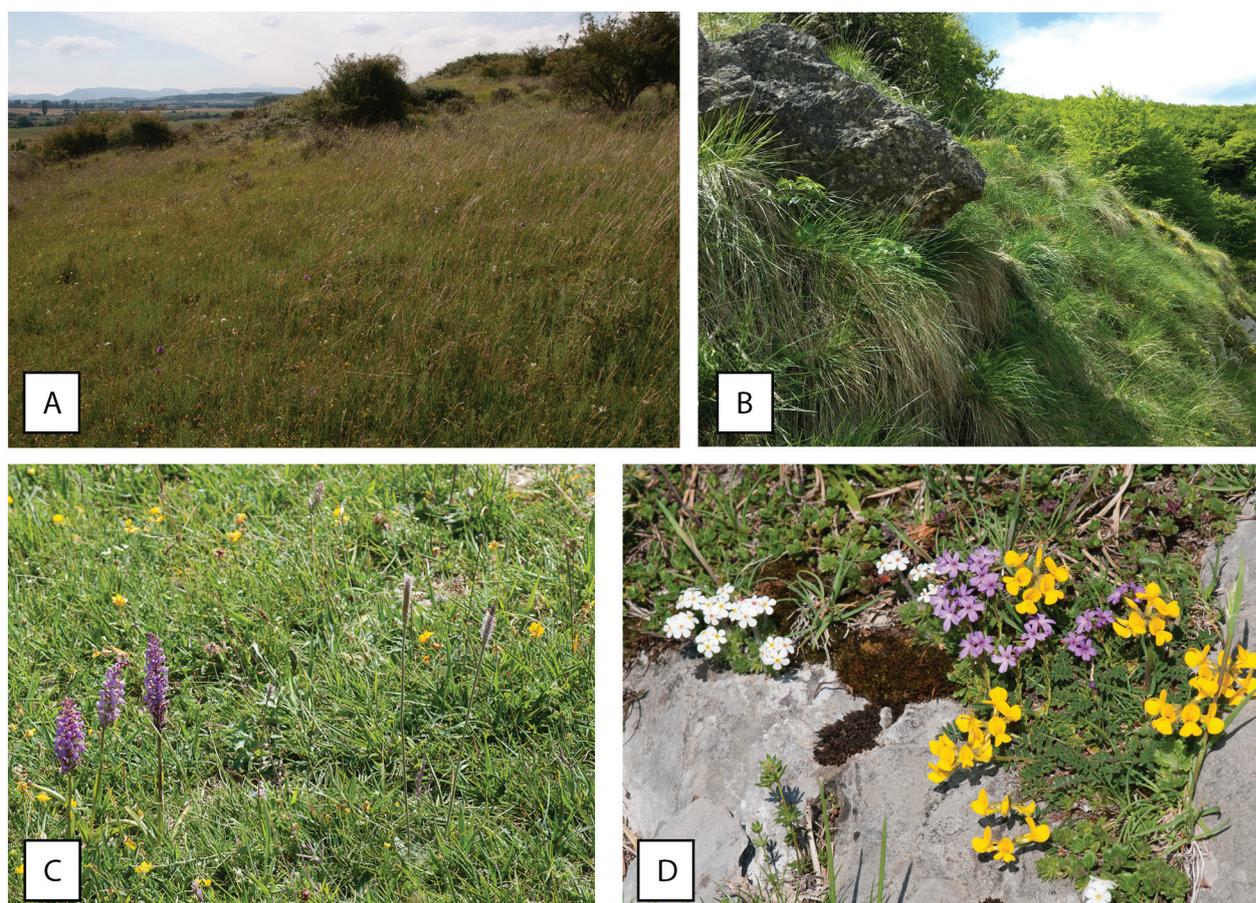
Figure 13. Photo plate showing typical stands of the associations included in order 1 of the *Festuco-Brometea*. A *Thymelaeo ruizii-Aphyllanthetum monspeliensis*, A1 Overview, A2 *Orchis papilionacea*, endangered in Navarre; B *Jurineo humilis-Festucetum hystricis*, B1 *Festuca hystrix*, B2 *Anthyllis montana*; C *Helianthemo incani-Koelerietum vallesianae*, C1 *Festuca rectifolia*, C2 overview. Photos: A. Berastegi (A2, B1, B2, C1); J. Dengler (A1, C2).

Ecology and distribution: The association represents pastures which are subject to intense livestock use, mainly by sheep, especially in the summer period. It occurs on different types of carbonate substrates (limestones, calcarenites, conglomerates, flysch), although mainly on limestone. They develop in the mountain ranges of the transition between the Atlantic and Mediterranean regions, also reaching the westernmost Pyrenean mountains, mostly in the montane belt.

Syntaxonomy: This unit matches well with the association *Helianthemo incani-Koelerietum vallesianae*, which was originally included in the class *Festuco-Ononidetea*, order *Ononidetalia striatae*, alliance *Genistion occidentalis* (Berastegi 2013), due to the floristic and ecological affinities to other rocky dry grasslands also included in this alliance. However, we would like to acknowledge that *Genistion occidentalis* originally included cushion shrub communities from Cantabrian mountains and Western Pyrenees (Díaz and Fernández-Prieto 1994), and only recently rocky dry grasslands from the Basque-Cantabrian mountains (*Helictotricho-Seslerietum hispanicae* and *Carici-Teucrietum pyrenaici*) were moved to this alliance and consequently to the class *Festuco-Ononidetea* (Rivas-Martínez 2011) from the class *Festuco-Brometea* where they had been previously placed (Rivas-Martínez et al. 1991a).

Association 2.1.1 – *Prunello hyssopifoliae-Plantaginetum serpentinae*
(relevès in Suppl. material 14; distribution in Figure 9)

Characterisation: These communities are characterised by species like *Festuca capillifolia*, *Jasonia tuberosa*, *Plantago maritima* subsp. *serpentina* or *Prunella hyssopifolia*. Other species with high frequency are *Blackstonia perfoliata*, *Carex flacca* subsp. *flacca*, *Centaurea jacea* or *Dorycnium pentaphyllum* subsp. *pentaphyllum*.

Ecology and distribution: They are typical of the submediterranean climate and can be found at elevations from 410 to 1,000 m a.s.l., in the colline and montane belts. These communities develop in micro-depressions in loamy or clayey soils, which, due to their impermeable nature, are subject to temporary waterlogging. During the rainy season, these areas can become flooded, while in periods of strong sunshine they dry out completely. They are relatively frequent in the areas of blue-grey loams in the central part of Navarre, as serial stages of *Quercus pubescens* and *Q. faginea* forests, and main land use are the cereal crops.

Syntaxonomy: This unit matches quite well with the *Prunello hyssopifoliae-Plantaginetum serpentinae* association, originally placed in the class *Molinio-Arrhenatheretea*, although as a quite deviant community from the alliance *Deschampsion mediae* that often occurs in mosaic with meso-xeric grasslands; thus, typical dry grassland species are common (Biurrun 1999; Berastegi 2013).

Association 2.1.2 – *Carduncello mitissimi-Brachypodietum phoenicoidis*
(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: Grasslands growing usually on the middle or bottom part of slopes, characterised by *Blackstonia perfoliata*, *Brachypodium phoenicoides* (including its hybrid with *B. rupestre*), *Bromopsis erecta* subsp. *erecta*, *Carex flacca* subsp. *flacca*, *Eryngium campestre* or *Phleum pratense*. Some other typical *Festuco-Brometea* species also occur: *Carthamus mitissimus*, *Centaurea jacea*, *Ranunculus bulbosus* subsp. *bulbosus* or *Trifolium ochroleucon*. Species of the class *Molinio-Arrhenatheretea* are also common, including *Lotus corniculatus*, *Plantago lanceolata*, *Trifolium campestre* and *T. pratense*.

Ecology and distribution: These dry grasslands are typical for the submediterranean climate type and can be found at elevations between 400 and 1,040 m a.s.l., in the supramediterranean and mesotemperate belts. They appear on clayey soils developed from calcareous materials (marl and limestone). They are distributed in the middle area of Navarre region, as serial stages of *Quercus pubescens* and *Q. faginea* forests, and main land use are the cereal crops. The sampled stands are grazed with low intensity or have been recently abandoned.

Syntaxonomy: This unit matches well with the association *Carduncello mitissimi-Brachypodietum phoenicoidis*, originally included in the order *Brachypodietalia phoenicoidis* (Berastegi 2013).

Association 2.2.1 – *Helictotricho cantabrici-Seslerietum hispanicae*
(relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: These communities, dominated by the grasses *Brachypodium rupestre*, *Helictotrichon cantabricum* or *Sesleria autumnalis*, develop on rocky, steep slopes on limestone, usually with large crevices. In addition to the abovementioned species, it is common to find species such as *Bromopsis erecta* subsp. *erecta*, *Carex flacca* subsp. *flacca*, *Dactylis glomerata*, *Galium pumilum*, *Teucrium pyrenaicum* or *Vincetoxicum hirundinaria* subsp. *intermedium*. Some scrub species such as *Dorycnium pentaphyllum* subsp. *pentaphyllum*, *Erica vagans* or *Genista hispanica* subsp. *occidentalis* are also present, sometimes with relevant cover.

Ecology and distribution: These rocky grasslands are typical for the temperate climate and can be found at elevations between 460 and 1,050 m a.s.l., in the colline and montane belts These communities develop mainly in the context of the series of *Quercus ilex*, *Fagus sylvatica* and *Quercus pubescens*. However, their main role is as a permanent natural community on steep calcareous slopes.

Syntaxonomy: This unit roughly matches with the association *Helictotricho cantabrici-Seslerietum hispani-*

Figure 14. Photo plate showing typical stands of the associations included in order 2 of the *Festuco-Brometea*. A *Carduncello mitissimi-Brachypodietum phoenicoidis*; B *Helictotricho cantabrici-Seslerietum hispanicae*; C *Calamintho acini-Seselietum montani*, D *Carici ornithopodae-Teucrietum pyrenaici*. Photos: J. Dengler (A, C, D); A. Berastegi (B).

cae described by Braun-Blanquet (1967) in more atlantic areas of nearby Basque Country. Originally placed in the *Potentillo-Brachypodion pinnati* (Braun-Blanquet 1967; Rivas-Martínez et al. 1991a), the Spanish checklist of phytosociological syntaxa (Rivas-Martínez 2011) included it in the alliance *Genistion occidentalis*, therefore in the class *Festuco-Ononidetea*, although, it has also been assigned to the alliance *Bromo erecti-Teucrion pyrenaici* Rivas-Mart. et al. 1997 (Loidi et al. 1997).

Association 2.2.2 – *Calamintho acini-Seselietum montani* (relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: Basophilous grasslands characterised by *Brachypodium rupestre*, *Briza media* subsp. *media*, *Bromopsis erecta* subsp. *erecta*, *Carex flacca* subsp. *flacca*, *Lotus corniculatus* or *Plantago media*. Some other taxa typical in these communities are *Carthamus mitissimus*, *Helictochloa pratensis* subsp. *iberica*, *Linum catharticum* subsp. *catharticum*, *Potentilla tabernaemontani*, *Ranunculus bulbosus* subsp. *bulbosus*, *Thymus praecox* and *Trifolium ochroleucon*. Species such as *Achillea millefolium* or *Trifolium pratense* are also common within the most mesic stands.

Ecology and distribution: These meso-xeric grasslands are typical for the temperate climate with submediterranean features and can be found at elevations between 230 and 1,400 m a.s.l., in the colline and montane belts. They develop on more or less deep soils, as serial stages of *Fagus sylvatica* and *Quercus pubescens* forests.

Syntaxonomy: This unit matches quite well with the association *Calamintho acini-Seselietum montani* described by Braun-Blanquet (1967) from temperate areas in Navarran inner valleys. In the Atlantic valleys in Navarre and nearby Basque Country it is replaced by the association *Seseli cantabrici-Brachypodietum rupestris* Br.-Bl. 1967 corr. Rivas-Mart. et al. 1984 (Rivas-Martínez et al. 1991a), linked to a more oceanic and humid climate. However, we could not reproduce this unit in our classification, as we had very sparse data from these Atlantic valleys.

Association 2.2.3 – *Carici ornithopodae-Teucrietum pyrenaici* (relevès in Suppl. material 14; distribution in Figure 9; photos in Figure 14)

Characterisation: These grasslands are characterised by species such as *Clinopodium alpinum* subsp. *pyrenaeum*, *Festuca rectifolia*, *Helictochloa pratensis* subsp. *iberica*, *Ses-*

eli montanum subsp. *montanum* or *Teucrium pyrenaicum*, and some orophilous plants such as *Poa alpina* and *Vicia pyrenaica*. Typical elements of *Festuco-Brometea* such as *Bromopsis erecta* subsp. *erecta*, *Carex caryophyllea*, *Helianthemum nummularium*, etc. also occur, as well as others of *Nardetea* and *Molinio-Arrhenatheretea* such as *Festuca microphylla*, *Lotus corniculatus* or *Plantago lanceolata*.

Ecology and distribution: They are typical for the temperate climate and can be found at elevations between 560 and 1,720 m a.s.l., mostly in the montane belt. They usually grow on shallow soils (rendzina) developed on limestones, in the beech forest belt, and main land use is summer grazing (transterminant herds).

Syntaxonomy: This unit roughly matches with the association *Carici ornithopodae-Teucrietum pyrenaici* described by Loidi (1983), although it also includes some relevés originally included in *Festucion scopariae* and an important number of relevés originally classified in *Helianthemo incani-Koelerietum vallesianae*. Originally placed in the alliance *Potentillo-Brachypodion pinnati* (Loidi 1983; Rivas-Martínez et al. 1991a), the Spanish checklist of phytosociological syntaxa (Rivas-Martínez 2011) included it in the alliance *Genistion occidentalis*, therefore in the class *Festuco-Ononidetea*, although it has also been assigned to the alliance *Bromo erecti-Teucrion pyrenaici* Rivas-Mart. et al. 1997 (Loidi et al. 1997).

Discussion

Delimitation of the grassland classes

Although our results largely concur with the previous classification of grasslands in Navarre (Berastegi 2013), our analyses suggest a different treatment of the classes *Festuco-Brometea*, *Festuco-Ononidetea* and *Ononido-Rosmarinetea* compared to the Iberian tradition (Rivas-Martínez et al. 1991b; Rivas-Martínez 2011). Dry and rocky grasslands and dwarf-shrub communities have been traditionally assigned to the class *Festuco-Ononidetea* and those scrublands with a more Mediterranean character to *Ononido-Rosmarinetea*. Nevertheless, we could not recognise any of these two classes in Navarre in the context of the grasslands. Rather, they would remain within the communities dominated by dwarf shrubs and chamaephytes, while the communities dominated by grasses would belong to *Festuco-Brometea* or *Elyno-Seslerietea*. This new arrangement would tally with the European perspective of placing rocky grasslands in *Festuco-Brometea* (Willner et al. 2017, 2019; Dengler et al. 2020b), although their distinction from the remaining units in the classes *Festuco-Ononidetea* and *Ononido-Rosmarinetea* mentioned above, is still to be clarified.

The class *Festuco-Ononidetea* was proposed by Rivas-Martínez et al. (1991b) to separate grasslands rich in tussock grasses and dwarf shrubs with submediterranean continental supra-oromediterranean distribution from the communities dominated by nanophanerophytes and

dwarf shrubs with broad Mediterranean distribution of the class *Rosmarinetea officinalis* Rivas-Mart. et al. 2002. The authors recognised two orders within the class, *Ononidetalia striatae* and *Festuco hystricis-Poetalia ligulatae*. Subsequently, Mucina et al. (2016) also included in *Festuco-Ononidetea* the order *Erysimo-Jurineetalia bocconei*, which includes submediterranean xeric calcicolous grasslands on skeletal soils of the Apennine Peninsula and the oromediterranean belt of Sicily. Nevertheless, the assignment of the orders *Ononidetalia* and *Erysimo-Jurineetalia* to the class *Festuco-Ononidetea* has been controversial (Bardat et al 2004; Biondi et al. 2014). In the Iberian Peninsula, the order *Ononidetalia striatae* has a Pyrenean and Cantabrian distribution, encompassing seven alliances that include a very heterogenous set of communities: dry grasslands, dwarf shrublands and cushions, occurring from the sea level to the subalpine belt (Rivas-Martínez 2011). According to our results, grasslands of *Ononidetalia* in Navarre should be included either in *Festuco-Brometea* or in *Elyno-Seslerietea*. The full set of communities of this order, including its type alliance *Ononidion striatae*, should be analysed together with dry grasslands in order to decide on its potential complete integration in *Festuco-Brometea*.

The class *Elyno-Seslerietea* gathers alpine and subalpine calcicolous swards of the nemoral mountain ranges of Europe. In Navarre, they belong to the Alpine-Pyrenean order *Seslerietalia caeruleae* and the alliance *Primulion intricatae* (Mucina et al. 2016). However, our analyses pose the question whether subalpine grasslands of *Festucion scopariae* should also be included in this class. Actually, this alliance had been originally included by Braun-Blanquet (1948) in *Elyno-Seslerietea*, but subsequently Rivas-Martínez et al. (1991b) transferred it to *Ononidetalia striatae*. Peyre and Font (2011) conducted a syntaxonomic revision by means of numerical analysis of the subalpine and alpine grasslands of the Pyrenees and Cantabrian Mountains and concluded that *Festucion scopariae* should be included in the order *Seslerietalia caeruleae*, even though it contains some thermophilous species. Our results also support the reclassification of *Festucion scopariae* into the class *Elyno-Seslerietea* as it presents a number of species of this class (*Euphrasia salisburgensis*, *Gentiana verna* subsp. *verna*, *Helictotrichon sedenense* subsp. *sedenense*, *Trifolium thalii*), which differentiates them from the rest of the *Festuco-Ononidetea* communities.

As regards the class *Carici-Kobresietea bellardii*, although our analysis included these communities in *Elyno-Seslerietea*, we kept it as a separate class, as it was only represented by two relevés in our dataset. Actually, these cryophytic alpine grasslands are very scarce in Navarre, so our geographic scope is not suitable to decide on the separation or grouping of both classes.

The class *Nardetea strictae* was defined as secondary oligotrophic grasslands and groups mesophilous or acidophilous, fairly grazed, tussock grasslands dominated by *Nardus stricta* from the montane to alpine belts with humid and hyper-humid ombroclimate (Rivas Goday

and Rivas-Martínez 1963). Our relevés were included by Berastegi (2013) in the alliances *Violion caninae* and *Carici macrostylidi-Nardion strictae* (sub suballiance *Carici-Nardenion strictae*), following the classification of Rivas-Martínez (2011). However, the *Carici macrostylidi-Nardion,* grouping mat-grass chionophilous swards at high elevations of the Pyrenees and the Cantabrian Mountains (Rivas-Martínez et al. 1984) was transferred by Mucina et al. (2016) to the class *Juncetea trifidi*, within the order *Festucetalia spadiceae*. This new classification is based on the differentiation of the secondary mat-grass swards growing at low and mid-elevations included within the class *Nardetea*, from the primary oligotrophic pastures/grasslands occurring at high elevations, placed within the *Juncetea trifidi* (Mucina et al. 2016). Further analyses supported the separation of high and mid-low elevation swards (Rodriguez-Rojo et al. 2020), although Gavilán et al. (2017) included *Nardus stricta* grasslands from high elevations in the Pyrenees in the *Festucion eskiae* alliance, not in *Carici macrostylidi-Nardion*. Our analyses do not support the separation of low and high elevation swards, as all relevés originally assigned to the alliances *Violion caninae* and *Carici macrostylidi-Nardion* were grouped in the same cluster. In Navarre, the class *Juncetea trifidi* according to Rivas-Martínez (2011, as *Caricetea curvulae*) is represented by the association *Carici pseudotristis-Festucetum eskiae*, within the alliance *Festucion eskiae*. These communities have a central Pyrenean distribution and only occasionally reach the highest siliceous peaks in Navarre (Lakora Mountain). The scarcity of data from this alliance does not allow us to establish a clear differentiation between the classes *Nardetea* and *Juncetea trifidi* in the territory, as only one relevé from *Juncetea trifidi* was available, which was of course included in *Nardetea*. A more in-depth study would be necessary to decide definitively in this respect, since the high presence of acidophilous species in the communities of *Violion caninae, Carici macrostylidi-Nardion* and *Festucion eskiae* (Berastegi 2013) determines their grouping compared to the rest of the grasslands and pastures analysed in the context of this study.

According to our results, the association *Merendero-Cynosuretum* should also be included in the class *Nardetea strictae*. This association was originally included in the alliance *Cynsurion cristati* of the *Molinio-Arrhenatheretea* class (Tüxen and Oberdorfer 1958), although the high constancy of *Nardus stricta* and *Danthonia decumbens* is noteworthy. These pastures originate from the oligotrophic grasslands after intense grazing (Berastegi 2013). The position of this association within *Nardetea* would be justified by the high presence of acidophilous species diagnostic of this group, such as *Festuca microphylla, Galium saxatile* and *Polygala serpyllifolia*. However, they are enriched by species of the alliance *Cynosurion* due to livestock pressure.

Our analysis included relevés previously classified in the alliance *Sedion pyrenaici* from the class *Sedo-Scleranthetea* in *Nardetea strictae*. However, we have to consider the reduced context of our study, so we kept this class as a separate unit. In Navarre, these communities shaped by

succulent species and dwarf chamaephytes growing on siliceous lithosols and rock surfaces (Rivas-Martínez et al. 2002) develop in montane and subalpine areas forming mosaics with grasslands of *Nardetea strictae*. Consequently, they share some acidophilous plants such as *Agrostis curtisii, Festuca microphylla* and *Galium saxatile*.

Molinio-Arrhenetheretea is the most diverse class in Navarre regarding the number of associations. Berastegi (2013) recognised twelve alliances grouped within four orders. Although some associations were not well represented in our data, especially the most hygrophilous ones, the TWINSPAN analysis did reproduce a structure with three branches interpreted as corresponding to the orders *Arrhenatheretalia elatioris, Molinietalia caeruleae* and *Holoschoenetalia*. The only changes regarding this class are the new positions of the associations *Merendero-Cynosuretum* (*Cynosurion, Arrhenatheretalia*) and *Prunello-Plantaginetum serpentinae* (*Deschampsion mediae, Holoschoenetalia*). We suggest moving the former to the class *Nardetea strictae*, as explained above, while the latter should be placed in *Festuco-Brometea*, as has been also explained in the results section.

The class *Lygeo-Stipetea* gathers Mediterranean pseudo-steppes on calcareous substrates and relict Mediterranean steppes on deep clayey soils (Mucina et al. 2016). In Navarre this class encompasses communities dominated by *Lygeum spartum* on the one hand and *Brachypodium retusum* grasslands on the other (Berastegi 2013). The former develops on the bottom of slopes receiving regular downslope input of fine materials (silt, clay) and can tolerate short periods of hydromorphy. *Lygeum spartum* communities are characterised by the co-occurrence of many annual species (*Asterolinon linum-stellatum, Filago pyramidata, Linum strictum, Trachynia distachya*) (Marcenò et al. 2019). However, the delimitation of *Brachypodium retusum* grasslands is another unresolved syntaxonomic issue (Apostolova et al. 2014). Two associations belonging to two different classes are recognised in the territory (Berastegi 2013), which is also reflected in our results. Within *Lygeo-Stipetea*, the association *Ruto angustifolio-Brachypodietum retusi* groups the typically Mediterranean grasslands of the Ebro valley (Braun-Blanquet and Bolòs 1958). The other syntaxon including grasslands rich in *Brachypodium retusum* is *Thymelaeo-Aphyllanthetum brachypodietosum retusi,* which was classified in *Festuco-Brometea* and is thus discussed in the next section.

Our analyses placed relevés of the classes *Poetea bulbosae* and *Stipo-Trachynietea distachyae* in *Lygeo-Stipetea*. However, our dataset contained only a small number of relevés from these classes and thus we cannot make any decision about the grouping of these classes within *Lygeo-Stipetea*. Therefore, we kept both classes as independent units.

Subdivision of the *Festuco-Brometea*

In Navarre, the class *Festuco-Brometea* is composed of dry grasslands dominated by hemicryptophytes that develop

on non-hygromorphic soils in temperate and submediterranean climates (Berastegi 2013). According to our results, the class *Festuco-Brometea* in Navarre includes, besides the associations previously assigned to this class (*Calamintho-Seselietum montani* and *Carduncello-Brachypodietum phoenicoidis*), several associations that had been included in the class *Festuco-Ononidetea striatae* (Rivas-Martínez 2011; Berastegi 2013): *Carici-Teucrietum pyrenaici*, *Helianthemo-Koelerietum vallesianae* and *Helictotricho-Seslerietum hispanicae* from the order *Ononidetalia striatae,* and *Jurineo-Festucetum hystricis* from the order *Festuco-Poetalia ligulatae.* Additionally, the association *Thymelaeo-Aphyllanthetum monspeliensis,* classified in *Ononido-Rosmarinetea* by the Spanish checklist (Rivas-Martínez 2011) has also been included in *Festuco-Brometea*, as well as the association *Prunello-Plantaginetum serpentinae*, previously classified in *Molinio-Arrhenatheretea* (Rivas-Martínez 2011)

The numerical analysis clearly separates two groups that can be interpreted as two orders. Order 1 groups the more xerophytic relevès with Mediterranean influence which occupy an intermediate position between the orders *Brachypodietalia pinnati* and the more Mediterranean communities of *Festuco-Ononidetea* and *Ononido-Rosmarinetea*. This order would be a vicariant of *Astragalo-Potentilletalia* and *Stipo-Festucetalia pallentis* from central-southern Europe (Aćić et al. 2015).

Communities in this order 1 are included in two alliances. Alliance 1 includes the association *Thymelaeo-Aphyllanthetum monspeliensis,* originally included in the alliance *Helianthemo italici-Aphyllanthion monspeliensis* (class *Ononido-Rosmarinetea*) by Braun-Blanquet (1966). Subsequently most Spanish phytosociologists have also placed it there, including the Spanish checklist (Rivas-Martínez 2011), where it sits well due to the high cover of dwarf shrubs in the typical subassociation. A new comprehensive analysis including all basophilous grasslands and dwarf-shrublands from Mediterranean and submediterranean areas in Europe would help us decide not only on the syntaxonomic position of *Thymelaeo-Aphyllanthetum*, but also on the position of the alliance *Helianthemo-Aphyllanthion*. Consequently, we put forward the question whether a new alliance and order should be proposed for these grasslands rich in dwarf shrubs which would be transitional to *Lygeo-Stipetea* and *Ononido-Rosmarinetea.*

Alliance 2 in this order 1 includes two associations that were previously classified in two different orders of the class *Festuco-Ononidetea*: *Jurineo humilis-Festucetum hystricis* in the order *Festuco-Poetalia ligulatae* and *Helianthemo incani-Koelerietum vallesianae* in the order *Ononidetalia striatae* (Berastegi 2013). These communities contain a number of species diagnostic for perennial rocky calcareous grasslands of subatlantic-submediterranean Europe belonging to the *Xerobromion,* the *Festuco-Bromion* or the *Artemisio-Dichantion* (Chytrý et al. 2020), which justifies their inclusion within *Festuco-Brometea.* The identity of this alliance also remains unresolved un-til a comprehensive analysis including all basophilous grasslands and dwarf-shrublands in southern Europe is conducted.

Order 2 is related to *Brachypodietalia pinnati* and includes grasslands that usually develop in areas with a temperate climate, in well-constituted soils with relatively good water retention capacity and normally high total vegetation cover. *Calamintho-Seselietum* represents one of the typical associations of this order. This order also includes grasslands growing in rocky steep slopes from areas of high rainfall (*Helictotricho-Seslerietum hispanicae* and *Carici-Teucrietum pyrenaici*), as well as dry grasslands from submediterranean areas, but the latter ones are restricted to soils or topographic situations that allow relatively good water retention (*Prunello-Plantaginetum serpentinae* and *Carduncello-Brachypodietum phoenicoidis*).

Rocky grasslands from this order 2 (*Helictotricho-Seslerietum hispanicae* and *Carici-Teucrietum pyrenaici*) are included in *Ononidetalia striatae* in the Spanish checklist, but our analysis has shown that they have a strong floristic relationship with grasslands of *Brachypodietalia pinnati.* In fact, both associations were originally included in this order (Braun-Blanquet 1967; Loidi 1983).

Alliance 2.1, which includes the associations *Prunello-Plantaginetum serpentinae* and *Carduncello-Brachypodietum phoenicoidis* in Navarre, could be assigned to the alliance *Brachypodion phoenicoidis*. More comprehensive analyses would be needed to confirm, as this alliance is distributed along the Western Mediterranean region, and its type association *Brachypodietum phoenicoidis* Br.-Bl. 1924 was described in Mediterranean France (Rivas-Martínez 2011).

Proposed syntaxonomic scheme for the class *Festuco-Brometea* in Navarre

Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Klika et Hadač 1944
    Order 1: ???
      Alliance 1.1: ???
        1.1.1: *Thymelaeo ruizii-Aphyllanthetum monspeliensis* Br.-Bl. et P. Montserrat in Br.-Bl. 1966
      Alliance 1.2: ???
        1.2.1: *Jurineo humilis-Festucetum hystricis* Peralta et al. in Berastegi 2013
        1.2.2: *Helianthemo incani-Koelerietum vallesianae* Berastegi et al. in Berastegi 2013
    Order 2: *Brachypodietalia pinnati* Korneck 1974 nom. cons. propos. (= *Brometalia erecti* Koch 1926)
    Nomenclatural remark: Dengler et al. (2003) proposed to reject the name *Brometalia erecti* Koch 1926 as nomen ambiguum, and Kuzemko et al. (2014) proposed to conserve the name *Brachypodietalia pinnati* Korneck 1974. This proposal was also adopted by Mucina et al. (2016), but no formal proposal has been submitted so far.

Alliance 2.1: ???
  2.1.1: *Prunello hyssopifoliae-Plantaginetum serpentinae* F. Prieto et al. ex Biurrun 1999
  2.1.2: *Carduncello mitissimi-Brachypodietum phoenicoidis* García-Mijangos et al. in Berastegi 2013
Alliance 2.2: *Potentillo montanae-Brachypodion pinnati* Br.-Bl. 1967
  2.2.1: *Helictotricho cantabrici-Seslerietum hispanicae* Br.-Bl. 1967
  2.2.2: *Calamintho acini-Seselietum montani* Br.-Bl. 1967
  2.2.3: *Carici ornithopodae-Teucrietum pyrenaici* Loidi 1983

Biodiversity

Grasslands of *Festuco-Brometea* showed the highest total species richness, and specifically meso-xeric grasslands of the association *Calamintho-Seselietum montani*, which have previously been highlighted as species rich grasslands (Dengler et al. 2016b; Boch et al. 2020). However, differences with mesic grasslands are not significant. In fact, only bryophyte richness is significantly higher in *Festuco-Brometea* than in *Molinio-Arrhenatheretea* in the Navarran context. This may be due to the continued agricultural extensive management of these secondary mesic grasslands, at least in part of the region, as it has been demonstrated that intensively managed grasslands tend to be species poor (Hilpold et al. 2018). In any case, the high bryophyte richness of *Festuco-Brometea* grasslands is comparable to that of alpine grasslands of *Elyno-Seslerietea*, which is the richest vegetation type when both bryophytes and lichens are considered. This significant cryptogam-richness of alpine grasslands was already shown by Dengler et al. (2020c) and has recently been evidenced using a very large dataset by Biurrun et al. (2021). We would also like to highlight the high lichen richness in the Mediterranean grasslands of *Lygeo-Stipetea*, which is comparable in this respect to *Elyno-Seslerietea*. Our results show that these Mediterranean grasslands, although being quite species-poor regarding total species richness and richness of vascular plants, host a high proportion of bryophytes and especially lichens, which was already observed by Biurrun et al. (2021).

Relevance of bryophytes and lichens

Up to now vegetation ecologists in the Southern European countries, and particularly in the Mediterranean region, rarely considered bryophytes and lichens as part of the vegetation - unlike many of their colleagues in temperate and boreal Europe. This is reflected by the fact that for example, Rivas-Martínez et al. (2002) in their overview of the syntaxa of the Iberian Peninsula did not list any non-vascular plant species (apart from

few *Characeae* spp. and *Sphagnum* spp.) as diagnostic for any of the hundreds of syntaxa of the region. Also, Mucina et al. (2016), while listing some bryophytes and lichens as diagnostic for temperate and boreal classes, do not mention any for the Mediterranean classes. Even Dierßen (2001), who characterised the phytosociological prevalences of all European bryophyte species, systematically under-reported their presence in Mediterranean classes. As already highlighted by Guarino et al. (2012) in the report from the EDGG Field Workshop in Sicily, the non-vascular flora of Mediterranean grasslands can be quite rich. In fact, while amongst all grasslands of Navarre, those of the Mediterranean class *Lygeo-Stipetea* were poorest in vascular plants, they hosted the highest lichen diversity together with the *Elyno-Seslerietea*. We also found that bryophytes and lichens are not randomly distributed across communities but have clear and often narrow prevalences which makes them equally effective diagnostic species as many vascular plants. All this calls for a better consideration of non-vascular plants in syntaxonomic studies in South European countries.

Conclusions and outlook

The combination of numerical methods allows a standardisation of the classification of grassland types. In fact, with our expert system we could largely reproduce the associations previously recognised in the region. Moreover, some often "diagnostic" species mentioned in the literature could be confirmed by our numerical analyses of a large dataset, while others were not supported by the data. However, at the class level, we found significant deviations from the Iberian syntaxonomic tradition (Rivas-Martínez et al. 2002; Rivas-Martínez 2011) and we propose a new system that matches the Iberian data more appropriately, and is consistent with the European concept of the class *Festuco-Brometea*. In any case, questions still remain regarding classification at order and alliance level, which can only be solved by means of a comprehensive analysis of all basophilous grasslands and dwarf-shrub communities in southern Europe. This analysis will also allow for the delimitation of the controversial class *Festuco-Ononidetea*.

Our study provides, for the first time, an electronic expert system for the grasslands of Navarre, which allows a standardised assignment of any new relevé, thus is of enormous value, particularly for practitioners. We provide, also for the first time, a detailed databased characterisation and comparison of the syntaxa in terms of their environmental conditions and biodiversity. We were also able to show that bryophytes and lichens, contrary to past assumptions, are core elements of these grasslands and in particular, the Mediterranean ones of *Lygeo-Stipetea*, both in terms of biodiversity and of diagnostic species. Therefore, they should also be taken into account in Mediterranean phytosociology.

Once the main five phytosociological classes were differentiated, our study focused on the analysis of the *Festuco-Brometea*. Therefore, an in-depth analysis based on expert systems of the rest of the classes would be desirable. Moreover, classes whose status could not be resolved due to a small/marginal dataset or due to plot sizes being too small, should be specifically addressed in future studies with better/more data from a larger area.

Finally, it can be emphasised that we have provided important insights from the western part of Europe that complement the extensive studies of Willner et al. (2017, 2019) from Central and Eastern Europe. Thus, we have taken a new step on the pan-European classification of the *Festuco-Brometea*. With this aim, we acknowledge that these comprehensive analyses would be facilitated if the hierarchical expert system and hierarchical determination of diagnostic species could be directly implemented in JUICE.

Data availability

The vegetation-plot data underlying this study are stored and available in the GrassPlot database (https://edgg.org/databases/GrassPlot; dataset code ES_A; Dengler et al. 2018a, Biurrun et al. 2019), from which they can be requested according to the GrassPlot Bylaws, and in the Vegetation-Plot Database of the University of the Basque Country (BIOVEG) (Biurrun et al. 2012), which is available in the European Vegetation Archive (Chytrý et al. 2016) and the Global Vegetation Database sPlot (Bruelheide et al. 2019) as dataset EU-00-011.

Author contributions

I.G.M, I.B. and A.B. organized the 7th EDGG Field Workshop in Navarre (Spain); as EDGG Field Workshop Coordinator during the Field Workshop, J.D. ensured consistent application of the EDGG methodology, I.G.M. identified the vascular plant species collected during the Field Workshop, J.E. identified the lichens, R.N. identified the bryophytes and added ecological aspects, and O.Y. analysed the soil samples and described methodological aspects; A.B. compiled 839 relevés used in the paper from 1996 to 1999; I.G.M. together with J.D. developed the numerical classification, implemented the expert system and identified the diagnostic species with the collaboration of I.B., A.B., A.K., M.J., and D.V.; M.J. developed the NMDS ordination, I.D. and D.V. analysed differences between syntaxa by means of ANOVAs and J.D. calculated and analysed biodiversity patterns; I.G.M. led the writing of the manuscript with substantial inputs from A.B., I.B. and J.D.; all authors critically revised the manuscript.

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References

Aćić S, Šilć U, Petrović M, Tomović G, Stevanović ZD (2015) Classification, ecology and biodiversity of Central Balkan dry grasslands. Tuexenia 35: 329–353.

Apostolova I, Dengler J, Di Pietro R, Gavilan RG, Tsiripidis I (2014) Dry grasslands of Southern Europe: Syntaxonomy, management and conservation. Hacquetia 13: 5–18. https://doi.org/10.2478/hacq-2014-0015

Bardat J, Bioret F, Botineau M, Boullet V, Delpech R, Géhu J-M, Haury J, Lacoste A, Rameau J-C, ... Touffet J (2004) Prodrome des végétations de France. Patrimoines naturels 61: 1–171.

Bengtsson J, Bullock JM, Egoh B, Everson C, Everson T, O'Connor T, O'Farrell PJ, Smith HG, Lindborg R (2019) Grasslands — more important for ecosystem services than you might think. Ecosphere 10: e02582. https://doi.org/10.1002/ecs2.2582

Berastegi A (2013) Pastizales y prados en Navarra: descripción, tipificación y ecología. Guineana 19: 1–510.

Berastegi A, Peralta J, Loidi J (2005) La transición entre los pastizales mesoxerófilos templados y los mediterráneos en las montañas cantábricas y prepirenaicas (Navarra, NE de la Península Ibérica). Bulletin de la Société d'Histoire Naturelle de Toulouse 141: 91–95.

Berastegi A, Biurrun I, Campos JA, García-Mijangos I, Herrera M, Loidi J (2010) La alianza *Sedion pyrenaici* Tüxen ex Rivas-Martínez et al. 1994 en el norte de Navarra (España). Braun-Blanquetia 46: 107–110.

Biondi E, Blasi C, Allegrezza, M, Anzellotti I, Azzella MM, Carli E, Casavechia S, Copiz R, Del Vico E, ... Zivrovic L (2014) Plant communities of Italy: The vegetation Prodrome. Plant Biosystems 148: 728–814. https://doi.org/10.1080/11263504.2014.948527

Biurrun I (1999) Flora y vegetación de los ríos y humedales de Navarra. Guineana 5: 1-338.

Biurrun I, García-Mijangos I, Campos JA, Herrera M, Loidi J (2012) Vegetation-plot database of the University of the Basque Country (BIOVEG). Biodiversity & Ecology 4: 328–328. https://doi.org/10.7809/b-e.00121

Biurrun I, García-Mijangos I, Berastegi A, Ambarli D, Filibeck G, Jandt U, Janišová M, Jaunatre R, Kącki Z, ... Dengler J (2014) Diversity of dry grasslands in Navarre (Spain). Bulletin of the Eurasian Dry Grassland Group 25: 15–24.

Biurrun I, Burrascano S, Dembicz I, Guarino R, Kapfer J, Pielech R, García-Mijangos I, Wagner V, Palpurina S, ... Dengler J (2019) GrassPlot v. 2.00 – first update on the database of multi-scale plant diversity in Palaearctic grasslands. Palaearctic Grasslands 44: 26–47.

Biurrun I, Pielech R, Dembicz I, Gillet F, Kozub Ł, Marcenò C, Reitalu T, Van Meerbeek K, Guarino R, ... Dengler J (2021) Benchmarking plant diversity of Palaearctic grasslands and other open habitats. Journal of Vegetation Science 32: e13050. https://doi.org/10.1111/jvs.13050

Boch S, Biurrun I, Rodwell J (2020) Grasslands of Western Europe. In: Goldstein MI, DellaSala DA, DiPaolo DA (Eds) Encyclopedia of the world's biomes. Volume 3: Forests – trees of life. Grasslands and shrublands – sea of plants. Elsevier, Amsterdam, NL, 678–688. https://doi.org/10.1016/B978-0-12-409548-9.12095-0

Braun-Blanquet J (1932) Plant sociology. The study of plant communities. McGraw-Hill, New York, US, 439 pp.

Braun-Blanquet J (1948) La végétation alpine des Pyrénées orientales. Étude the phytosociologie comparée. Consejo Superior de Investigaciones Científicas, Barcelona, ES, 306 pp.

Braun-Blanquet J (1967) Vegetationsskizzen aus dem Baskenland mit Ausblicken auf das weitere Ibero-Atlantikum. II. Teil. Vegetatio 14: 1–126. https://doi.org/10.1007/BF02639845

Braun-Blanquet J, Bolòs O (1958) Les groupements végétaux du bassin moyen de l'Ebre et leur dynamisme. Anales Estación Experimental Aula Dei 5: 1–266. https://doi.org/10.1111/jvs.12710

Bruelheide H, Dengler J, Jiménez-Alfaro B, Purschke O, Hennekens SM, Chytrý M, Pillar VD, Jansen F, Kattge J, ... Zverev A (2019) sPlot – A new tool for global vegetation analyses. Journal of Vegetation Science 30: 161–186. https://doi.org/10.1111/jvs.12710

Cancellieri L, Rosatti L, Brunetti M, Mancini LD, Primi R, Ronchi B, Scoppola A, Filibeck G (2020) The dry grasslands of Abruzzo National Park, the oldest protected area in the Apennines (Central Italy): overview of vegetation composition, syntaxonomy, ecology and diversity. Tuexenia 40: 547–571.

Chytrý M, Tichý L, Holt J, Botta-Dukát Z (2002) Determination of diagnostic species with statistical fidelity measures. Journal of Vegetation Science 13: 79–90. https://doi.org/10.1111/j.1654-1103.2002.tb02025.x

Chytrý M, Hennekens SM, Jiménez-Alfaro B, Knollová I, Dengler J, Jansen F, Landucci F, Schaminée JHJ, Aćić S, ... Yamalov S (2016) European Vegetation Archive (EVA): an integrated database of European vegetation plots. Applied Vegetation Science 19: 173–180. https://doi.org/10.1111/avsc.12191

Chytrý M, Tichý L, Hennekens SM, Knollová I, Janssen JAM, Rodwell JS, Peterka T, Marcenò C, Landucci F, ... Schaminée JHJ (2020) EUNIS Habitat Classification: Expert system, characteristic species combinations and distribution maps of European habitats. Journal of Vegetation Science 23: 648–675. https://doi.org/10.1111/avsc.12519

Darquistade A, Berastegi A, Campos JA, Loidi J (2004) Pastizales supratemplados Cántabro-Euskaldunes de *Agrostis curtisii*: caracterización y encuadre fitosociológico. Silva Lusitana 12: 135–149.

Del Valle Lersundi J, García de Domingo A, Díaz de Neira A, Salvany JM, Cabra P, Ramírez, J (1997) Mapa geológico de Navarra. Escala 1:200.000. Government of Navarra, Pamplona-Iruña, ES.

Dengler J (2003) Entwicklung und Bewertung neuer Ansätze in der Pflanzensoziologie unter besonderer Berücksichtigung der Vegetationsklassifikation. Archiv naturwissenschaftlicher Dissertationen 14: 1–297.

Dengler J, Tischew S (2018) Grasslands of Western and Northern Europe – between intensification and abandonment. In: Squires VR, Dengler J, Feng H, Hua L (Eds) Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton, US, 27–63.

Dengler J, Berg C, Eisenberg M, Isermann M, Jansen F, Koska I, Löbel S, Manthey M, Päzolt J, ... Wollert H (2003) New descriptions and typifications of syntaxa within the project 'Plantcommunities of Mecklenburg-Vorpommern and their vulnerability'. Part I. Feddes Repertorium 114: 587–631. https://doi.org/10.1002/fedr.200311017

Dengler J, Berg C, Jansen F (2005) New ideas for modern phytosociological monographs. Annali di Botanica Nuova Serie 5: 193–210.

Dengler J, Chytrý M, Ewald J (2008) Phytosociology. In: Jörgensen SE, Fath BD (Eds) Encyclopedia of ecology. Elsevier, Amsterdam, NL, 2767–2779. https://doi.org/10.1016/B978-008045405-4.00533-4

Dengler J, Löbel S, Dolnik C (2009) Species constancy depends on plot size – a problem for vegetation classification and how it can be solved. Journal of Vegetation Science 20: 754–766. https://doi.org/10.1111/j.1654-1103.2009.01073.x

Dengler J, Boch S, Filibeck G, Chiarucci A, Dembicz I, Guarino R, Henneberg B, Janišová M, Marcenò C, ... Biurrun I (2016a) Assessing plant diversity and composition in grasslands across spatial scales: the standardised EDGG sampling methodology. Bulletin of the Eurasian Grassland Group 32: 13–30.

Dengler J, Biurrun I, Apostolova I, Baumann E, Becker T, Berastegi A, Boch S, Cancellieri L, Dembicz I, ... Weiser F (2016b) Scale-dependent plant diversity in Palaearctic grasslands: a comparative overview. Bulletin of the Eurasian Dry Grassland Group 31: 12–26.

Dengler J, Wagner V, Dembicz I, García-Mijangos I, Naqinezhad A, Boch S, Chiarucci A, Conradi T, Filibeck G, ... Biurrun I (2018a) GrassPlot – a database of multi-scale plant diversity in Palaearctic grasslands. Phytocoenologia 48: 331–347. https://doi.org/10.1127/phyto/2018/0267

Dengler J, Vassilev K, Bergmeier E, Boch S, Pedashenko H, Sopotlieva D, Tsiripidis I, Aposotolova I, Fotiadis G, ... Vrahnakis M (2018b) Joining hierarchical clustering, diagnostic species and expert system definitions into a coherent classification approach: dry grasslands of the Balkan Peninsula as an example. Presentation at the 61st Annual Symposium of the IAVS Bozeman, Montana, USA, 22-27 July 2018.

Dengler J, Biurrun I, Boch S, Dembicz I, Török P (2020a) Grasslands of the Palaearctic biogeographic realm: introduction and synthesis. In: Goldstein MI, DellaSala DA, DiPaolo DA (Eds) Encyclopedia of the world's biomes. Volume 3: Forests – trees of life. Grasslands and shrublands – sea of plants. Elsevier, Amsterdam, NL, 617–637. https://doi.org/10.1016/B978-0-12-409548-9.12432-7

Dengler J, Guarino R, Moysiyenko I, Vynokurov D, Boch S, Cykowska-Marzencka B, Babbi M, Catalano C, Eggenberg S, ... Dembicz I (2020b) On the trails of Josias Braun-Blanquet II: First results from the 12thEDGG Field Workshop studying the dry grasslands of the inneralpine dry valleys of Switzerland. Palaearctic Grasslands 45: 59–88.

Dengler J, Cykowska-Marzencka B, Bruderer T, Dolnik C, Neumann P, Riedel S, Seiler H, Zhang J, Dembicz I (2020c) Sampling multi-scale and multi-taxon plant diversity data in the subalpine and alpine habitats of Switzerland: Report on the 14th EDGG Field Workshop. Palaearctic Grasslands 47: 14–42.

Dierßen K (2001) Distribution, ecological amplitude and phytosociological characterization of European bryophytes. Bryophytorum Bibliotheca 56: 1–289.

Díaz TE, Fernández-Prieto JA (1994) La vegetación de Asturias. Itinera Geobotanica 8: 243–258.

Euro+Med (2006–2021) Euro+Med PlantBase – the information resource for Euro-Mediterranean plant diversity. http://ww2.bgbm.org/EuroPlusMed/ [accessed 09 May 2021].

European Commission (2013) Interpretation Manual of European Union Habitats. EUR 28. European Commission. DG Environment. Nature ENV B.3, Brussels, BE.

Evans D (2013) Interpreting the habitats of Annex I: past, present and future. Acta Botanica Gallica 157: 677–686. https://doi.org/10.1080/12538078.2010.10516241

García-Madrid AS, Rodríguez-Rojo MP, Cantó P, Molina JA (2016) Diversity and classification of tall humid herb grasslands (*Molinio-Holoschoenion*) in Western Mediterranean Europe. Applied Vegetation Science 19: 736–749. https://doi.org/10.1111/avsc.12249

Gavilán RG, Vilches B, Font X, Jiménez-Alfaro B (2017) A review of high-mountain acidophilous vegetation in the Iberian Peninsula. Applied Vegetation Science 20: 513–526. https://doi.org/10.1111/avsc.12314

Gee GW, Bauder JW (1986) Particle-size analysis. In: Knute A. (Ed.) Methods of soil analysis. Part 1 – Physical and mineralogical analysis. 2nd ed. American Society of Agronomy and Soil Science Society of America, Madison, US, 383–411. https://doi.org/10.2136/sssabookser5.1.2ed.c15

Guarino R, Becker T, Dembicz I, Dolnik C, Kącki Z, Kozub Ł, Rejžek M, Dengler J (2012) Impressions from the 4th EDGG Research Expedition to Sicily: community composition and diversity of Mediterranean grasslands. Bulletin of the European Dry Grassland Group 15: 12–22.

Hilpold A, Seeber J, Fontana V, Niedrist G, Rief A, Steinwandter M, Tasser E, Tappeiner U (2018) Decline of rare and specialist species across multiple taxonomic groups after grassland intensification and abandonment. Biodiversity and Conservation 27: 3729–3744. https://doi.org/10.1007/s10531-018-1623-x

Hodges NG, Söderström L, Blockeel TL, Caspari S, Ignatov MS, Konstantinova NA, Lockhart N, Papp B, Schröck, ... Porley D (2020) An annotated checklist of bryophytes of Europe, Macaronesia and Cyprus. Journal of Bryology 42: 1-116. https://doi.org/10.1080/03736687.2019.1694329

Hoekstra JM, Boucher TM, Ricketts TH, Roberts C (2005) Confronting a biome crisis: global disparities of habitat loss and protection. Ecology Letters 8: 23–29. https://doi.org/10.1111/j.1461-0248.2004.00686.x

Illyés E, Chytrý M, Botta-Dukát Z, Jandt U, Škodová I, Janišová M, Willner W, Hájek O (2007) Semi-dry grasslands along a climatic gradient across Central Europe: Vegetation classification with validation. Journal of Vegetation Science 18: 835–846. https://doi.org/10.1111/j.1654-1103.2007.tb02600.x

Karger DN, Conrad O, Böhner J, Kawohl T, Kreft H, Soria-Auza RW, Zimmermann NE, Linder HP, Kessler M (2017) Climatologies at high resolution for the earth's land surface areas. Scientific Data 4: e170122. https://doi.org/10.1038/sdata.2017.122

Kuzemko A (2016) Classification of the class *Molinio-Arrhenatheretea* in the forest and forest-steppe zones of Ukraine. Phytocoenologia 46: 241–256. https://doi.org/10.1127/phyto/2016/0083

Kuzemko A, Becker T, Didukh YP, Ardelean IA, Becker U, Beldean M, Dolnik C, Jeschke M, Naqinezhad A, ... Dengler J (2014) Dry grassland vegetation of Central Podolia (Ukraine) – a preliminary overview of its syntaxonomy, ecology and biodiversity. Tuexenia 34: 391–430.

Llimona X, Hladun N, Burgaz AR, Gómez-Bolea A, Giralt M, Navarro-Rosinés P, Barbero M, Boqueras M (2001) Checklist of the lichens and lichenicolous fungi of the Iberian Peninsula and Balearic Islands. Bocconea 14: 5–581.

Loidi J (1983) Estudio de la flora y la vegetación de la cuenca de los ríos Deva y Urola en la provincia de Guipúzcoa. Publ. Universidad Complutense de Madrid, Madrid, ES.

Loidi J, Báscones JC (2006) Memoria del mapa de series de vegetación de Navarra. Gobierno de Navarra, Pamplona, ES.

Loidi J, Biurrun I, Herrera M (1997) La vegetación del centro-septentrional de España. Itinera Geobotanica 9: 161–618.

Marcenò C, Guarino R, Mucina L, Biurrun I, Deil U, Shaltout K, Finckh M, Font X, Loidi J (2019) A formal classification of the *Lygeum spartum* vegetation of the Mediterranean Region. Applied Vegetation Science 22: 593–608. https://doi.org/10.1111/avsc.12456

McCune B, Grace JB (2002) Analysis of ecological communities. MJM, Gleneden Beach, OR, US.

Mucina L, Bültmann H, Dierßen K, Theurillat J, Raus T, Čarni A, Šumerová K, Willner W, Dengler J, ... Tichý L (2016) Vegetation of Europe: hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. Applied Vegetation Science 19 (Suppl. 1): 3–264. https://doi.org/10.1111/avsc.12257

Nimis PL, Martellos S (2021) ITALIC 6.0 – the Information System on Italian Lichens. URL: http://italic.units.it/?procedure=idkeys [accessed 20 April 2021]

Peralta J, Olano JM (2001) La transición mediterráneo-eurosiberiana en Navarra: caracterización de los tomillares y aliagares submediterráneos (*Thymelaeo-Aphyllanthetum monspeliensis*). Pirineos 156: 27–56. https://doi.org/10.3989/pirineos.2001.v156.79

Peralta J, Biurrun I, García-Mijangos I, Remón JL, Olano JM, Lorda M, Loidi J, Campos JA (2018) Manual de interpretación de hábitats de Navarra. 2nd ed. Gobierno de Navarra y Gestión Ambiental de Navarra, Pamplona, ES, 576 pp.

Peyre G, Font X (2011) Syntaxonomic revision and floristic characterization of the phytosociological alliances corresponding to subalpine and alpine grasslands of the Pyrenees and Cantabrian Mountains (classes *Caricetea curvulae*, *Carici-Kobresietea*, and *Festuco-Seslerietea*). Plant Biosystems 145: 220–232. https://doi.org/10.1080/11263504.2011.602732

Quinn GP, Keough MJ (2002) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK. https://doi.org/10.1017/CBO9780511806384

R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, AT.

Rivas Goday S, Rivas-Martínez S (1963) Estudio y clasificación de los pastizales españoles. Publ. Ministerio de Agricultura, Madrid, ES, 269 pp.

Rivas-Martínez S (1996) Clasificación bioclimática de la Tierra. Folia Botanica Matritensis 16: 1–32.

Rivas-Martínez S (2011) Mapa de series, geoseries y geopermaseries de vegetación de España - Parte II. Itinera Geobotanica 18: 5–424.

Rivas-Martínez S, Díaz TE, Fernández-Prieto JA, Loidi J, Penas A (1984) La vegetación de la alta montaña cantábrica: Los Picos de Europa. Ediciones Leonesas, León, ES, 295 pp.

Rivas-Martínez S, Báscones JC, Díaz TE, Fernández-González F, Loidi J (1991a) Vegetación del Pirineo occidental y Navarra. Itinera Geobotanica 5: 5–456.

Rivas-Martínez S, Díaz TE, Fernandez-Prieto JA, Loidi J (1991b) *Festuco hystricis-Ononidetea striatae* y *Rosmarinetea officinalis*, clases de vegetación independientes. Itinera Geobotanica 5: 505–516.

Rivas-Martínez S, Fernández-González, F, Loidi J, Lousã M, Penas A (2002) Vascular plant communities of Spain and Portugal. Addenda to the syntaxonomic checklist of 2001. Itinera Geobotanica 15: 433–922.

Rodríguez-Rojo MP, Fernández-González F (2014) Diversity patterns and typology of *Cynosurus cristatus* grasslands (*Cynosurion cristati* Tüxen 1947) in the Iberian Peninsula. Folia Geobotanica 49: 461–485. https://doi.org/10.1007/s12224-014-9191-7

Rodríguez-Rojo MP, Fernández-González F, Tichý L, Chytrý M (2014) Vegetation diversity of mesic grasslands (*Arrhenatheretalia*) in the

Iberian Peninsula. Applied Vegetation Science 17: 780–796. https://doi.org/10.1111/avsc.12118

Rodríguez-Rojo MP, Jiménez-Alfaro B, Jandt U, Bruelheide H, Rodwell J, Schaminée JHJ, Perrin PM, Kącki Z, Willner W, … Chytrý M (2017) Diversity of lowland hay meadows and pastures in Western and Central Europe. Applied Vegetation Science 20: 702–719. https://doi.org/10.1111/avsc.12326

Rodríguez-Rojo MP, Font X, García-Mijangos I, Crespo G, Fernández-González F (2020) An expert system as an applied tool for the conservation of semi-natural grasslands on the Iberian Peninsula. Biodiversity and Conservation 29: 1977–1992. https://doi.org/10.1007/s10531-020-01963-1

Roleček J, Tichý L, Zelený D, Chytrý M (2009) Modified TWINSPAN classification in which the hierarchy respects cluster heterogeneity. Journal of Vegetation Science 20: 596–602. https://doi.org/10.1111/j.1654-1103.2009.01062.x

Škvorc Ž, Ćuk M, Zelnik I, Franjić J, Igić R, Ilić M, Krstonošić D, Vukov D, Čarni A (2020) Diversity of wet and mesic grasslands along a climatic gradient on the southern margin of the Pannonian Basin. Applied Vegetation Science 23: 676–697. https://doi.org/10.1111/avsc.12497

ter Braak CJF, Šmilauer P (2012) Canoco reference manual and user's guide: Software for ordination (version 5.0). Microcomputer Power, Ithaca, NY, US.

The British Lichen Society (2021) Lichen Taxon Dictionary. URL: https://www.britishlichensociety.org.uk/content/lgbi3?s=03 [accessed 20 April 2021]

Theurillat J-P, Willner W, Fernández-González F, Bültmann H, Čarni A, Gigante D, Mucina L, Weber H (2021) International Code of Phytosociological Nomenclature. 4th edition. Applied Vegetation Science 24: e12491. https://doi.org/10.1111/avsc.12491

Thomas GW (1996) Soil pH and soil acidity. In: Sparks DL, Page AL, Helmke PA, Loeppert RH (Eds) Methods of Soil Analysis - Part 3 - Chemical Methods. Soil Science Society of America and American Society of Agronomy, Madison, WS, US, 475–490. https://doi.org/10.2136/sssabookser5.3.c16

Tichý L (2002) JUICE, software for vegetation classification. Journal of Vegetation Science 13: 451–453. https://doi.org/10.1111/j.1654-1103.2002.tb02069.x

Tichý L, Chytrý M (2006) Statistical determination of diagnostic species for site groups of unequal size. Journal of Vegetation Science 17: 809–818. https://doi.org/10.1111/j.1654-1103.2006.tb02504.x

Török P, Dengler J (2018) Palaearctic grasslands in transition: overarching patterns and future prospects. In: Squires VR, Dengler J, Feng H, Hua L (Eds) Grasslands of the world: diversity, management and conservation. CRC Press, Boca Raton, US, 15–26.

Tsiripidis I, Bergmeier E, Fotiadis G, Dimopoulos P (2009) A new algorithm for the determination of differential taxa. Journal of Vegetation Science 20: 233–240. https://doi.org/10.1111/j.1654-1103.2009.05273.x

Tsiripidis I, Xystrakis F, Kallimanis A, Panitsa M, Dimopoulos P (2018). A bottom–up approach for the conservation status assessment of structure and functions of habitat types. Rendiconti Lincei. Scienze Fisiche e Naturali 29: 267–282. https://doi.org/10.1007/s12210-018-0691-x

Tüxen R, Oberdorfer E (1958) Die Pflanzenwelt Spaniens II Teil: Eurosiberische Phanerogamen-Gesellschaften Spaniens. Veröffentlichungen des Geobotanischen Institutes der ETH Rübel Zürich 32(2): 1–328.

Vassilev K, Apostolova I, Pedashenko H (2012) *Festuco-Brometea* in western Bulgaria with an emphasis on *Cirsio-Brachypodion pinnati*. Hacquetia 11: 227–248. https://doi.org/10.2478/v10028-012-0011-4

Visa S, Ramsay B, Ralescu A, van der Knaap E (2011) Confusion matrix-based feature selection. Proceedings 22nd Midwest Artificial Intelligence and Cognitive Science Conference 2011, Cincinatti, Ohio, US.

Willner W, Kuzemko A, Dengler J, Chytrý M, Bauer N, Becker T, Biţă-Nicolae C, Botta-Dukát Z, Čarni A, … Janišová M (2017) A higher-level classification of the Pannonian and western Pontic steppe grasslands (Central and Eastern Europe). Applied Vegetation Science 20: 143–158. https://doi.org/10.1111/avsc.12265

Willner W, Roleček J, Korolyuk A, Dengler J, Chytrý M, Janišová M, Lengyel A, Aćić S, Becker T, … Yamalov S (2019) Formalized classification of semi-dry grasslands in central and eastern Europe. Preslia 91: 25–49. https://doi.org/10.23855/preslia.2019.025

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Supplementary material

Supplementary material 1
Geographic, environmental and structural data of the relevés
Link: https://doi.org/10.3897/VCS/2021/69614.suppl1

Supplementary material 2
Ordered relevé table and complete constancy table of the five classes
Link: https://doi.org/10.3897/VCS/2021/69614.suppl2

Supplementary material 3
Definition of the aggregates used
Link: https://doi.org/10.3897/VCS/2021/69614.suppl3

Supplementary material 4
Confusion matrix comparing TWINSPAN and original classification
Link: https://doi.org/10.3897/VCS/2021/69614.suppl4

Supplementary material 5
Information on type relevés
Link: https://doi.org/10.3897/VCS/2021/69614.suppl5

Supplementary material 6
Expert system for the five classes
Link: https://doi.org/10.3897/VCS/2021/69614.suppl6

Supplementary material 7
Expert system for the *Festuco-Brometea* orders
Link: https://doi.org/10.3897/VCS/2021/69614.suppl7

Supplementary material 8
Expert system for the *Festuco-Brometea* order 1 alliances
Link: https://doi.org/10.3897/VCS/2021/69614.suppl8

Supplementary material 9
Expert system for the *Festuco-Brometea* order 2 alliances
Link: https://doi.org/10.3897/VCS/2021/69614.suppl9

Supplementary material 10
Expert system for the *Festuco-Brometea* alliance 1.2 associations
Link: https://doi.org/10.3897/VCS/2021/69614.suppl10

Supplementary material 11
Expert system for the *Festuco-Brometea* alliance 2.1 associations
Link: https://doi.org/10.3897/VCS/2021/69614.suppl11

Supplementary material 12
Expert system for the *Festuco-Brometea* alliance 2.2 associations
Link: https://doi.org/10.3897/VCS/2021/69614.suppl12

Supplementary material 13
Synoptic table with seven clusters from TWINSPAN
Link: https://doi.org/10.3897/VCS/2021/69614.suppl13

Supplementary material 14
Ordered relevé table and complete constancy table of the *Festuco-Brometea*
Link: https://doi.org/10.3897/VCS/2021/69614.suppl14