Abstract

Aims: We studied the syntaxonomic position, biodiversity, ecological features, nature conservation value and current status of dry grasslands investigated by Josias Braun-Blanquet more than 60 years ago. Study area: Inner-alpine valleys of Austria. Methods: We sampled 67 plots of 10 m², following the standardized EDGG methodology. We subjected our plots to an unsupervised classification with the modified TWINSPAN algorithm and interpreted the branches of the dendrogram syntaxonomically. Biodiversity, structural and ecological characteristics of the resulting vegetation units at association and order level were compared by ANOVAs. Results: All the examined grasslands belong to the class Festuco-Brometea. From ten distinguished clusters, we could assign four clusters to validly published associations, while the remaining six clusters were named tentatively. We classified them into three orders: Stipo-Festucetalia pallentis (Armerio elongatae-Potentilletum arenariae, Phleo phleoidis-Pulsatilletum nigricantis, Medicago minima-Melica ciliata community, Koelerio pyramidatae-Teucrietum montani), Festucetalia valesiacae (Sempervivum tectorum-Festuca valesiaca community); Brachypodietalia pinnati (Astragalo onobrychidis-Brometum erecti, Agrostis capillaris-Avenula adsurgens community, Anthericum ramosum-Brachypodium pinnatum community, Ranunculus bulbosus-Festuca rubra community, Carduus defloratus-Brachypodium pinnatum community). Conclusions: The ten distinguished dry grassland communities of the Austrian inner-alpine valleys differ in their ecological affinities as well as their vascular plant, bryophyte and lichen diversity. We point out their high nature conservation importance, as each of them presents a unique habitat of high value.
Introduction

The European Alps ("Alps") form a nearly 1,200 km long arc from Nice in the southwest to Vienna in the northeast, with the widest sector in the centre of the Eastern Alps, stretching approximately 240 km from north to south (Ozenda 1988). The Alps represent a biodiversity hotspot in Central Europe, with 4,491 observed vascular plant species (Aeschimann et al. 2004; Barthlott et al. 2005). The inner-alpine valleys are the central parts of the great longitudinal valleys between the highest ridges of the Alps and represent islands of continentality within the relatively oceanic climate of the mountain ranges. One important aspect of continentality is the low precipitation, caused by the high altitudes of the mountains that cast rain shadows towards the south and southeast, leeward of the prevailing rain-bringing northwestern winds. While even the driest parts of the Alps are more humid than true steppes (Ozenda 1988), these valleys provide refugial habitats to many species with a distribution centred in the steppe biome of Eastern Europe (Kirschner et al. 2020). Similar intra-montane valleys with continental climate and Festuco-Brometea grasslands are known from other high mountain ranges, like the Caucasus (Belonovskaya et al. 2016).

The inner valleys of the Alps have been inhabited by humans since the Bronze Age (Sydow 1995; Bätzing 2005) or even earlier (Patzelt 1996), up to elevations exceeding 2,000 m (Braun-Blanquet 1961; Schwabe and Kratochwil 2012). Therefore, the contemporary landscape has been influenced by millennia of land use, mainly as pastures and meadows. It is evident that the traditional agro-pastoral practice exerted a positive feedback on the Festuco-Brometea grasslands, as already noticed by Braun-Blanquet (1961), who described the succession from the Astragalo-Brometum to Larix decidua or Pinus sylvestris forests after the cessation of management. Both the isolated relic character of these steppe elements and the requirement of adequate management underline the need of skilled nature protection measures in these unique habitats. Phytosociological studies are well suited for evidence-based decisions in nature conservation. However, most studies of the inner-alpine dry grasslands (Buschardt 1979; Wagner 1979; Schwabe and Kratochwil 2004, 2012; Wiesner et al. 2015; Dengler et al. 2019) focused on the more (south)western parts of the Alps with a severe summer drought, and merely touched the Eastern Alps, which have only a moderately continental climate that is influenced by cyclones from the Adriatic Sea.

Our study is part of a long-term project of the Eurasian Dry Grassland Group (EDGG) that will cover the inner-alpine dry grasslands in the whole Alps (Dengler et al. 2020a; Magnes et al. 2020). In the present paper, we focus on the dry grassland vegetation of the inner-alpine valleys of the Austrian Alps, revisiting sites that were already described by Braun-Blanquet (1961). More specifically, we provide a preliminary syntaxonomic classification using modern multivariate methods, describe the biodiversity and ecology of these grasslands and discuss their conservation management.

Study area

We mainly sampled in three regions of Austria: the Upper Inn valley in North Tyrol, the Virgen valley in East Tyrol and the central Mur valley in Styria. Additionally, one site in the Carinthian Basin was visited (Figure 1). Aridity is most pronounced in the Upper Inn valley (Magnes et al. 2018), and although Landeck is located highest among the three weather stations presented (Figure 2), the annual mean temperature is higher and annual precipitation is lower than at stations in the other two.

Upper Inn valley

Sampling localities: Fließ (FL), Kaunerberg (KA), Laudegg castle in Ladis (LA) (Figure 1).
The sampling was performed in the Nature Park Kaunergrat, southwest of Landeck, in one of the driest regions of the Austrian Alps. Our study area is close to the Engadin in Switzerland and the most continental area of the Eastern Alps, the Vinschgau in South Tyrol (Italy). Braun-Blanquet (1961) described the dry grasslands of the Austrian Upper Inn Valley in conjunction with those of the Lower Engadin because of the proximity and the similarity in geology, climate and species composition.

Geologically, the Kaunerberg (KA) and the study sites below the castle Laudegg (LA) belong to the easternmost part of the Engadin window. Kauns-Kaunerberg is located above Bündner schist, a metamorphic marine sediment from the Cretaceous period that is rich in calcium carbonate (Gruber et al. 2010). In contrast, the study sites below the Laudegg castle are situated above a much older, Triassic bedrock of metamorphic quartzite sandstone (Gruber et al. 2010). However, both rock materials favoured the formation of shallow soils at these localities. Another process that had a large influence on the composition of the soils at the studied sites was the deposition of drift and moraine material by the Inn glacier during the Würm Glacial. In course of this, rocks from a wider glacial catchment (e.g. Bündner schists, but also dolomites) were distributed and deposited along the valley slopes. This propagated the
formation of calcareous soils at the study sites below Fließ (FL), although the bedrock below is exclusively made up of acidic mica schists of the Variscan Silvretta crystalline (Gruber et al. 2010).

The studied dry grassland sites bear witness of an old cultural landscape. Traditionally, these sites were communal pastures (“Allmende”) for small livestock (mainly sheep, to a lesser amount goats) in spring and autumn, before and after summering on alpine pastures at higher elevations. This kind of management is documented back to the medieval ages, but likely is much older. Until the 1940s and early 1950s, several hundred animals were herded in the slopes below Fließ. However, this practice was abandoned alongside the economic upturn of the post-war era, leading to a reforestation of the sites. This negative trend lasted until 2002, when, following the long-lasting pressure of regional conservationists, the sites at Fließ were finally put under protection and integrated into the Naturra 2000 network. The sites at Kauns-Kaunerberg followed shortly after and are protected under Tyrolean law since 2006. Since then, both sites have been managed by the Kauenergrat Nature Park. Management measures include the initial re-establishment of abandoned areas by removal of bushes and trees, and subsequent, targeted grazing by cattle, goats and sheep. Since their implementation, these activities have been regularly evaluated via monitoring studies on vegetation and selected insect taxa (butterflies, ants). The area is the best example of inner-alpine dry valleys in Austria concerning size and extent of dry and semi-dry grassland vegetation.

Virgen valley

Sampling localities: Obermauern (OM), Marin (MA), Zinizachspitze (ZS) (Figure 1).

The Virgen valley runs in a west-east direction south of the main ridge of the Alps. It is quite remote from modern traffic routes and accessible only from the east, following the Isel river upstream. Due to its position south of the giant mountain massif Großvenediger (3,662 m), the climate is rather dry with an average annual precipitation of about 900 mm. The nearest climate station (Lienz, 30 km to the southeast) shows sub-Mediterranean characteristics with a relatively low precipitation in late summer (Figure 2), while the precipitation in Virgen is probably significantly lower (Wagner 1979). The main settlements are found from 1,200 to 1,300 m. North of the valley the geological bedrock is dominated by the schist shell of the Upper Tauern Penninicum.

The valley has been populated since prehistoric times. *Triticum aestivum* was cultivated until the 1980s and up to an elevation of approximately 1,400 m. Cattle breeding is another important land use. Traditionally, the animals were brought across mountain passes to markets on the northern side of the main ridge (Oberwalder 1999). Since the 19th century, markets that are more distant have become relevant. The settlement structure in the valley is characterised by small villages surrounded by a structurally rich cultural landscape called “Virger Feldflur” (Michor 1999). Part of it are hedges with *Berberis vulgaris, Rosa spp.* and *Sorbus aucuparia.* The former arable fields were gradually transformed into grasslands, resulting in a saying in local dialect: “Virgn isch grin woagn” (“Virgen has become green”) (Oberwalder 1999).

The montane and subalpine zones reach from the valley bottom up to more than 2,000 m. On the northern slopes, *Picea abies* forests are dominant. On the sunny southern slopes, the forests were replaced by grasslands centuries ago. The forest remnants are usually dominated by *Larix decidua* with low cover and are still used as reserve pastures for dry years. The often very steep slopes were not only grazed by cattle, sheep and goats, but also used as mountain hay meadows as farmers could not produce enough hay in the lower parts of the valley. Hay was used as forage in winter in addition to harvested leaves and straw. The mountain meadows, sometimes even above the timberline, were traditionally mown only every second year. They are situated in the neighbourhood of the mountain pastures, which are mainly used for young cattle (Oberwalder 1999).

The bedrock of the sampling localities is mainly calcareous slate, partly covered with moraine material, and only on the southern border of OM there is also some dark phyllite together with the calcareous slate (Frank et al. 1987).

Mur valley and Carinthian Basin

Sampling localities: Puxer Loch (PU), Neumarkt in der Steiermark (NM), Pöls (PÖ), Griffen (GR), Gulsen (GU) (Figure 1).

The studied part of the Mur valley is situated along the upper reaches of the river, approximately 80 to 120 km east of its source. Braun-Blanquet (1961) identified this area as the easternmost extension of the inner-alpine dry valleys. In comparison to the climate of Lienz (Figure 2), the precipitation is lower without a depression in late summer (Figure 2, climate station of Zeltweg). Additional to the two sites within the Mur valley itself (GU, PU), we include here plots in the area of an adjacent pass traversal (NM), one site in the Carinthian Basin (GR) and one site in a tributary valley of the Mur with the last population of the endemic *Stipa styriaca* (PÖ). The latter locality was not investigated by Braun-Blanquet (1961), because this species, probably a remnant of the glacial steppe-tundra, was discovered and described from this place only later (Melzer 1962; Martinovský 1970).

Although all sites are situated in the Austrian Central Alps, the geological bedrock is very diverse (Flügel and Neubauer 1984). While the westernmost site (PU) is located on a steep slope of Palaeozoic limestone (Murauer Palaeozoikum), the bedrock in NM consists of moraine material with quartzite. The habitat of *Stipa styriaca* in PÖ is a steep southern slope on black mica schist, and GU
is part of the greatest connected serpentinite outcrop of Central Europe (Brooks 1987), its steep southern slopes being one of the most peculiar habitats in Austria (Magnes 2018). The castle hill of Griffen (GR), a landmark visible for miles around, is an isolated block of marble (Gleirscher and Pacher 2005).

Methods
Vegetation and environmental data

In total, we sampled 67 plots of 10 m² (15 nested-plot series with two 10-m² subplots each and additional 37 normal plots, Suppl. materials 1, 2) with the EDGG methodology (Dengler et al. 2016) between the 6th and 13th July 2018. Each nested-plot series ("EDGG Biodiversity Plots") consists of a 100-m² plot, with nested series of 0.0001, 0.001, 0.01, 0.1, 1 and 10 m² in two opposite corners. All terricolous vascular plants, bryophytes and lichens were recorded with the shoot presence method (Dengler 2008) for all plot sizes, and their cover value in percent was estimated in the 10-m² plots.

Soil of the uppermost 10 cm was collected in each plot by mixing five random samples. The following soil parameters were measured (all measured environmental variables as header data are provided in Suppl. material 1): skeleton content (mass fraction of particles > 2 mm), percentages of sand, clay and silt, texture class estimated with Robinson pipette method after removing organic matter with 6% H₂O₂, field capacity (%), drainage rate (cm/h), available water (%), permanent wilting point (%), pH (in a suspension of 10 g dry soil in 25 ml aqua dest.), electrical conductivity (EC) (in a suspension of 10 g dry soil in 50 ml aqua dest., dS/m), organic matter (as loss at ignition at 430°C, %), organic carbon (%), N content estimated with the Kjeldahl method (%), C/N, available P (estimated with the Mehlich 3 method (PM3), mg/kg).

Other recorded environmental and structural parameters were (for methodological details, see Dengler et al. 2016): geographical position (with precision of 1 m), elevation (m), aspect (°), inclination (°), maximum micromeas (cm), soil depth (cm, mean of five measurements per plot), total vegetation cover (%), cover shrub layer (%), cover herb layer (%), cover bryophyte/lichen layer (%), cover litter (%), cover stones and rocks (%), cover gravel (%), cover fine soil (%), maximum height of shrubs (m), maximum height of herbs (cm), height of herb layer (mean of five measurements per plot), relief (topographic) position, and land use, with indication of grazing, mowing, burning or abandonment. For each relevé, mean ecological indicator values for temperature, continentality, light, moisture, nutrients and soil reaction were calculated in the JUICE 7.1 software (Tichý 2002), based on the values published by Ellenberg et al. (1991).

The complete data are stored in and available from the GrassPlot database (Dengler et al. 2018; Biurrun et al. 2019; https://edgg.org/databases/GrassPlot) as data-set AT_E. The 10-m² plots are also provided in Suppl. material 1 (header data) and Suppl. material 2 (sorted relevé table).

Data analysis

The compositional data, along with the header data, were entered into TURBOVEG (Hennekens and Schaminé 2001) and then imported into the program JUICE (Tichý 2002). Prior to the numerical analysis, occurrences of species in the shrub and herb layer were combined, using the formula of Fischer (2015). We conducted a TWINSPIAN (Two-Way Indicator Species Analysis; Hill 1979) in the modified version proposed by Roleček et al. (2009), with the following settings: three pseudospecies cut levels (0%, 5% and 25%); total inertia as measure of heterogeneity; minimum group size: 2.

We tried cluster numbers up to 15 and finally selected the solution with 11 clusters as the basis for our classification, as it corresponded most closely to what we consider the association level. One cluster containing a single relevé was joined with another cluster, so finally ten relevé groups were distinguished. Moreover, three clusters were subdivided into regional variants. These variants partly corresponded to TWINSPIAN clusters of finer resolution, but the assignment of relevés to regional variants was based on their geographical distribution.

Fidelity of species to relevé groups was calculated using the phi coefficient of association (Chytrý et al. 2002), assuming equal cluster size (Tichý and Chytrý 2006). To provide diagnostic species both at order and association level, the calculations were done in Excel, which precluded the application of Fisher's exact test. However, we set phi-value thresholds so high that essentially no non-significant species were chosen at the association level. Species were considered as diagnostic with phi ≥ 0.25 at order level and phi ≥ 0.45 at association level. Additionally, we required in both cases that the drop in phi-value to the syntaxon with the next highest phi-value was at least 0.25; otherwise, the species was also considered diagnostic in the latter syntaxon. If such a drop of 0.25 did not occur anywhere in the sequence of syntaxa ordered by decreasing phi-values, a species was considered not diagnostic. If a species was diagnostic at both order and association level, it was assigned to the level where the phi-value was higher, provided all other conditions were fulfilled. The term “diagnostic species” is used here in a data-set specific context and should not be understood as equivalent to character species (see Willner et al. 2009).

We tried to assign our relevé groups to phytosociological associations, alliances and orders described in the literature by comparing the species composition. If such an assignment was ambiguous, we used informal community names. We refrained from formally describing new syntaxa, as this will be the task of a future, more comprehensive revision of all dry grasslands of the Eastern Alps. To facilitate the syntaxonomic interpretation, we
calculated for each relevé the total percentage cover of the diagnostic species of orders according to Willner et al. (2019) using the function “total cover of <colour> species” in JUICE.

To visualize the relation of the species composition of the relevé groups (and relevés) to measured or calculated factors we performed a DCA using Canoco 5 (ter Braak and Šmilauer 2012) with downweighting of rare species and log-transformation of cover values.

The number and cover of red list species were calculated in JUICE based on Niklfeld and Schratt-Ehrendorfer (1999) for vascular plants, Grims and Köckinger (1999) and Saukel and Köckinger (1999) for bryophytes and Türk and Hafellner (1999) for lichens.

**Results**

**Numerical classification**

The first TWINSPLAN division resulted in two groups roughly corresponding to the orders *Stipo-Festucetalia pallentis* (clusters 1–7) and *Brachypodietalia pinnati* (clusters 8–11) of the class *Festuco-Brometea* (Figure 3). Cluster 4 was transitional between the two orders, with most of its relevés having a higher total cover of *Brachypodietalia* species (Figure 4). Cluster 7 was transitional between the *Stipo-Festucetalia pallentis* and *Festucetalia valesiacae* with several relevés clearly belonging to the latter order (Figure 4). Cluster
6, containing a single relevé, showed a clear prevalence of Brachypodietalia species (Figure 4). As it shared several otherwise rare species with cluster 8 (e.g., Allium carniatum, Avenula adsurgens, Jasione montana, Potentilla argentea), and the relevés of both clusters were from the same location, we joined these two clusters into a single community. Otherwise, we refrained from moving single relevés between clusters based on their affinity to phytosociological orders, but potentially misclassified relevés are mentioned in the description of the individual communities.

Therefore, we classified our relevés into ten vegetation units at association level, which in turn were grouped in the three orders (A) Stipo-Festucetalia pallentis, (B) Festucetalia valesiacae and (C) Brachypodietalia pinnati (Table 1, Suppl. material 2). The alliance level remained unresolved (see Discussion).

Table 1. Abridged synoptic table of the associations, based on the 10-m² plots. For each syntaxon, the 10 species with the highest phi-values are shown plus all species with 10% or higher constancy across all plots. The number of presented vs. total species in each group is given in brackets. Values are percentage constancies. Species are sorted by decreasing fidelity within the respective syntaxon and by decreasing overall constancy in case of accompanying species. The complete synoptic and relevé table is provided in Suppl. material 2. B: bryophyte, L: lichen, V: vascular plant.

| Syntaxon                      | Number of plots | A1 | A2 | A3 | A4 | A5 | B1 | C1 | C2 | C3 | C4 | C5 |
|-------------------------------|-----------------|----|----|----|----|----|----|----|----|----|----|----|
| Diagnostic species order A (3) |                 |    |    |    |    |    |    |    |    |    |    |    |
| Hypnum cupressiforme          | B 16            | 43 | 7  | 11 | 50 | 50 | 60 | 7  | 20 | 14 | 20 | 8  |
| Geranium colubrinum           | V 7             | 21 | 5  | 33 | 50 | 20 | 13 | 20 | 14 | 20 | 20 |
| Echium vulgare                | V 4             | 14 | 3  | 33 | 50 | 60 | 14 | 14 | 14 | 14 | 14 | 14 |
| Diagnostic species association A.1 (11 of 15) |              |    |    |    |    |    |    |    |    |    |    |    |
| Alyssum montanum             | V 6             | 29 | 100|    |    |    |    |    |    |    |    |    |
| Apium graveolens             | V 6             | 29 | 100|    |    |    |    |    |    |    |    |    |
| Dorycnium germanicum         | V 6             | 29 | 100|    |    |    |    |    |    |    |    |    |
| Koeleria pyramidalata var. pubiculmis | V 6         | 29 | 100|    |    |    |    |    |    |    |    |    |
| Potentilla incana            | V 6             | 29 | 100|    |    |    |    |    |    |    |    |    |
| Fastuca pallens              | V 7             | 29 | 3  | 100|    |    |    |    |    |    |    |    |
| Lepraria lobicicana           | L 4             | 21 | 100|  75|    |    |    |    |    |    |    |    |
| Erysimum sylvestre           | V 15            | 50 | 13 | 3  | 100|    | 60 | 13 | 13 |    |    |    |
| Jovibarba globifera subsp. hirta| V 6            | 21 | 3  | 75 |    |    |    |    |    |    |    |    |
| Nototheca marantae           | V 3             | 14 | 50 |    |    |    |    |    |    |    |    |    |
| Weissia brachycarpa          | B 12            | 21 | 7  | 11 | 75 |    | 7  | 25 |    |    |    | 15 |
| Diagnostic species association A.2 (10 of 13) |              |    |    |    |    |    |    |    |    |    |    |    |
| Alliaria petiolata           | V 3             | 14 |    |    | 67 |    |    |    |    |    |    |    |
| Myosotis ramosissima         | V 3             | 14 |    |    | 67 |    |    |    |    |    |    |    |
| Origanum vulgare             | V 10            | 21 | 11 | 100|    |    |    |    |    |    |    | 57 |
| Fallopia convolvulus         | V 10            | 21 | 11 | 100|    |    |    |    |    |    |    | 60 |
| Stachys recta                | V 12            | 29 | 11 | 100|  50|    | 13 | 43 |    |    |    |    |
| Scabiosa ochroleuca          | V 6             | 14 | 5  | 67 |    |    |    |    | 29 |    |    |    |
| Taecium chamadrys            | V 19            | 21 | 13 | 21 | 100|    | 13 | 38 | 20 | 57 |    |    |
| Aster amellus                | V 12            | 14 | 27 | 5  | 67 |    | 27 | 25 |    |    |    |    |
| Bromus inermis               | V 1             | 7  |    |    |    |    |    |    |    |    |    | 33 |
| Galeopsis pubescens          | V 1             | 7  |    |    |    |    |    |    |    |    |    | 33 |
| Diagnostic species association A.3 (10 of 15) |              |    |    |    |    |    |    |    |    |    |    |    |
| Medicago minima              | V 10            | 14 | 20 | 5  | 100|    | 20 | 25 |    |    |    |    |
| Agrimonia eupatoria          | V 12            | 14 | 16 |    | 100|    | 25 | 57 |    |    |    |    |
| Amblystegium serpens         | B 1             | 7  |    |    | 50 |    |    |    |    |    |    |    |
| Clinopodium nepeta agg.      | V 1             | 7  |    |    | 50 |    |    |    |    |    |    |    |
| Erigeron acris               | V 1             | 7  |    |    | 50 |    |    |    |    |    |    |    |
| Lapsana communis             | V 1             | 7  |    |    | 50 |    |    |    |    |    |    |    |
| Silene latifolia             | V 1             | 7  |    |    | 50 |    |    |    |    |    |    |    |
| Torilis arvensis             | V 1             | 7  |    |    | 50 |    |    |    |    |    |    |    |
| Melica citata                | V 18            | 21 | 40 | 8  | 33 | 100| 40 | 38 |    |    |    |    |
| Artemisia absinthium         | V 3             | 7  | 7  |    | 50 | 7  |    |    |    |    |    |    |
| Galium lucidum               | V 24            | 36 | 33 | 16 | 33 | 100| 40 | 33 | 50 | 14 | 8  |    |
| Diagnostic species association A.4 (12 of 19) |              |    |    |    |    |    |    |    |    |    |    |    |
| Poa baderioides agg.         | V 9             | 36 | 7  |    |    | 100| 7  |    |    |    |    |    |
| - Poa malnieri               | V 4             | 14 | 7  |    | 40 |    |    |    |    |    |    |    |
| Toninia sedifolia            | L 6             | 29 |    |    | 80 |    |    |    |    |    |    |    |
| Tortella inclinata           | B 6             | 29 |    |    | 80 |    |    |    |    |    |    |    |
| Dinitrichium flexicaule      | B 7             | 29 | 3  |    | 80 |    |    |    |    |    |    |    |
| Peltigera rufescens          | L 7             | 29 | 3  |    | 80 |    |    |    |    |    |    |    |
| Saxifraga paniculata         | V 4             | 21 |    |    | 60 |    |    |    |    |    |    |    |
| Piora decipiens              | L 6             | 21 | 7  |    | 80 |    |    |    |    |    |    |    |
| Cladonia symphycarpa         | L 15            | 29 | 40 |    | 80 |    |    |    |    |    |    |    |
| Physconia muscigera          | L 7             | 21 | 13 |    | 60 |    |    |    |    |    |    |    |
| Cladonia macrophyllodes      | L 3             | 14 |    |    | 40 |    |    |    |    |    |    |    |
| Endocarpan pusillum          | B 10            | 21 | 27 |    | 60 |    |    |    |    |    |    |    |
| Tortella tartuosa            | B 22            | 29 | 40 | 13 | 80 |    |    |    |    |    |    | 31 |
| Diagnostic species order B (21 of 35) |              |    |    |    |    |    |    |    |    |    |    |    |
| Fastuca valesiae             | V 33            | 14 | 93 | 16 | 50 | 20 | 93 | 38 | 20 | 15 |    |
| Sempervivum tectorum         | V 16            | 67 | 3  |    |    | 67 | 13 |    |    |    |    |    |
| Diagnosic species association C.1 (2) | All | A | B | C | A.1 | A.2 | A.3 | A.4 | B.1 | C.1 | C.2 | C.3 | C.4 | C.5 |
|--------------------------------------|-----|---|---|---|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|
| **Fragaria viridis**                 | V   | 3 |   |   |     |     |     |     |     |     |     |     |     |     |
| **Astragalus obnubilis**              | V   | 9 |   |   |     |     |     |     |     |     |     |     |     |     |
| **Diagnosic species association C.2 (12 of 16)** |     |    |    |    |     |     |     |     |     |     |     |     |     |     |
| **Potentilla argentea**               | V   | 10 | 13 | 13 |     |     |     |     | 13   |     |     |     |     |     |
| **Allium carinatum**                 | V   | 10 | 7  | 16 |     |     |     | 7    |     | 100 |     |     |     |     |
| **Genista tinctoria**                | V   | 4  |   | 8  |     |     |     |     | 60   |     |     |     |     |     |
| **Jasione montana**                  | V   | 4  |   | 8  |     |     |     |     | 60   |     |     |     |     |     |
| **Papulus tremula**                  | V   | 4  |   | 8  |     |     |     |     | 60   |     |     |     |     |     |
| **Potentilla rupestris**              | V   | 6  |   | 8  |     |     |     |     | 60   |     |     |     |     |     |
| **Avenula adsurgens subsp. adsurgens** | V    | 15 | 7  | 24 | 33  |     |     | 100  | 43   |     |     |     |     |     |
| **Campanula rotundifolia**           | V   | 10 | 7  | 16 |     |     |     | 7    | 80   |     |     |     |     |     |
| **Viola arvensis**                   | V   | 6  |   | 11 |     |     |     |     | 60   |     |     |     |     |     |
| **Ceratodon purpureus**              | B   | 7  | 11 | 13 |     |     |     | 7    | 80   |     |     |     |     |     |
| **Silene nutans**                    | V   | 15 |   | 26 |     |     |     |     | 80   | 14  | 20  |     |     |     |
| **Cladonia fimbriata**               | B   | 12 | 7  | 13 | 13  | 25  |     | 13   | 60   |     |     |     |     |     |
| **Diagnosic species association C.3 (10 of 18)** |     |    |    |    |     |     |     |     |     |     |     |     |     |     |
| **Anthemiscum Ramosum**              | V   | 7  |   | 13 |     |     |     |     | 71   |     |     |     |     |     |
| **Campanula trachelium**             | V   | 7  |   | 13 |     |     |     |     | 71   |     |     |     |     |     |
| **Centarea scabiosa**                | V   | 7  |   | 13 |     |     |     |     | 71   |     |     |     |     |     |
| **Tragopogon orientalis**            | V   | 7  |   | 13 |     |     |     |     | 71   |     |     |     |     |     |
| **Peucedanum oreoselinum**           | V   | 13 | 20 | 16 |     |     |     | 20   | 13   |     |     |     |     |     |
| **Astragalus glycyphyllos**          | V   | 9  | 7  | 13 | 33  |     |     | 7    | 86   |     |     |     |     |     |
| **Polygala comosa**                  | V   | 4  |   | 8  |     |     |     |     | 43   |     |     |     |     |     |
| **Clinopodium vulgare**              | V   | 13 | 7  | 21 | 50  |     |     | 13   | 20   | 86  |     |     |     |     |
| **Viola hirta**                      | V   | 16 | 7  | 26 | 50  |     |     | 38   | 86   |     |     |     |     |     |
| **Vicia cracca agg.**                | V   | 10 | 7  | 18 |     |     |     |     | 52   | 20  | 15  |     |     |     |
| **Diagnosic species association C.4 (11 of 19)** |     |    |    |    |     |     |     |     |     |     |     |     |     |     |
| **Ranunculus bulbosus**              | V   | 9  |   | 16 |     |     |     |     | 14   | 100 |     |     |     |     |
| **Festuca rubra agg.**               | V   | 12 | 21 |   |     |     |     |     | 100  |     |     |     |     |     |
### Vegetation Classification and Survey

#### Syntaxons and Diagnostic Species

| Syntaxons | Number of plots |
|-----------|----------------|
|           | All | A | B | C | A1 | A2 | A3 | A4 | B1 | C1 | C2 | C3 | C4 | C5 |
|           | 67  | 14 | 15 | 4 | 3 | 2 | 5 | 15 | 8 | 5 | 7 | 5 | 13 |
| Festuca rubra | 6  | 7  | 17  | 70 | 8  | 60  | 8  |
| Knautia arvensis | V | 4  | 8  | 60  |
| Lolium perenne | V | 4  | 8  | 60  |
| Veronica officinalis | V | 4  | 8  | 60  |
| Calliergonella cuspidata | B | 7  | 13 | 60  |
| Ranunculus acris | V | 7  | 13 | 60  |
| Thuidium philiberti | B | 7  | 13 | 60  |
| Hieracium pilosella | V | 25  | 27  | 34  | 27  | 40  | 100  |
| Avenula pratensis | V | 3  | 29  | 100  |
| Plantago lanceolata | V | 25  | 7  | 20  | 34  | 50  | 20  | 38  | 43  | 100  |
| **Diagnostic species association C.5 (21 of 55)** |
| Persicaria vivipara | V | 13  | 24  | 69  |
| Potentilla erecta | V | 24  | 42  | 60  |
| Phyteuma orbiculare | V | 10  | 18  | 54  |
| Plantago atrata | V | 10  | 18  | 54  |
| Ranunculus nemorus | V | 10  | 18  | 54  |
| Thesium alpinum | V | 15  | 26  | 20  |
| Centaurea pseudophyra | V | 9  | 16  | 46  |
| Gymnadenia conopsea | V | 9  | 16  | 46  |
| Laserpitium latifolium | V | 9  | 16  | 46  |
| Molinia caerulea | V | 9  | 16  | 46  |
| Pimpinella major | V | 13  | 26 | 60  |
| Polygala chamaebuxus | V | 13  | 24 | 20  |
| Carlina acaulis | V | 27  | 7  | 45  | 7  | 29  | 60  | 92  |
| Euphrasia officinalis | V | 16  | 29  | 40  |
| Galium album | V | 16  | 29  | 40  |
| Carduus nutans | V | 19  | 7  | 12  | 25  | 13  | 77  |
| Trifolium montanum | V | 33  | 13  | 53  | 13  | 13  | 43  | 100  |
| Campanula scheuchzeri | V | 12  | 21  | 20  |
| Seslia caerulea | V | 12  | 21  | 20  |
| Anthyllis vulneraria | V | 19  | 14  | 29  | 40  | 14  | 69  |
| Hippocrepis comosa | V | 12  | 21  | 13  | 20  |
| **Diagnostic species for more than one order (3)** |
| Carex caryophyllea | V | 52  | 7  | 60  | 66  | 20  | 60  | 63  | 100  | 29  | 80  |
| Allium unifolium | V | 42  | 71  | 73  | 18  | 50  | 100  | 100  | 73  | 13  | 14  | 38  |
| Thymus praecox | V | 33  | 50  | 63  | 13  | 100  | 50  | 60  | 67  | 50  | 14  |
| **Diagnostic species for more than one association (18 of 25)** |
| Thymus pulegioides | V | 37  | 29  | 20  | 47  | 80  | 20  | 25  | 80  |
| Briza media | V | 33  | 13  | 53  | 13  | 71  | 60  |
| Salvia pratensis | V | 31  | 7  | 60  | 29  | 50  | 60  | 63  | 86  |
| Plantago media | V | 25  | 7  | 42  | 7  | 38  |
| Teucrium montanum | V | 24  | 29  | 33  | 18  | 80  | 33  | 88  |
| Agrostis capillaris | V | 22  | 39  | 100  |
| Trifolium pratense | V | 22  | 7  | 37  | 50  | 14  | 100  |
| Leucanthemum vulgare agg. | V | 21  | 37  | 100  |
| Linum catharticum | V | 21  | 37  | 80  |
| Verbascum chaixii subsp. austriacum | V | 21  | 36  | 24  | 50  | 100  | 80  | 57  | 8  |
| Arrhenatherum elatius | V | 18  | 7  | 29  | 7  | 60  | 71  | 20  |
| Taraxacum sect. Ruderalia | V | 16  | 29  | 71  |
| Primula veris | V | 15  | 26  | 57  |
| Hylotelephium maximum | V | 13  | 29  | 13  | 13  | 33  |
| Genista sagittalis | V | 12  | 21  | 80  |
| Hamamelis triloba (Avenula) pubescens | V | 12  | 21  | 60  |
| Prunella vulgaris | V | 12  | 21  | 60  |
| Trifolium arvense | V | 12  | 7  | 27  | 8  | 50  | 27  | 60  |
| **Other species (22 of 209)** |
| Abietina abietina | B | 57  | 43  | 53  | 63  | 33  | 100  | 53  | 63  | 100  | 71  |
| Euphorbia cyparissias | V | 57  | 60  | 63  | 50  | 50  | 60  | 63  | 100  |
| Carex humilis | V | 55  | 57  | 73  | 47  | 75  | 100  | 100  | 73  |
| Helianthemum nummularium subsp. obscurum | V | 52  | 36  | 47  | 61  | 33  | 80  | 47  | 63  | 20  |
| Fagopyrum esculentum | V | 48  | 50  | 27  | 55  | 100  | 80  | 27  | 38  |
| Rhytidiadelphus squamosus | B | 46  | 43  | 45  | 45  | 35  | 80  | 53  | 25  |
| Medicago sativa | V | 28  | 21  | 33  | 33  | 50  | 20  | 33  | 88  |
| Eryngium yuccifolium | V | 18  | 21  | 27  | 13  | 60  | 27  | 13  |
| Hyssopus officinalis | V | 16  | 14  | 24  | 25  |
| Sanguisorba minor | V | 16  | 17  | 21  | 33  | 13  | 38  | 43  |
| Cuscuta epithymum | V | 15  | 14  | 7  | 18  | 7  | 38  | 20  |
| Arenaria serpyllifolia agg. | V | 13  | 29  | 20  | 50  |
| Asperula cynanchica | V | 13  | 14  | 7  | 16  |
| Medicago lupulina | V | 13  | 14  | 18  | 33  | 20  | 13  |
| Rosa canina agg. | V | 12  | 14  | 7  | 33  |
| Securigera varia | V | 12  | 14  | 13  | 11  | 33  |
| Cladonia furcata | L | 10  | 13  | 13  | 13  | 20  |
| Clinopodium alpinum | V | 10  | 7  | 16  | 20  |
| Dactylorhiza rigidula | B | 10  | 14  | 27  | 3  |
| Leucanthemum vulgare | V | 10  | 14  | 27  | 13  |
| Prunus spinosa | V | 10  | 7  | 16  | 50  | 20  | 40  |
| Sedum acre | V | 10  | 21  | 20  | 3  | 25  | 40  | 20  | 13  |
Ordination

The first axis of the DCA graph (Figure 5) corresponds to a gradient of skeleton content and partly soil depth, supporting the division between the *Stipo-Festucetalia pallen*tis (clusters A.1–A.4) on the left (high skeleton content, low soil depth) and the *Brachypodietalia pinnati* (clusters C.1–C.5) on the right, with cluster B.1 (*Festucetalia valesiacae*) in an intermediate position. Axis 2 depicts mainly litter cover, a good proxy for abandonment of management in the lower parts of the graph. The neatly grazed grassland of cluster A.4 (OM) in the upper part of the graph, having a high number of bryophytes and lichens, contrasts with the abandoned sites of PU and PO of clusters A.2 and A.3 having high litter cover and higher indicator values for nutrients.

Biodiversity and vegetation cover

Maximum species richness for all taxa increased from 9 in 0.0001 m² to 103 in 100 m² (Table 2). Across grain...
sizes, maximum species richness was much higher for vascular plants (e.g. 94 species in 100 m²) compared to bryophytes and lichens (e.g. 17 species each in 100 m²) (Table 2). When comparing the mean species richness of vascular plants across the three orders, for all taxa as well as for vascular plants alone, order C was by far the richest, as for vascular plants alone, order C was by far the richest, order C (meso-xeric) they ranged from 27 in C.1 to 54 in C.5. Mean richness of non-vascular taxa in 10 m² varied strongly within the orders, ranging from 0.3 to 16.6 in order A and from 1.3 to 9.6 in order C. Herb layer cover was generally higher in the meso-xeric communities (order C) compared to the xeric and rocky ones (orders A and B) (Tables 3 and 4, Figure 6), while cover values of non-vascular taxa varied independently of the order and were largely consistent with the respective richness patterns (Figure 6).

While we found the highest mean species richness of vascular plants in the mountain meadows of C.5

### Table 3. Biodiversity, structural and ecological characteristics of all 10 m² plots across the three orders. The p-values and significance levels refer to ANOVAs.

| Parameter | All (n = 67) | Order A (n = 14) | Order B (n = 15) | Order C (n = 38) | p-value | Significance |
|-----------|-------------|-----------------|-----------------|-----------------|---------|--------------|
| Species richness (all taxa) | 40.4 ± 18 | 28.8 ± 6.9 | 34.4 ± 5.6 | 47.0 ± 15.8 | <0.001 | *** |
| Species richness (vascular plants) | 34.2 ± 16 | 20.9 ± 4.2 | 26.1 ± 3.7 | 42.4 ± 14.6 | <0.001 | *** |
| Species richness (bryophytes + lichens) | 6.1 ± 0 | 7.9 ± 7.9 | 8.3 ± 3.4 | 4.6 ± 4.1 | 0.021 | * |
| Species richness (red-listed species) | 2.5 ± 0 | 9 ± 2.5 | 3.1 ± 1.5 | 2.1 ± 1.6 | 0.109 | |
| Vegetation structure | | | | | | |
| Cover vegetation [%] | 78 ± 30 | 64 ± 15 | 58 ± 18 | 90 ± 15 | <0.001 | *** |
| Cover herb layer [%] | 72 ± 20 | 58 ± 22 | 47 ± 16 | 87 ± 18 | <0.001 | *** |
| Cover bryophyte + lichen layer [%] | 13 ± 0 | 14 ± 20 | 18 ± 20 | 11 ± 15 | 0.423 | |
| Cover litter [%] | 29 ± 0 | 22 ± 23 | 21 ± 16 | 35 ± 28 | 0.091 | |
| Herb layer height mean [cm] | 14.1 ± 1.4 | 62.6 ± 11.5 | 8.4 ± 5.6 | 17.3 ± 12.5 | 0.018 | * |
| Herb layer height SD [cm] | 6.8 ± 0.8 | 33.4 ± 8.3 | 5.6 ± 0.6 | 6.7 ± 6.4 | 0.564 | |
| Ecological indicator values (not weighted by cover) | | | | | | |
| EV light | 7.5 ± 0.6 | 8.1 ± 7.7 | 7.8 ± 0.1 | 7.3 ± 0.2 | 0.001 | *** |
| EV temperature | 5.4 ± 3.2 | 5.8 ± 5.9 | 5.1 ± 0.1 | 5.1 ± 0.9 | 0.001 | *** |
| EV biodiversity | 4.2 ± 3.5 | 5.0 ± 4.4 | 4.5 ± 0.2 | 4.1 ± 0.3 | 0.001 | *** |
| EV moisture | 3.4 ± 2.6 | 4.9 ± 3.0 | 2.8 ± 0.1 | 3.9 ± 0.6 | 0.001 | *** |
| EV reaction | 6.9 ± 5.4 | 8.1 ± 7.3 | 6.8 ± 0.4 | 6.9 ± 0.7 | 0.031 | * |
| EV nutrients | 2.7 ± 1.6 | 4.6 ± 2.3 | 2.2 ± 0.2 | 3.1 ± 0.6 | <0.001 | *** |
| Topography | | | | | | |
| Elevation [m] | 1180 ± 549 | 1945 ± 1078 | 1114 ± 120 | 1243 ± 390 | 0.191 | |
| Inclination [%] | 36 ± 8 | 59 ± 40 | 38 ± 7 | 33 ± 10 | 0.017 | * |
| Southing | 0.76 ± 0.97 | 1.00 ± 0.79 | 0.86 ± 0.31 | 0.71 ± 0.46 | 0.518 | |
| Heat index | 0.36 ± 0.98 | 1.19 ± 0.36 | 0.42 ± 0.38 | 0.34 ± 0.38 | 0.820 | |
| Maximum microrelief [cm] | 15 ± 2 | 105 ± 20 | 23 ± 25 | 11 ± 7 | 0.011 | * |
| Soil parameters [general] | | | | | | |
| Cover rocks and stones [%] | 18 ± 0 | 85 ± 37 | 34 ± 28 | 5 ± 11 | <0.001 | *** |
| Cover gravel [%] | 7 ± 0 | 50 ± 16 | 8 ± 11 | 3 ± 10 | 0.002 | * |
| Cover fine soil [%] | 73 ± 1 | 100 ± 41 | 62 ± 29 | 89 ± 23 | <0.001 | *** |
| Soil depth mean [cm] | 17 ± 1 | 56 ± 11 | 9 ± 5 | 22 ± 15 | <0.001 | *** |
| Soil depth CV | 58 ± 12 | 225 ± 73 | 89 ± 66 | 40 ± 21 | <0.001 | *** |
| Soil parameters [physical] | | | | | | |
| Skeleton content [%] | 31 ± 0 | 77 ± 44 | 26 ± 8 | 28 ± 12 | <0.001 | *** |
| Sand content [%] | 70 ± 48 | 81 ± 70 | 74 ± 3 | 68 ± 9 | 0.036 | * |
| Silt content [%] | 14 ± 6 | 31 ± 14 | 12 ± 3 | 15 ± 6 | 0.170 | |
| Clay content [%] | 16 ± 11 | 29 ± 16 | 14 ± 1 | 17 ± 4 | 0.046 | |
| Water at saturation [%] | 42.7 ± 4.7 | 48.3 ± 43.3 | 42.4 ± 0.6 | 42.6 ± 6.6 | 0.863 | |
| Water at field capacity [%] | 20.5 ± 17.9 | 27.7 ± 20.5 | 19.3 ± 0.7 | 21.1 ± 2.5 | 0.028 | * |
| Water at permanent wilting point [%] | 11.3 ± 9.4 | 16.7 ± 11.3 | 10.5 ± 0.5 | 11.6 ± 1.8 | 0.063 | |
| Plant-available water [%] | 9.2 ± 8.1 | 12.2 ± 9.2 | 8.8 ± 0.4 | 9.4 ± 1.0 | 0.080 | |
| Drainage rate [cm/h] | 1.3 ± 0.3 | 2.2 ± 1.3 | 1.6 ± 0.3 | 1.2 ± 0.5 | 0.053 | |
| Soil parameters [chemical] | | | | | | |
| pH [in aqua dest.] | 6.87 ± 4.34 | 8.34 ± 7.37 | 6.87 ± 0.55 | 6.67 ± 1.02 | 0.040 | * |
| Electrical conductivity [µS/cm] | 148 ± 25 | 214 ± 511 | 90 ± 53 | 147 ± 110 | 0.011 | * |
| Organic matter [%] | 14.2 ± 6.0 | 32.3 ± 16.4 | 11.8 ± 5.1 | 14.4 ± 7.2 | 0.209 | |
| Organic carbon [%] | 8.2 ± 3.5 | 18.8 ± 9.5 | 6.8 ± 3.0 | 8.3 ± 4.2 | 0.212 | |
| N content [%] | 1.4 ± 0.1 | 4.6 ± 2.0 | 1.0 ± 0.6 | 1.4 ± 0.8 | 0.004 | ** |
| C/N ratio | 7.9 ± 2.8 | 61.8 ± 4.8 | 9.0 ± 6.8 | 8.6 ± 10.6 | 0.326 | |
| P available [ppm] | 18.5 ± 8.8 | 47.3 ± 23.1 | 17.5 ± 5.0 | 17.2 ± 8.9 | 0.120 | |

*Vegetation Classification and Survey*
(58.5 species in 10 m²), the record (87 species on 10 m²) occurred in a plot of C.4 with shallow, acidic soil, grazed by cattle, sheep and goats in Fließ (Suppl. material 1). The highest cryptogam species richness was in a stand of A.4, a historically and recently grazed hill on calcareous slate in the Virgen valley in East Tyrol (Suppl. material 1). Concerning red list species, the non-managed steep grasslands on serpentinite (cluster A.1) had the highest values (Suppl. material 1), as many of the species are edaphic specialists with a restricted distribution.

**Site conditions**

According to all ecological indicator values except soil reaction, orders A and B were indistinguishable, but different from the meso-xeric order C, whose species composition stands for less light, lower temperature, lower continentality, more moisture and more nutrients (Table 3, Figure 7). By contrast, EIVs for soil reaction were high in order A, low in order B and intermediate in order C (Table 3, Figure 7). In general, measured topographic and soil variables showed only weak or no systematic difference between the orders, except skeleton content, which was clearly higher in the rocky grassland order A (Table 3).

At the association level, there were also strong differences for most of the measured variables (Table 4), with the most prominent ones shown in Figure 8: Within both the rocky and the meso-xeric order, the associations were segregated along an elevation gradient, with A.1 and C.3 occurring at the lowest and A.4 and C.5 at the highest elevations. Rock and stone cover generally was higher and more variable in the associations of the rocky and xeric orders (except A.3) compared to the meso-xeric associations. Soil depth in most communities was low (around 10–15 cm), but much higher in C.3 and C.5 (around 30 cm). Soil pH was high in most of the associations (6.9–7.4), but lower in C.4 (6.3) and much lower in C.2 (4.7). Nutrient concentrations (N and P) were generally low, with the noticeable exception of association A.2 with approximately two times higher values than all other associations.

**Description of the associations and communities**

In the following paragraphs, the ten accepted vegetation units at association level are described, and their syntaxonomic position is discussed. Four units could be unambiguously assigned to described associations, while the six remaining ones are labelled with informal community names.
A.1 Armerio elongatae-Potentillatetum arenariae (relevés 1–4 in Suppl. material 2, Table 1, Figure 9a)

Characterisation: Rocky grasslands on serpentine bedrock with low vegetation cover (48–80%). They are dominated by Festuca pallens and Potentilla incana with Carex humilis, Dorycnium germanicum and Thymus praecox as occasional subdominants. Among the species diagnostic or constant for this association, Asplenium cuneifolium, Erysimum sylvestre, Koeleria pyramidata var. pubilicinus, Notholaena marantae and Silene oitīs were recorded in our relevés. The cryptogam layer covered 1% to 10% of the surface and was dominated by Rhytidium rugosum and Weissia brachycarpa. The latter species, together with Fissidens dubius and Mannia fragrans, belongs to the diagnostic species of the association in our data set.

Ecology and distribution: Our relevés were recorded on very steep slopes with predominantly southern aspect and elevation between 785 and 830 m. The rugged terrain had a high cover of rocks and gravel on the surface and very shallow soils rich in skeleton. The high soil pH is typical for serpentine (in this case it corresponds quite well with mean EIV-R of 7.2). N and P are rather low, but organic matter is high, even if there is a strikingly low litter cover (Table 4). Most of these species are adapted to the high magnesium soil content of the serpentine habitats. There is no management on these steep and dry southern slopes, although there is some moderate grazing by
Nevertheless, there is no litter accumulation, and the low productivity seems in balance with the humification, as shown by the high organic matter content. In this cluster, we found the highest number and cover of red-list species, although the total species number was low. The special weathering of the serpentinite, which leads to very steep slopes, the dark soil surface caused by the high organic content, the low soil depth, the high soil magnesium content, and the position at a narrow section of the valley that increases wind velocity, interact to a very dry and specific habitat type. The history of this habitat might date back to the Neogene, as indicated by the occurrence of the palaeoendemic *Sempervivum pittonii* (Magnes et al. 2020), which has its closest relative in Bulgaria (Lippert 1995). The association is probably endemic to Styria, besides Gulsen occurring also near Kirchdorf und Trafoß ("Tragoß") about 30 km downstream the Mur river where the serpentinite layer reaches the surface again (Mucina and Kolbek 1993).

**Syntaxonomy**: Our relevés are from the locus classicus of this association, which was described by Braun-Blanquet (1961) and included in the alliance *Stp-Poio xe-rophilae* and in the order *Festucetalia valesiacae*. Mucina and Kolbek (1993) described a new alliance *Avenulo adsurgentis-Festucion pallentis* within the *Stipo-Festucetalia pallentis*, based on the *Armerio-Potentilletum* as holotype. This alliance was intended to include all dry grasslands on serpentinite in Austria. However, the alliance name is invalidly published as the name-giving *Avenula adsurgens* is not present in the original diagnosis (Art. 3f ICPN, Theurillat et al. 2021).

**Figure 7**: Comparison of six mean ecological indicator values among the plots of the three orders A (Stipo-Fes-tucetalia pallentis), B (Festucetalia valesiacae) and C (Brachypodietalia pinnati). Letters represent homogeneous groups (at \( \alpha = 0.05 \)) according to Tukey’s post-hoc test following a significant ANOVA.

**Figure 8**: Comparison of six measured ecological variables among the plots of the 10 communities at association rank. Letters represent homogeneous groups (at \( \alpha = 0.05 \)) according to Tukey’s post-hoc test following a significant ANOVA.
A.2 Phleo pleoidis-Pulsatilletum nigricantis
(relevés 5–7 in Suppl. material 2, Table 1, Figure 9b–d)

**Characterisation:** Rocky grasslands on steep, south-facing slopes at elevations between 861 and 935 m. The vegetation is almost closed with bryophyte and lichen layers nearly absent (Table 4). The community is dominated by Carex humilis and Festuca rupicola with a constant occurrence of Allium lasianicum, Fallopia convolvulus, Origaniun vulgaris, Stachys recta, Teucrium chamaedrys, and Verbacum chaixii subsp. austriacum. The endangered *Stipa styriaca* reached its highest cover in this association.

**Ecology and distribution:** The sampled stands were not managed. They have deep soils, the second highest organic matter content among all clusters and also relatively high litter cover, P and N (Table 4). The plots show clear indication of grassland abandonment. Apart from Pöls (PO) we recorded this vegetation around the Puxer Loch (PU), a medieval cave castle in a Paleozoic lime cliff, where *Galium mollugo* agg. was dominant.

**Syntaxonomy:** This unit perfectly matches the association *Phleo-Pulsatilletum nigricantis* described by Braun-Blanquet (1961) from various locations in Carinthia and one location in Styria. As in the previous unit, Braun-Blanquet included this association in the alliance *Stipo-Poion xerophila*. Following a proposal by Franz (1988), Mucina and Kolbek (1993) merged the Phleo-Pulsatilletum nigricantis with the Potentillo puberulae-Festucetum sulcatae. Then in 1993, Mucina and Kolbek raised it to the alliance *Festucion valesiacae*. However, while the Potentillo puberulae-Festucetum sulcatae has a strong affinity to the Festucion valesiacae, the Phleo-Pulsatilletum nigricantis clearly belongs to the Stipo-Festucetalia pallentis. We therefore suggest maintaining the Phleo-Pulsatilletum nigricantis as a separate association, which probably includes all rocky grasslands on relatively well-developed soils in the Styrian and Carinthian part of the Austrian central Alps. As in other regions of Central Europe, these moderate rocky grasslands have a more or less closed herb layer and are dominated by Carex humilis and Festuca rupicola (Janišová and Dúbravková 2010; Willner et al. 2013). The exact delimitation towards the *Seselietum austriaca* Br.-Bl. 1961, which comprises the more extreme, open rocky grasslands with Festuca pallens in the same region, requires further studies.

A.3 Medicago minima-Melica ciliata community
(relevés 8–9 in Suppl. material 2, Table 1, Figure 9e)

**Characterisation:** Cluster A.3 only includes two relevés from the Upper Inn valley, dominated by *Melica ciliata*. The vegetation cover is 70% while the cryptogam layer is poorly developed, covering only below 2%. Along with *Melica ciliata*, some other species have a high cover, such as Artemisia absinthium, Brachypodium pinnatum, Bromus erectus, Galium lucidum and Thymus praecox. Less abundant are Agrimonia eupatoria, Carex humilis and Medicago minima.

**Ecology and distribution:** The shallow soils on the steep south-facing upper slopes show a high skeleton content, high pH and P, but low N and organic matter, although the litter cover is very high (Table 4). Both sites were not managed. One is overgrown by shrubs (*Berberis vulgaris, Euonymus europaeus, Prunus spinosa*), and the other one has a strongly developed litter layer covering 80% of the soil surface. The number of species is low in all categories. We recorded this community in the Upper Inn valley, in FL and LA.

**Syntaxonomy:** This unit does not match any described association from the Eastern Alps. The closest syntaxon from the literature is the Astragalo-Brometum stipetosum capillatae of Kielerhauser (1954), which was raised to association rank by Mucina and Kolbek (1993) under the name *Achnathero-Stipetum capillatae*.

A.4 Koelerio pyramidatae-Teucrietum montani
(relevés 10–14 in Suppl. material 2, Table 1, Figure 9f)

**Characterisation:** Rocky grasslands on extremely shallow soils on calcareous slate (Table 4). The most constant and abundant species in the herb layer are *Festuca rupicola*, *Koeleria pyramidata* and *Potentilla pusilla*. Further, *Allium lasianicum*, *Artemisia campestris*, *Dianthus sylvestris*, *Juniperus sabina*, *Sedum album*, *Sempervivum wulfenii* and *Teucrium montanum* were constantly present. The most important diagnostic species are *Poa badensis* agg., *Saxifraga paniculata*, the lichens *Peltigera rufescens* and *Toninia sedifolia* as well as the bryophytes *Tortella inclinata* and *T. tortuosa*. Numerous further lichen species show high constancy and fidelity to this plant community, e.g. Buellia elegans, *Cladonia symphycarpa*, *C. pyxidata*, *Endocarpon pusillum*, *Physconia muscigena* and *Psora decipiens*. The most frequent bryophytes are *Abietinella abietina*, *Ditrichum flexicaule* and *Tortella inclinata*.

**Ecology and distribution:** Most of the surface (30–90%) is covered by rocks or gravel. Litter cover and organic content are low, like N and P content, with a high pH (Table 4). The plant layer is open, covering between 40 and 60%, and it is quite species poor, containing only 16 to 19 vascular plant species in 10 m². The cryptogam layer is well-developed, covering between 40 and 60% of the soil surface, and rich in species (median species number is 17, maximum 23 including both bryophytes and lichens), being the highest values of all clusters. In the past (until several decades ago) most of these grasslands were grazed by sheep. The lichen *Thamnolia vermicularis* subsp. *subuliformis*, which has its preferred habitat on alpine wind-heathland on stony open soil (Wirth et al. 2013; Nimis et al. 2018), is a witness for transport of thallus fragments by sheep because this wormlike fruticose chalk-white lichen never develops vegetative propagules such as isidia or soredia. Recently, all of these grasslands have been moderately grazed by cattle. We recorded the association in Obermauern (OM) in the Virgen valley (East Tyrol) on the top and southern and southeastern slopes of a hill called “Burg”, at elevations of about 1,400 m.

**Syntaxonomy:** This unit corresponds to the association *Koelerio pyramidatae-Teucrietum montani*, first proposed by Franck (1988) and validly described in Mucina and
Kolbek (1993). While Franz (l.c.) originally placed the association in the *Festucion valesiacae*, the latter authors classified it in the alliance "*Diantho lumnitzeri-Seslerion albicanis*". The community has some similarity with the *Teucrio-Caricetum humilis* Br.-Bl. 1961, which is traditionally classified in the *Stipo-Poion xerophila* and includes rocky grasslands in the Upper Inn valley (Braun-Blanquet 1961; Mucina and Kolbek 1993). However, according to the species list in Franz (1988) and our own relevés, *Carex humilis* seems to be absent in this association. The floristic
relationship between *Teucrio-Caricetum humilis* and *Koelerio-Teucrietum montani* should be further addressed in future studies.

**B.1 Sempervivum tectorum-Festuca valesiaca community**
(relevés 15–29 in Suppl. material 2, Table 1, Figure 10a)

**Characterisation:** This unit was documented from the Upper Inn valley, between 983–1,295 m on steep slopes. The rather low litter cover is connected with a high number and cover of cryptogams, indicated by the saxicolous species *Grimmia ovalis*, *G. laevigata* and *Hedwigia ciliata* occurring on the rocks and *Crossidium squamiferum* and *Tortula ruralis* as bryophytes from open dry soil, interwoven by the common pleurocarpous dry grassland species *Abitinella abietina* and *Rhytidium rugosum*. Among grasses, *Festuca valesiaca* has a high constancy and cover. A fairly high number of annual species, typical of the *Sedo-Scleranthetea*, form the largest bulk of diagnostic species.

**Ecology and distribution:** Shallow soils with rather low litter cover and organic content, and low N and P (Table 4). The community was recorded only in the Upper Inn valley (KA, FL and LA).

**Syntaxonomy:** This cluster is transitional between the orders *Stipo-Festucetalia pallentis* and *Festucetalia valesiacae*. In five relevés, the diagnostic species of the first order are more abundant, in seven relevés those of the second order, while in three relevés both species groups have more or less the same total cover (Figure 4). Diagnostic species of the order *Festucetalia valesiacae* that are present in this unit are both *Brachylochloa ischaemum*, *Festuca valesiaca*, *Medicago minima*, *Stipa capillata* and *Trifolium arvense*. Kielhauser (1954) included similar grasslands of the same region in the *Astragalo-Brometum*. However, since the *Astragalo-Brometum* is a *Brachypodietalia* community (see below), this association name cannot be applied to unit B.1. Here, we provisionally include this unit in the alliance *Festucion valesiacae*. Without a comprehensive revision of all inner-alpine dry grasslands it is impossible to say if it might be assigned to one of the numerous associations described by Braun-Blanquet (1961) from South Tyrol and Switzerland, or if it must be described as a new association.

**C.1 Astragalus onobrychidis-Brometum erecti**
(relevés 30–37 in Suppl. material 2, Figure 10b)

**Characterisation:** Grasslands in the Upper Inn valley dominated by *Bromus erectus* and/or *Brachypodium rupestre*, *Carex humilis* and *Festuca rupestris*. This unit is similar to the previous one, but it has a much lower cover of stones and deeper soils. *Festuca valesiaca*, *Sempervivum tectorum* and other diagnostic species of unit B.1 are rare or absent.

**Ecology and distribution:** Our plots have open and shallow soils, which are poor in skeleton, organic matter, N and P, with a rather high litter cover (Table 4). Braun-Blanquet (1961) considered the association as typical for the calcareous Bündner schist of the geological unit “Lower Engadine Window”, from Ardez in Switzerland to Landeck in Austria.

**Syntaxonomy:** This cluster can be assigned to the *Astragalo-Brometum*, described from the Lower Engadine (Switzerland) by Braun-Blanquet (1949) and originally included in the *Stipo-Poion xerophilae*. Braun-Blanquet’s alliance assignment was followed by Mucina and Kolbek (1993). However, the type relevé of the association (selected by Terzi et al. 2017) clearly belongs to the *Brachypodietalia pinnati*. Likewise, the *Brachypodietalia* species prevail in most relevés of this cluster, although the *Stipo-Festucetalia pallentis* species also have a high proportion (Figure 4). We therefore follow the interpretation of Willner et al. (2019) who included the *Astragalo-Brometum* in the *Cirso-Brachypodion*. Relevé 49, which contains almost no *Brachypodietalia* species, is probably misclassified. Kielhauser (1954), who studied the dry grasslands in the Tyrolian Upper Inn Valley, distinguished two subassociations within the *Astragalo-Brometum*: the A.-B. *stipetosum capillatae* on steep, rocky slopes (see unit A.3.), and the A.-B. *festucetosum valesiacae* on less rocky or even deep soils. However, the latter subassociation is a heterogeneous unit, including both xeric grasslands of the *Festucetalia valesiacae* (corresponding to our unit B.1) and meso-xeric (semi-dry) grasslands of the *Brachypodietalia* (corresponding to the *Astragalo-Brometum s.str.* and our unit C.1).

**C.2 Agrostis capillaris-Avenula adsurgens community**
(relevés 38–42 in Suppl. material 2, Table 1, Figure 10c)

**Characterisation:** This is a semi-dry grassland with dominant *Agrostis capillaris* and *Koeleria pyramidata* and the presence of several acidophytes like *Avenella flexuosa*, *Potentilla argentea* or *Trifolium arvense*. Remarkable is the occurrence of some very rare lichens like *Rinodina cana* and *R. vezdae (= R. moziana, new for Styria!).

**Ecology and distribution:** This unit occurs on siliceous soils (significantly lowest pH of all clusters, Table 4) over quartzite bedrock north of Neumarkt in der Steiermark (NM). Litter cover and organic matter are high (the latter is the highest of all clusters, Table 4), a consequence of abandonment as the grassland management was re-adopted just the year previous to our sampling, and also the high P and N contents are indicative for accumulation processes. The bryophytes *Bryum argenteum* and *Ceratodon purpureus* indicate high nutrient levels.

**Syntaxonomy:** This community has some similarity with the associations *Chamacytisiro hirsuti-Koelerietum* and *Genistro sagittalis-Festucetum rubicolae*, both (invalidly) described from southern Styria – near to the Slovenian border – by Steinbich (1995). In the revision of the semi-dry grasslands of Central and Eastern Europe by Willner et al. (2019), the *Chamacytisiro hirsuti-Koelerietum* was partly assigned to the *Festuco rubricole-Brometum* Zielonkowski 1973, and partly to the *Colchico-Festucetum rubicolae* Lengyel et al. 2016 while the *Genistro-Festucetum rubicolae* remained unclassified, indicating that there are still some unresolved problems in the classification of semi-dry grasslands in Austria. There is also a slight similarity to the *Brachypodio-Avenuletum adsurgentis* that was (also invalidly) described from the Köszeg Mts. in western
Hungary (Kovács 1994). Here, we prefer to use an informal community name for this cluster, leaving the clarification of its syntaxonomic status to a future revision.

**C.3 Anthericum ramosum-Brachypodium pinnatum community**
(relevés 43–49 in Suppl. material 2, Table 1, Figure 10d)

**Characterisation:** These semi-dry grasslands on calcareous soils are dominated by *Brachypodium pinnatum* and *Festuca rupicola*. *Clinopodium vulgare*, *Salvia pratensis*, *Vincetoxicum hirundinaria*, *Viola hirta*, and together with *Molinio-Arrhenatheretea* taxa such as *Achillea millefolium* agg., *Arrhenatherum elatius*, *Dactylis glomerata*, *Taraxacum* sect. *Ruderalia* and *Tragopogon orientalis* are also common.

**Ecology and distribution:** This cluster mainly includes the semi-dry grasslands on base rich, very deep and fine soils near Pöls (PÖ) that had been abandoned for years before grassland management was started again by clearing shrubs only a few years ago. Because of the occurrence of *Stipa styriaca*, the site was declared as a Natura 2000 protected area. With the reintroduction of
grazing by sheep in 2020, there is a good chance that Stipa will be able to spread again from the rocky areas (see unit A.2) to the parts with deep soils. In this community, there is nearly no rock and gravel cover and also skeleton soil content, P and N are low (Table 4). The high litter cover does not lead to high organic matter, but suppresses the development of a bryophyte layer as well as the germination of most vascular plant species. The one relevé from Griffen (variant a) represents a grassland parcel within the bounding walls of the castle that was cleared from trees a few years ago, and the grassland management was started only after that. One relevé from Tyrol (KA) is included in this cluster as well.

**Syntaxonomy:** Three geographical variants can be distinguished in this cluster: The relevé from Griffen (variant a) is a strongly disturbed, ruderalized grassland of doubtful phytosociological position. The relevé from Kaunert-berg (variant c) might represent a more mesic variant of the Astragalo-Brometum (see unit C.1). The remaining relevés (variant b) could be assigned to the Scabioso ochro- leucae-Brachypodietum Klika 1933, which was described in Bohemia (Klika 1933). This association has not been reported from Austria before, but its presence in the Eastern Alps was predicted by the expert system developed by Willner et al. (2019). Against its Pannonian vicariant Polygalo majoris-Brachypodietum Wagner 1941, the Scabioso ochroleucae-Brachypodietum is only negatively differentiated.

**C.4 Ranunculus bulbosus-Festuca rubra community** (relevés 50–54 in Suppl. material 2, Table 1, Figure 10e)

**Characterisation:** This unit lacks dominant species, but some Molinio-Arrhenatheretum species show high constancy, like Achillea millefolium agg., Festuca rubra agg., Plantago lanceolata and Trifolium pratense. Species number is very high, especially in variant (b) from FL, as well as cryptogam species number and cover.

**Ecology and distribution:** The soils are shallow and pH is remarkably low (with the exception of variant c) and both litter cover and organic soil matter are low (Table 4). P is low, while N has high values, especially in variant (b). The bryophyte layer with Calliergonella cuspidata, Plagiommium undulatum and Thuidium philibertii shows a good water supply. The cluster includes relevés from three locations from each of the investigated main valley systems (NM, MA, FL).

**Syntaxonomy:** This is a rather heterogeneous cluster consisting of three geographical variants. Variant (a) includes a single relevé from Neumarkt in der Steiermark (NM), which is dominated by Arrhenatherum elatius and might belong to the alliance Arrhenatherion (class Molinio-Arrhenatheretum). Variant (b) contains two relevés from the Upper Inn Valley (FL), which have a high portion of acidophilous species (e.g. Calluna vulgaris, Danthonia decumbens, Viola canina). These relevés have some similarity with the Agrostio-Dianthetum deltoidis, which was described by Braun-Blanquet (1976) in the Lower Engadin and the Val Müstair (Switzerland). Variant (c) comprises two relevés from Virgen (MA) that share some species with the next unit.

**C.5 Carduus defloratus-Brachypodium pinnatum community** (relevés 55–67 in Suppl. material 2, Table 1, Figure 10f)

**Characterisation:** Semi-dry grasslands in the montane and subalpine belt on steep southern slopes dominated by Brachypodium pinnatum agg. and Laserpitium lattifolium and with (sub)alpine species such as Astragalus penduliflorus, Campanula scheuchzeri, Carex sempervirens, Festuca norica, Plantago atrata, Rhinanthus glacialis and Soldanella alpina.

**Ecology and distribution:** Grasslands on deep soils with low organic matter and low P and N (Table 4), mainly found in the Virgen valley. The subalpine plots from ZS and FL represent subalpine hay-meadows. The montane grassland in MA was managed similarly, mown only once and late in the year (August) without any fertilization. Although the subalpine grassland from ZS, an avalanche corridor, is not mown anymore, litter cover is low in all plots. Together with cluster 10b (part of C.4) we found here the highest vascular species number.

**Syntaxonomy:** This community is characterised by the presence of several subalpine and alpine species and therefore is transitional towards the class Elyno-Seslerietea. In this respect, it is similar to the Carlino-Caricetum sempervirentis Lutz et Paul 1947 of the northern Alps. According to the alliance concept of Willner et al. (2019), the Carlino-Caricetum sempervirentis belongs to the Mesobromion, while the grasslands in East Tyrol probably belong to the Cirsio-Brachypodion. However, the diagnostic species of the latter alliance are not very abundant in this cluster, and in some relevés they are even completely absent. Thus, the alliance assignment remains provisional. Another association that has similarity with this cluster is the Centau- ro-Gentianetum cruciatae, described by Braun-Blanquet (1976) from the Upper and Lower Engadine (Switzerland). Some relevés from the highest elevations might already belong to the Campanulo scheuchzeri-Festucetum noricae Isda 1986 (alliance Caricion ferruginei, see Grab- herr et al. 1993), that was mentioned from other alpine hay meadows in the Virgen valley (Isda 1986).

**Discussion**

**Alliances and orders**

While the assignment of the TWINSPLAN clusters to phytosociological orders was relatively straightforward, the identification of the alliances remains doubtful for the most part.

The rocky grasslands of the Eastern Alps were included in three alliances by Mucina and Kolbek (1993): Avenulo adsurgentis-Festucion pallentis (comprising the Armerio elongatae-Potentilletum arenariae as the only association),
**Diantho-Seslerion** (comprising the rocky grasslands on calcareous soils from East Tyrol and Salzburg eastwards) and **Stipo-Poion xerophilae** (comprising all dry grassland of the Inn valley). However, none of these names is acceptable because (1) the *Avenulo adsurgenti-Festucion pallentis* is not validly published (see description of unit A.1), (2) the **Diantho-Seslerion** is based on associations of the Bükk mountains in Hungary that are very different from the rocky grasslands of the Alps (see remark in the syntaxonomic scheme below), and (3) the **Stipo-Poion xerophilae** has been typified with a *Festucetalia valesiaca* community of the Vinschgau (Terzi et al. 2017). Thus, it seems that the rocky grasslands of the Eastern Alps are lacking a valid alliance name, unless they are included in a broadly conceived **Seslerio-Festucion pallentis** Kliska 1931. However, it is impossible to decide from our dataset whether all rocky grasslands belong to the same alliance, or if they can be included in one of the alliances described from the Pannonian Basin. Therefore, we refrain from assigning our **Stipo-Festucetalia pallentis** communities to an alliance and leave this question to a broad-scale syntaxonomic revision of the order.

Grass steps of the *Festucetalia valesiaca* are represented by a single community in our data set (**Semprevivum tectorum-Festuca valesiaca** community), which probably can be assigned to the *Festucetalia valesiaca*. It must be noted, however, that the current concept of the order *Festucetalia valesiaca* is much narrower than that of Braun-Blanquet (1961) who included all dry and semi-dry grasslands of the study area in this order. Whether the **Stipo-Poion xerophilae** can be maintained as an inner-alpine geographical variant of the *Festucetalia valesiaca*, remains to be further investigated.

Among the semi-dry grasslands of the **Brachypodietalia pinnati**, the communities of Styria (**Agrostis capillaris-Avenula adsurgenti-Avenulo adsurgenti-Festuca valesiaca** community), which probably can be assigned to the *Festucetalia valesiaca*. It must be noted, however, that the current concept of the order *Festucetalia valesiaca* is much narrower than that of Braun-Blanquet (1961) who included all dry and semi-dry grasslands of the study area in this order. Whether the **Stipo-Poion xerophilae** can be maintained as an inner-alpine geographical variant of the *Festucetalia valesiaca*, remains to be further investigated.

**Associations**

Perhaps surprisingly, only four clusters could be unambiguously assigned to described associations. The main reason is that a comprehensive syntaxonomic revision of the dry and semi-dry grasslands of the inner Eastern Alps is still lacking. Instead of adopting names of associations that might or might not correspond to our units, we preferred to use informal community names, thus making the insufficient knowledge clearly visible. The relationship between these communities and described associations such as the **Achnathero-Stipetum capillatae** and **Teucrio-Caricetum humilis** (Mucina and Kolbek 1993) could only be clarified in a revision based on all available plot data from the Eastern Alps. For the **Brachypodietalia pinnati** communities, it will be particularly important to include data from Italy and Switzerland, which both were not covered by the revision of Willner et al. (2019). For the syntaxonomic interpretation of the *Festucetalia valesiaca*, a comparison with data from the most continental part of the Eastern Alps, the Vinschgau in South Tyrol (Italy), will be crucial.

Beside the lack of comprehensive studies another reason for the lacking match with associations from the literature might be the unstable management of most of the sites during the last thirty years. Even at sites that have recently become protected under the Natura 2000 regime (like the grasslands of FL and KA in the Upper Inn valley or PO in the Mur valley), the current management is very different from the historical, much more intensive use, and it will take quite some time for the vegetation to get in balance with the new type of management.

Our results do not support a closer relationship of the dry and semi-dry grasslands of the Austrian inner-alpine dry valleys with the Pannonian steppes (see Willner et al. 2013), a finding that is also supported by genetic analyses of plant and animal species known from both regions (Kirschner et al. 2020, see paragraph nature conservation below).

**Proposed syntaxonomic scheme**

Class: *Festuco-Brometea* Br.-Bl. et Tx. ex Klika et Hadač 1944

A. Order: *Stipo pulcherrimae-Festucetalia pallentis* Pop 1968

Alliance: ??? [**Avenulo adsurgenti-Festucion pallentis** Mucina in Mucina et Kolbek 1993 nom. inval. (Art. 3f), "**Diantho lumnitzeri-Seslerion albicantis**" sensu Mucina et Kolbek 1993 p.p.]

Nomenclatural remark: The name **Diantho-Seslerion** (Soó 1971) Chytrý et Mucina 1993 is often used with wrong species
epithets and/or in a way that excludes its type. Neither Dianthus lanmitteri s.str. nor Seleria albiacns (= S. caerulea) occur in the original diagnosis of the alliance. Soó (1971) described this syntaxon as a suballiance of the Selerietum pallentis Klíka 1931 and listed three associations for it: (1) "Asplenio rutae-murariae-Melietum ciliatae", (2) "Diantho-Selerietum heugleriianae-hungariae" [= Selerietum heugleriianae Zólyomi 1936] and (3) "Selerietum pallentis" [= Campanulo diversifloro-Festucetum pallentis Zólyomi 1966]. We could not verify if the first association name is valid. However, Bothadi (Bothadi et al. 2012) classifies the Asplenio rutae-murariae-Melietum ciliatae in the alliance Alysso alysooidio-Sédiion Oberd. et Müller 1961, so it could hardly be a suitable lectotype. The two other associations, which were both described from the Bukk mountains in Hungary, are often classified in the Bromo pannonici-Festucion pallentis Zólyomi 1966 (e.g. Janišová and Durbavková 2010; Škodová et al. 2015). We are not aware of a published choice of a lectotype for the Diantho-Seleriorum. It could be argued, that Art. 20 (automatic type) is applicable in this case, but this interpretation needs further confirmation.

A.1 Armerio elongatae-Potentilietum arenariae Br.-Bl. 1961
A.2 Phleo phleoidis-Pulsatilietum nigrlicantis Br.-Bl. 1961
A.3 Medicago minima-Melica ciliata community
A.4 Koelerio pyramidalate-Teurctetum montani
Franz in Mucina et al. 1993

B. Order: Festucetalia valesiaceae Br.-Bl. et Tx. ex Br.-Bl. 1950; cons. propos. [= Festucetalia Soó 1940 = Festucetalia valesiaceae (Soó 1940) 1947 nom. illeg.]
Nomenclatural remark: For the nomenclatural problems surrounding the name Festucetalia valesiaceae and a formal proposal for a nomen conservandum, see Terzi et al. (2017).

Alliance: Festucion valesiaceae Klíka 1931 nom. cons. propos. (= Festucion sulcatae Soó 1930; incl. Stipo-Festucion xerophilae Br.-Bl. et Richard 1961)
Nomenclatural remark: Kuzemko et al. (2014) proposed to conserve the name Festucion valesiaceae Klíka 1931 against the earlier Festucion sulcatae Soó 1930, and this proposal was also adopted by Mucina et al. (2016). However, no formal proposal has been submitted so far.

B.1 Sempervivum tectorum-Festuca valesica community

C. Order: 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: Cirsio-Brachypodion pinnati Hadač et Klíka in Klíka et Hadač 1944
C.1 Astragalo onobrychidis-Brometum erecti Br.-Bl. 1950
C.2 Agrostis capillaris-Avenula adsurgens community
C.3 Anthricum ramosum-Brachypodium pinnatum community

Biodiversity

For vascular plants, our findings that meso-xeric stands were substantially richer in species than either rocky or xeric grasslands across all grain sizes, is consistent with results from various other regional studies (Dengler et al. 2012, 2019; Pedashenko et al. 2013) as well as a synthesis across the Palaearctic (Dengler et al. 2020b). Our scale-dependent richness values were similar to mean richness from nested-plot sampling in meso-xeric grasslands across the Palaearctic, but about 25% lower in the xeric grasslands and about 40% lower in the rocky grasslands (GrassPlot Diversity Explorer v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). By contrast, our values for the first two orders (20.0 species for rocky grasslands, 26.9 species for xeric grasslands in 10 m²) were rather similar to richness data found for such types in the inner-alpine valleys of Italy (Wiesner et al. 2015: 25 species in 10 m²) and Switzerland (Dengler et al. 2019: 26.3 species for rocky and 24.3 species for xeric grasslands in 10 m²). Actually, if we exclude the high-elevation associations (transitional to Elyno-Sélerietae) of the meso-xeric grasslands also there the richness values were below average and similar to those found in Aosta Valley and Valais (Wiesner et al. 2015; Dengler et al. 2019). While for the Austrian stands one might be tempted to explain the low plot-scale richness with the small size of the majority of remaining patches, this is not the case for the two other regions where there are still large and well-managed dry grasslands persisting. Therefore, we assume that it is rather due to an impoverished species pool in consequence of the glaciations and the isolated position compared to other dry grassland types, but this definitely requires further studies in a broader geographic context, for which the GrassPlot database provides excellent opportunities (Dengler et al. 2018). By contrast, the strong increase of the plot-scale vascular plant species richness with elevation in the meso-xeric order (Table 4, Figure 6: from 27 to 54 species in 10 m²) is a well-known phenomenon for grasslands of the Alps. Data from the Swiss Biodiversity Monitoring, for example, also show that mean vascular plant species richness across all grassland types increases from 28 via 33 to 44 species in 10 m², in the colline, montane and subalpine belts, respectively (Koordinationsstelle Biodiversitäts-Monitoring Schweiz 2009). Specifically, the high species richness in subalpine hay meadows is a well-known phenomenon (Isda 1986; Matouch et al. 2000; Mayer and Grabner 2004).

For bryophytes and lichens, the situation was reversed in comparison to mean values from nested-plot sampling throughout the Palaearctic (GrassPlot Diversity Explorer v.2.10; https://edgg.org/databases/GrasslandDiversityExplorer; Biurrun et al. 2021). Here, the Austrian stands of...
the rocky and xeric order were on average nearly twice as rich in species than the Palaeartic average, while in the meso-xeric order we had fewer bryophyte species normal-
ly with unclear pattern for lichens in the meso-xeric order. One possible explanation is the large species pool of terri-
colous cryptogams of open stands from the nearby alpine
habitats in case of the first two orders.

**Nature conservation**

Based on the similar floristic composition of their vegeta-
tion, traditional vegetation ecology has anticipated close ties
between the inner-alpine dry valleys and the Eastern Euro-
pean steppes (Braun-Blanquet 1961). Such scenarios assume
that the biota of inner-alpine steppes are relatively young
remnants of the cold-stage steppe belt. In other words, the
inner-alpine steppe vegetation was often seen as a young
and species poor derivative of the steppe vegetation of East-
ern Europe. Genetic data from multiple steppe plants and
insects challenged this scenario: The biota of the inner-al-
pine dry valleys were shown to consist of genetic lineages
that have evolved in long-term isolation, and are not closely
related to European steppe biota from Central and Eastern
Europe (Kirschner et al. 2020). It was also shown that the
 genetic separation between the biota of inner-alpine and
Eastern European steppes did not occur postglacial, i.e. at
the beginning of the Holocene, but dates back as early as the
mid-Pleistocene epoch (Kirschner et al. 2020). Accordingly,
these extrazonal lineages must have survived climate driven
range contractions throughout the Pleistocene climate fluc-
tuations, such as during the LGM and the mid-Holocene
forest optimum, in isolation, that is in refugia apart from the
Pannonian and Eastern European steppes. The palaeoen-
demic Sempervivum pittonii from Gelsen can support these
findings. Practically, the isolated nature of Alpine steppe out-
posts and their previously disregarded genetic uniqueness in
respect to the Eastern European steppes raises their conserva-
tion value significantly. Adequate management and skilled
nature protection activities are key to preserve the inner-al-
pine steppes and their rich genetic diversity for the future.
In this respect, the importance of even small remnants of spe-
cies-rich grasslands should be pointed out: they are often
the last resources for propagules of autochthonous species for
restoration projects (Kiehl et al. 2010; Bischoff et al. 2018).

**Conclusions and outlook**

Our study provides the first phytosociological overview
of dry and semi-dry grasslands of the Austrian inner-al-
pine valleys using new plot data since the seminal work of
Braun-Blanquet (1961). While a comprehensive syntaxo-
nomic revision remains a task for future studies, the investi-
gated plots are important references of the current situa-
tion. It is obvious that in regions with a still predominantly
traditional type of farming, like in the Virgen valley, or in
larger continuous areas with a proper management, like in
the Nature Park Kaunergrat (Upper Inn valley), biodiversity
of grassland-specialists is higher than on smaller grassland
parcels within a matrix of high-input agriculture. Regarding
the number and cover of red list species, the big serpentinite
outcrop Gelsen in the Styrian Mur valley is the leader –
without any management, but with very special habitat con-
ditions. With the exceptions of the serpentinite grasslands
and former hay meadows on avalanche corridors, all the
studied grasslands are depending on a proper management,
otherwise they would undergo mostly a natural succession
to forests. Many of the grasslands are not only hotspots of
biodiversity but also a cultural heritage, some of them may-
be for millennia, and therefore have an extraordinarily high
conservation value. The results of this study support the
importance of grazing animals for achieving conservation
targets in species-rich grasslands, as most of the detected
biodiversity records are located in grazed habitats.

**Data availability**

The plot data presented in this paper were recorded on the
occasion of the 11th EDGG Field Workshop 2018 in Aus-
tria. They are included in the Suppl. material of this paper
and are stored in and available from the GrassPlot database
(https://edgg.org/databases/GrassPlot; Dengler et al. 2018).

**Author contributions**

M.M. organized the 11th EDGG Field Workshop and guid-
ed it together with H.M. and P.K. As former and current
EDGG Field Workshop Coordinators, J.D. and I.D. en-
 sured consistent application of the EDGG methodology.
M.M identified critical vascular plant species and led the
writing of the manuscript. H.M. identified the lichens and
provided information about rare or stenoecious lichens.
E.A.K. analysed the soil samples, C.B. identified the bry-
ophytes and added ecological aspects. W.W. prepared the
syntaxonomic table and framework, wrote most of the syn-
taxonomic discussions and revised several other parts
of the manuscript, M.J. contributed the descriptions of the
Stipo-Festucetalia pallentis, J.D. prepared the vegetation ta-
bles. P.K. wrote the description of the Upper Inn valley and
contributed to the discussion of the nature conservation
value. R.G. supported the description of the Brachypodi-
etalia pinnati and revised the Introduction. H.R. wrote the
description of the Virgen valley. I.D. prepared the map and
conducted the inferential statistical analyses, while J.D.
drew the Results and Discussion on biodiversity aspects.
All authors revised and approved the whole text.

**Acknowledgements**

We are grateful to the IAVS for financial support for some
of the participants. We would like to give special thanks
to Dr. Ernst Partl, director of the Naturpark Kaunergrat
for authorizing sampling in the protected areas and for
helping with the organization of the field workshop.
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Supplementary material

Supplementary material 1

Geographic, environmental and structural data of the analysed plots (pdf)
Link: https://doi.org/10.3897/VCS/2021/68594.suppl1

Supplementary material 2

Complete, sorted relevé and synoptic table (pdf)
Link: https://doi.org/10.3897/VCS/2021/68594.suppl2