



The *Stipa dasyvaginata* subsp. *apenninicola* mountain grasslands of the Velino Massif (central Italy)*

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Abstract

The central Italian *Stipa* mountain grasslands are a fascinating vegetation type of notable biogeographic interest, having remained along the Apennine chain since the last Pleistocene glacial phases. The present study focuses on the phytosociological description of grasslands dominated by *Stipa dasyvaginata* subsp. *apenninicola*, an endemic Apennine species. We sampled twenty-five plots in the Velino Massif and surrounding areas facing the northwestern side of the Fucino Basin and performed a cluster analysis combining our dataset with all published relevés of *Stipa dasyvaginata* subsp. *apenninicola* dominated communities in the Italian peninsula. The floristic and environmental differences between our dataset and the other communities led us to describe the new association *Saponario bellidifoliae*-*Stipetum apenninicolae* (class *Helianthemo cani*-*Seslerietea nitidae*), showing a xerophilous ecology. We further analyzed the variance in environmental data within our dataset, as well as its biological and chorological spectra. The peculiar floristic and ecological characteristics of these steppic grasslands highlight the need of preserving this type of vegetation, which may represent a valuable example contributing to the understanding of the formation of the contemporary vegetation landscape.

Keywords

Central Apennines, dry grasslands, phytosociology, syntaxonomy

Introduction

The Eurasian Steppe is one of the largest continuous terrestrial natural habitats, spanning a wide area of the Palearctic region from central and eastern Europe to northern China (Willner et al. 2021). This habitat is mainly characterized by a dry continental climate with low annual precipitation and pronounced temperature seasonality (Török et al. 2020). It is also marked by high biodiversity and zonal vegetation typical of temperate grasslands and forest-steppes (Pokorný et al. 2015; Wesche et al. 2016). During the glacial phases of the Pleistocene, steppes were

widespread across most of central and northern Eurasia but retreated with the beginning of the Holocene, whose more humid climate led to the expansion of forests (Hejman et al. 2013; Dengler et al. 2014; Feurdean et al. 2018; Willner et al. 2021).

However, under pressure from herbivores and agricultural societies during the mid-Holocene climatic optimum (Pokorný et al. 2015), many species retreated to refugial areas, where they found favorable environmental conditions and suitable habitats, leading to the development of central European extrazonal steppes, as in the dry valleys of the Alps, the Pannonian Basin, the

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Rhine Valley, northern and central Bohemia, Thuringia and the lower Oder Valley, southern Moravia, and Lower Austria (Kajtoch et al. 2016; Kirschner et al. 2020; Chytrý et al. 2022; Divíšek et al. 2022). Several species with ancient continuous distribution throughout Eurasia are currently considered either rare or with a highly fragmented distributional range. This is the case for several species of the genus *Stipa*, occurring in many dry valleys of the Alps and the Apennines (Becker 2010; Hensen et al. 2010).

In the Italian peninsula, most of the species of the genus *Stipa* are found on calcareous substrates, preferably in semi-rocky habitats, where competition with other species is reduced (Pignatti 2017–2019). In the Apennines, three endemic species can be found: *S. aquilana* (Conti et al. 2007) and *S. crassiculmis* subsp. *picentina* (Spada et al. 2010), restricted to isolated patches, and *S. dasyvaginata* subsp. *apenninica*, which is common in mountainous areas. This latter species shows a fragmented distribution along central and southern Apennines (Martinovský and Moraldo 1980; Moraldo 1983, 1986), reaching up to 2000 m a.s.l. from Marche Region to Calabria (Pignatti 2017–2019). In central Apennines, as well as in the Alps, grasslands dominated by *Stipa capillata*, a relict steppic species with a Eurasian distribution, can also be found (Tammaro 1984).

A few studies on communities dominated by *Stipa dasyvaginata* subsp. *apenninica* have been conducted in the dry valleys of the central Apennines (Pirone et al. 2001; Taffetani et al. 2004; Ballelli et al. 2006; Catorci et al. 2007), but none of them regarded the Fucino Basin. The intermontane basins of central Italy provide remarkably suitable areas for this vegetation, with an overall species composition which resembles that of the central European steppes and rich in glacial relicts, endemic and rare species (Petriccione 1993; Di Pietro and Catonica 1999; Pezzetta 2011; Cancellieri et al. 2024). In the Fucino Basin and surrounding mountains, the peculiar environmental and land-use conditions of mountain sites hindered the development of forest vegetation, thus enabling the persistence of fragmented populations of steppic species in glacial refugia, as well documented by the recent findings of *Festuca valesiaca*, *Astragalus exscapus* subsp. *exscapus*, *Goniolimon tataricum* subsp. *italicum*, *Alyssum desertorum*, *Spiraea hypericifolia* subsp. *hypericifolia*, and *Adonis fucensis* (Bartolucci and Conti 2016; Cancellieri et al. 2017; Filibeck et al. 2020; Conti and Bartolucci 2023; Conti et al. 2023). Here, the presence of *Stipa dasyvaginata* subsp. *apenninica* has already been sporadically recorded (Cancellieri et al. 2020), but the grasslands dominated by this species have never been fully investigated.

Given the biogeographical and ecological importance of these communities along with the lack of studies in the area, the main aim of the present investigation was the phytosociological analysis, as well as the coenological and chorological characterization, of the *Stipa dasyvaginata* subsp. *apenninica* dominated grasslands in the Velino Massif.

Materials and methods

Study area

The study area is located on the Velino Massif and surrounding areas facing the northwestern side of the Fucino Basin in Abruzzo, which is the largest tectonic intermontane basin in central Italy. It hosted an ancient lake before being completely drained at the end of 19th century (Petriccione 1993; Cavinato et al. 2002). The sampling occurred in seven limestone mountain areas, namely the slopes between Mount Rozza (2064 m a.s.l.) and Mount Sevice (2355 m a.s.l.), Mount Velino (2487 m a.s.l.), Mount Caforina (2424 m a.s.l.), the access of Valle Majelama, the upper side of Forme, Mount Tino (1923 m a.s.l.), and the slopes near Collarmele (Fig. 1a).

The area belongs to the sub-mediterranean bioclimate, with upper orotemperate thermotype and upper subhumid ombrotype (Pesaresi et al. 2017; Cutini et al. 2021). Furthermore, the basin is affected by the rain shadow effect caused by the northern and southwestern mountain massifs of the Sirente-Velino and Simbruini Mountains, which drive moist air upslope and thus cause a dry continental climate with low annual precipitation, winter frosts, and summer drought (Petriccione 1993; Pirone and Cutini 2002), as shown in the ombrothermic diagram below (Fig. 1b).

Dataset and data analysis

Twenty-five phytosociological relevés were carried out in summers 2007 and 2012 (7 relevés) and in summer 2023 (18 relevés). The preferential sampling was performed according to the Braun-Blanquet (1932) method, along south-facing rocky outcrops on calcareous soils ranging from 930 m to 1820 m a.s.l. Relevés ranged in size from 30 to 100 m² and were located where *Stipa dasyvaginata* subsp. *apenninica* dominated communities were found. During the sampling, we recorded the geographic coordinates of each plot and also collected environmental data on elevation, aspect, slope, rockiness, stoniness, and total vegetation cover.

Taxonomic nomenclature follows Bartolucci et al. (2024), while life forms and chorotypes follow Pignatti (2017–2019). The syntaxonomical nomenclature follows Mucina et al. (2016) and Terzi et al. (2021).

For the statistical analyses, cover data were converted into van der Maarel (2007) ordinal scale and aspect was converted into a southing index (with the formula $S = -\cos(\text{aspect}) + 1$).

The cluster analysis of the vegetation data from our dataset, along with all existing published data of *Stipa dasyvaginata* subsp. *apenninica* dominated communities, was performed using the Bray-Curtis index as similarity measure (Bray and Curtis 1957) and complete linkage as the agglomerative criterion to reduce chaining effects (package “vegan”, Oksanen et al. 2025). Subsequently, all the relevés were organized into a synoptic table, to summarize the floristic and syntaxonomical differences among these communities (see Table 1, which

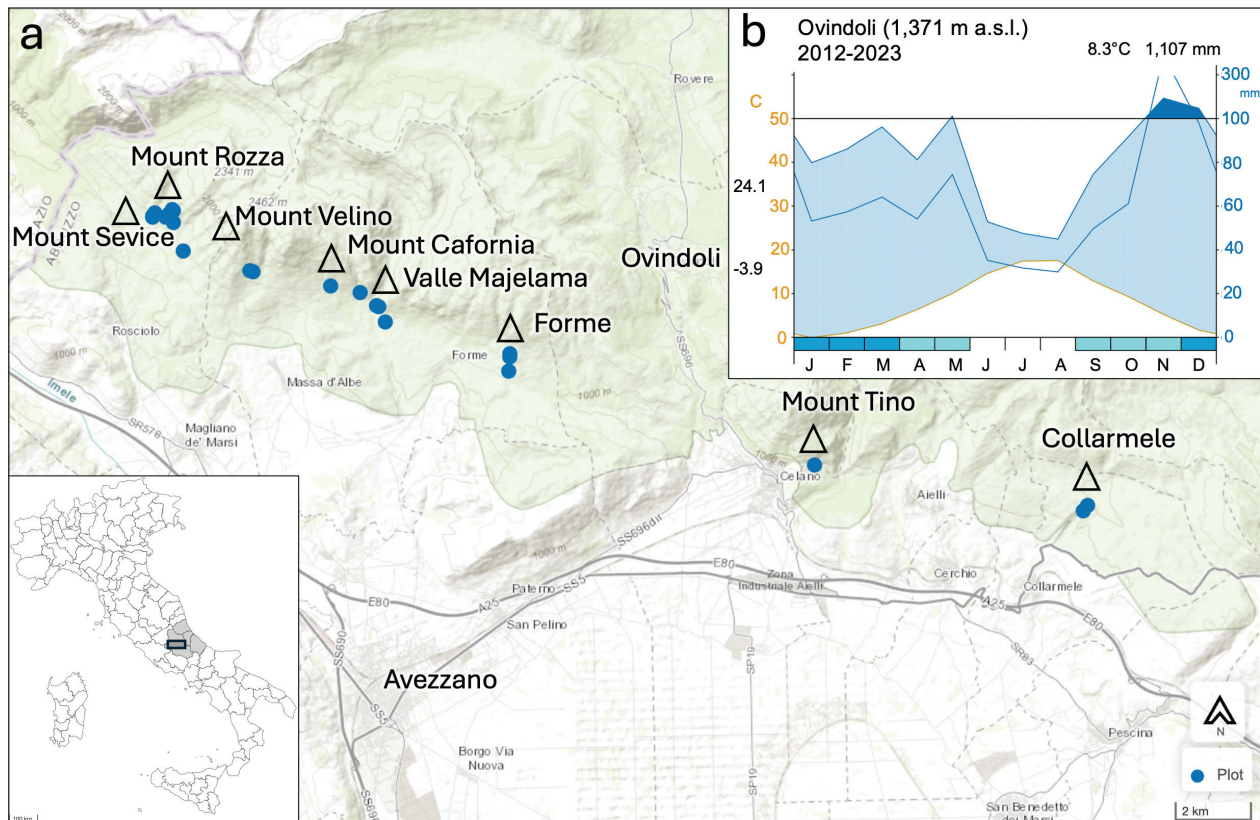


Figure 1. a) Map of the study area showing the mountain areas where field sampling occurred: sampling plots are represented by blue dots. **b)** Ombrothermic diagram *sensu* Walter and Breckle (2002) from Ovindoli station (L'Aquila, Italy): mean annual temperature and precipitation values are shown above the diagram, while mean maximum and minimum temperatures are shown on the left; frost months (in blue) and pre-frost months (in light blue) are shown below the diagram; the orange line represents the mean monthly temperature, while the blue lines represent, respectively, precipitation equal to three times the temperature (upper line) and precipitation equal to twice the temperature (lower line); the horizontal black line indicates the reference level above which the shaded blue area represents months with precipitation exceeding 100 mm, with one division corresponding to 200 mm (scale 1:10).

shows percentage values with cover ranges indicated as superscripts).

Furthermore, to provide a more detailed characterization of our dataset, the variance of environmental data among the resulting subclusters was tested using the non-parametric Kruskal-Wallis test. In addition, normal and weighted biological and chorological spectra were developed by grouping the plants' life forms and chorotypes into main categories (package "ggplot2", Wickham 2016; see Suppl. material 1), to better investigate the ecology of the sampled community.

All the statistical analyses were performed using R 4.5.1 (R Core Team 2025).

Results

The cluster analysis (Fig. 2) identified four main vegetation groups. Cluster A represents our dataset and can be further divided into two subclusters (A1 and A2). Cluster B–C represents respectively *Stipa dasyvaginata* subsp. *apenninica* dominated grasslands from Norcia Basin (Ballelli et al. 2006; subcluster B) and from Umbria-Marche and Marche Ridge (Catorci et al. 2007; subcluster C). Cluster D represents *Stipa dasyvaginata* subsp. *apenninica* dominated grasslands from Cingoli

Ridge (Taffetani et al. 2004). Lastly, cluster E represents *Stipa dasyvaginata* subsp. *apenninica* dominated grasslands from Tirino Valley (Pirone et al. 2001).

The groups identified through multivariate analysis differ both in species composition and in environmental characteristics, with elevation emerging as the primary differentiating factor (see Table 1). Cluster A, in particular, reaches much higher elevations compared to the other groups and is clearly well separated from the other clusters.

Regarding the two subclusters A1 and A2, as shown in Suppl. material 2, they differ both in elevational range and in the presence of high-elevation species. Moreover, subcluster A1 is the only group with a small number of relevés showing the presence of *Stipa capillata* (see Suppl. material 3). The results from ANOVA (Fig. 3) show a statistically significant difference in elevation (p -value: <0.001 ; Fig. 3a) and total cover (p -value: 0.014; Fig. 3f) between the two subclusters within our dataset. By contrast, the other environmental variables did not show any statistically significant difference (Fig. 3b, 3c, 3d, 3e).

In conclusion, the biological and chorological spectra enabled a better understanding of the sampled community (Fig. 4). The *Stipa dasyvaginata* subsp. *apenninica* mountain grasslands found in the Velino Massif and surrounding areas are mainly composed of hemicryp-

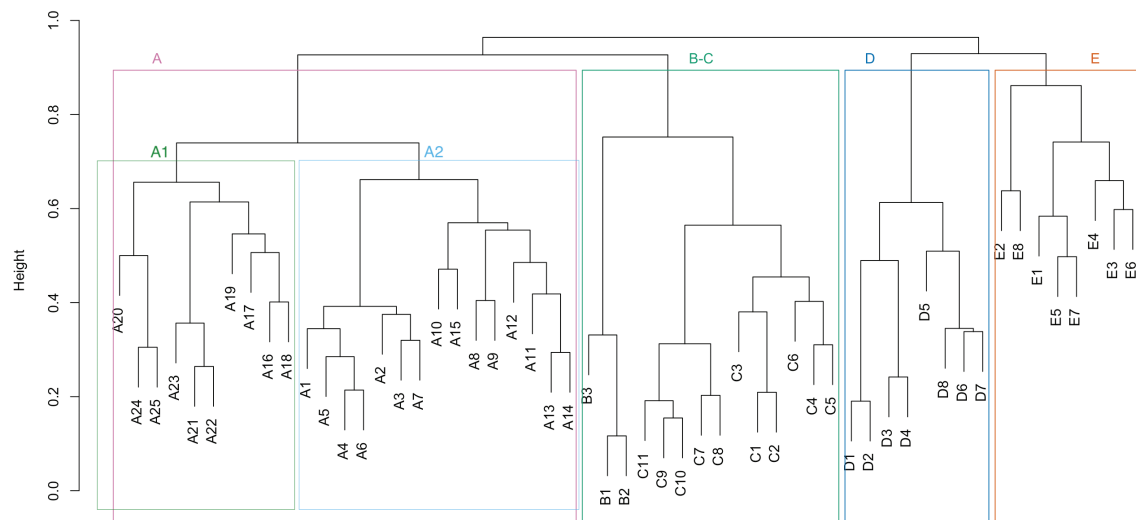


Figure 2. Dendrogram resulting from the cluster analysis. Letters refer to: Our dataset (A), Ballelli et al. 2006 (B), Catorci et al. 2007 (C), Taffetani et al. 2004 (D), and Pirone et al. 2001 (E).

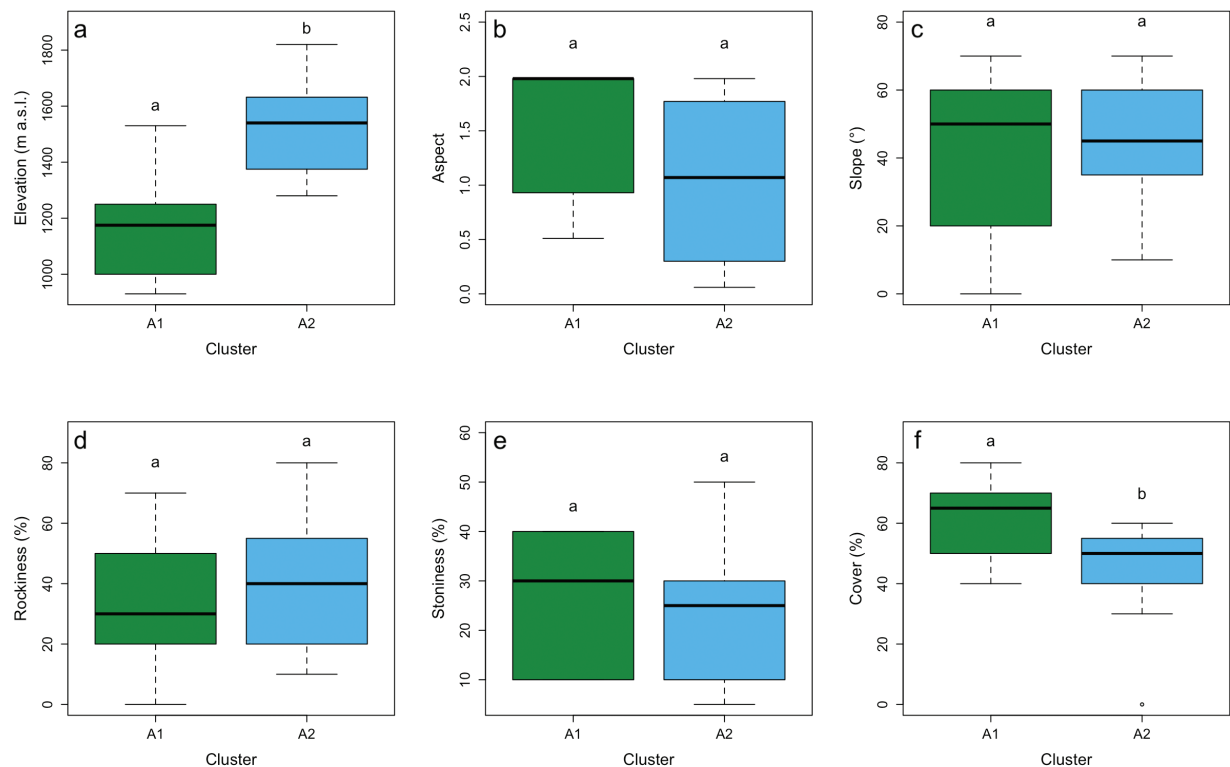


Figure 3. Boxplots of environmental variables with group comparisons between subclusters A1 and A2 based on ANOVA (different letters indicate significant differences between groups).

tophytes and to a lesser extent chamaephytes. Other life forms are very rare, especially phanerophytes (including only few shrubs). The chorotypes highlight the peculiarity of this vegetation, characterized by the predominance of endemic species, species with a Eurasian distribution and several Mediterranean and Pontic elements.

Discussion

In this study, we investigated the Velino Massif and surrounding areas facing the northwestern side of the Fuci-

no Basin, which host a fragment of the steppic grasslands typically occurring in refugia along the Apennines. These sites are characterized by local mesoclimatic and edaphic conditions that, over time, have favored the persistence of long-lasting grasslands, allowing the identification of primary grasslands (Cancellieri et al. 2017; Filibeck et al. 2020), as also observed in some *Stipa dasyvaginata* subsp. *apennincola* grassland sites. In fact, pollen analysis conducted in the Fucino Basin, and correlated with existing profiles from other sites in southern Europe, confirm the dominance of herbaceous vegetation characterized by xerophytic taxa (*Artemisia*, *Amaranthaceae*, *Ephedra*,

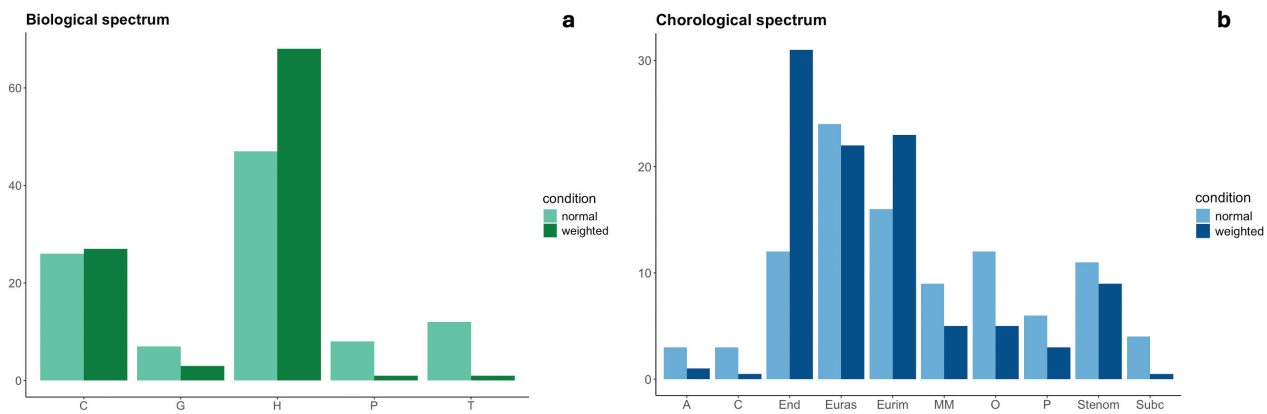


Figure 4. Normal and weighted biological and chorological spectra (see Suppl. material 1). **a)** Biological spectrum showing the following life forms: Chamaephytes (C), Geophytes (G), Hemicryptophytes (H), Phanerophytes (P), and Therophytes (T). **b)** Chorological spectrum showing the following distributional ranges: Atlantic (A), Circumboreal (C), Endemic (End), Eurasian (Euras), Eurimediterranean (Eurim), Mediterranean-Montane (MM), South-European Orophytes (O), Pontic (P), Stenomediterranean (Stenom), and Subcosmopolitan (Subc).

Hippophae), as indicators of pronounced cold and arid conditions during the transitional period between the Pleistocene and the Holocene (MIS 12-MIS11c transition, i.e. around 430–425 ka; Vera-Polo et al. 2024). These high-resolution pollen data (Giaccio et al. 2019; Vera-Polo et al. 2024; Roberts et al. 2025) have enabled the identification of several abrupt landscape transformation events, characterized by phases dominated by steppic herbaceous vegetation, alternating with climatically humid phases in which tree vegetation prevailed (*Ulmus*, *Acer*, *Tilia* and subsequently *Carpinus*, *Ostrya*, *Corylus*, *Celtis*, *Alnus*) during the transition between the Penultimate and Last Glaciations (138–129 ka; Roberts et al. 2025).

Although generalizations are difficult, a multifunctional use of ecosystems has been also repeatedly documented across different areas of the Mediterranean Basin, from Spain to Greece, varying according to the local characteristics of the biotopes (Mercuri et al. 2019). Farming communities progressively expanded northwards along the Italian Peninsula, promoting the maintenance of forest-free areas within which grassland species were preserved. The coexistence of herding and hunting activities was common during the Middle Neolithic (dating from the 6th to 5th millennia B.P.) and was later supplemented by mixed agriculture (Malone 2003) in the foothill landscapes of the Apennines (Abruzzo and Molise). Evidence emphasizes processes in which human activities, such as local deforestation, fire use and cultivation, modified an already open landscape (Sadori et al. 2004). In a comparable period (around 2800 BP, Copper Age), several evidence from the Abruzzo Apennines (Abruzzo, Molise, and Lazio National Park) indicate the first significant human impacts on forests, together with intensive livestock grazing reaching altitudes of up to 2000 m (Brown et al. 2013; Filibeck et al. 2020). From this perspective, faunal remains from the southernmost sector of the Fucino Basin (Grotta La Punta, near Ortucchio) have revealed the presence of red deer and sheep/goat remains (Malone 2003), indirectly confirming human presence and resource use during the Neolithic.

Therefore, both paleoclimatic factors and human activity played a role in shaping the relict herbaceous vegetation described by Vera-Polo et al. (2024) and Roberts et al. (2025). This vegetation occurs on calcareous, calcareous-marly, and calcarenitic substrates, and occasionally on detrital deposits, similarly to other syntaxa that describe xeric grasslands dominated by *Stipa dasyvaginata* subsp. *apenninica* in other central Apennines areas (Pirone et al. 2001; Taffetani et al. 2004; Ballelli et al. 2006; Catorci et al. 2007). These sites are invariably characterized by steep slopes and pronounced rocky outcrops, morphotypes that have allowed the conservation of relict species and communities (Kajtoch et al. 2016; Cancellieri et al. 2017; Filibeck et al. 2020; Divišek et al. 2022). A similar consideration can be applied to the vegetation dominated by *Stipa austroitalica* (Fanelli et al. 2001; Terzi and D'Amico 2016) and by *Achnatherum calamagrostis*, which is common in highly dynamic habitats of the southern Apennines such as scree slopes and sites with shallow soil (Corbetta and Pirone 1981; Brullo et al. 1998). Analogously to the *Stipa dasyvaginata* subsp. *apenninica* fragments found in central Apennines, this fragmented vegetation in southern Italy can be interpreted as a remnant of a much drier climatic period that occurred during the Quaternary (Spada et al. 2011).

The proposal of the new syntaxon *Saponario bellidifoliae-Stipetum apenninicae* (Fig. 5) is here justified by the absence of an association that adequately captures its floristic and ecological distinctiveness, as demonstrated by the clear separation of its cluster. Indeed, currently described associations refer either to sub-Mediterranean hill communities or to transitional submontane communities (*Lino tommasinii-Stipetum apenninicae* Pirone et al. 2001 and *Fumano procumbentis-Stipetum apenninicae* Taffetani et al. 2004 for the former; *Lino tommasinii-Stipetum apenninicae onobrychietosum albae* Ballelli et al. 2006 and *Stipo apenninicae-Seslerietum juncifoliae* Catorci et al. 2007 for the latter), but none of them exhibit a clear montane character with continental bioclimatic traits (Di Lena et al. 2014; Crespi et al. 2018; Cancellieri et al. 2024).

Moreover, the syntaxon we propose is more closely associated with shallow and poorly developed soils and occurs at much higher elevations (Table 1).

The new association includes *Stipa dasyvaginata* subsp. *apennincola*, *Saponaria bellidifolia*, and *Rhamnus saxatilis* as diagnostic species. Moreover, we found a transitional form with hilly grasslands on sites with a gentle slope, which we have interpreted as the new subassociation *stipetosum capillatae* with *Stipa capillata* as diagnostic species. This subassociation highlights the transition to other stepic grasslands dominated by *Stipa capillata*, which to date have been interpreted within the framework of *Globulario meridionalis-Stipetum capillatae*. This latter association was described in the inner areas of the Lazio-Abruzzi Apennines (in Marsica, Capestrano, Sulmona, L'Aquila and Barisciano Basins and in Salto valley; Tammara 1984) and later recorded in the Norcia Basin as well, where a transitional community to *Stipa dasyvaginata* subsp. *apennincola* dominated grasslands (subass. *stipetosum apennincolae*) was also identified (Ballelli et al. 2006).

Regarding the new syntaxon here proposed, the long-term persistence of this relict vegetation is generally associated with specific ecological constraints and the peculiar continental mesoclimate of the area (Cancellieri et al. 2024). This vegetation, in particular, is predominantly

found on steep slopes with shallow soils, where two factors act synergistically: first, the slow progression of vegetation dynamics, driven by limited soil depth and the presence of rocky outcrops (Petriccione 1993; Török et al. 2020); and second, reduced grazing pressure from sheep and horses, which preferentially utilize flatter areas with higher water availability (Adler 2001; Napoleone et al. 2021). In these areas, several shrub associations have been documented, highlighting phases of colonization of grasslands that indicate the abandonment or reduction of pastoral activities (Cutini et al. 2002; Pirone and Cutini 2002).

As shown by the biological and chorological spectra, these grasslands are mainly characterized by hemicryptophytes and chamaephytes, with a high percentage of endemic species (many of which are endemic to the Apennines, such as *Stipa dasyvaginata* subsp. *apennincola*, *Sesleria nitida*, and *Centaurea ceratophylla* subsp. *ceratophylla*). The presence of several species with Mediterranean and Eurasiatic distributions highlights the typical characteristics of dry grasslands in the central Apennines (Biondi et al. 2005; Di Pietro et al. 2015, 2017).

The synoptic table (Table 1; see Suppl. material 4) allowed us to better explain the distinctiveness of our group, in which the diagnostic species (*Saponaria bellidifolia* and *Rhamnus saxatilis*) are exclusive species. At the

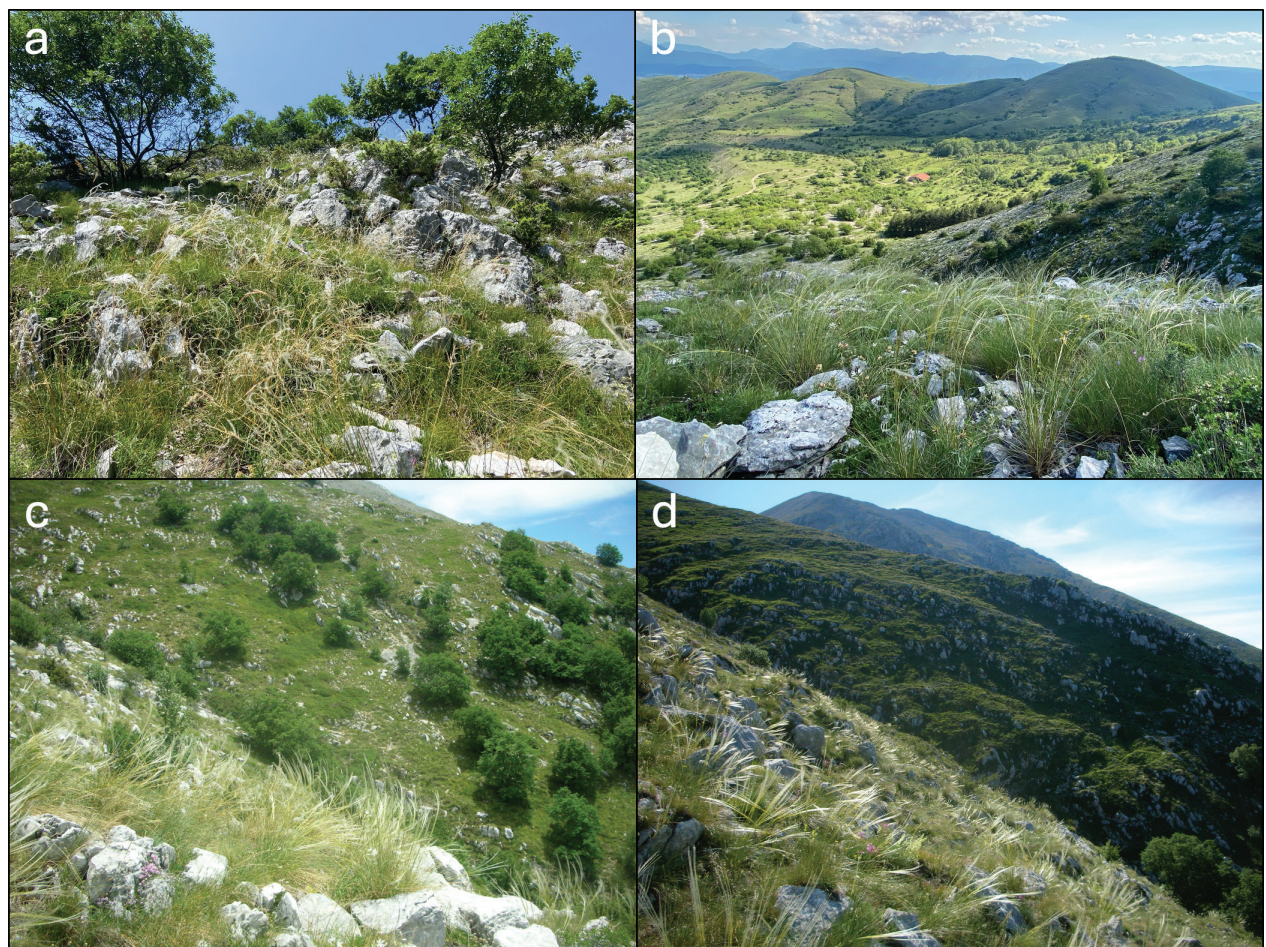


Figure 5. *Saponaria bellidifoliae-Stipetum apennincolae* ass. nova: **a–c–d**) southern slopes of Mount Velino; **b**) southern slopes of Mount Caforia. Photo credits: Claudia Zitarelli, Maurizio Cutini.

Table 1. Synoptic table. Cluster A: relevés from Fucino Basin, Abruzzo (our dataset); Cluster B: relevés from Norcia Basin, Umbria (Ballelli et al. 2006); Cluster C: relevés from Umbria-Marche and Marche Ridge, Marche (Catorci et al. 2007). Cluster D: relevés from Cingoli Ridge, Marche (Taffetani et al. 2004); and Cluster E: relevés from Tirino Valley, Abruzzo (Pirone et al. 2001). The diagnostic species identified in these associations align with those chosen by the cited authors. Values represent percentage frequencies, with superscripts showing cover ranges.

Cluster	A	B	C	D	E
Elevation range (m a.s.l.)	930–1820	1200–1250	1100–1350	580–695	320–880
Mean vegetation cover (%)	54	92	88	84	88
No. Plot	25	3	11	8	8
<i>Saponario bellidifoliae-STIPETUM APENNINICOLAE</i> ass. nova					
+ <i>stipetosum capillatae</i> subass. nova*					
<i>Stipa dasyvaginata</i> subsp. <i>apenninica</i>	100 ³⁻⁴	100 ³	64 ⁺¹	75 ¹⁻³	100 ¹⁻⁵
<i>Saponaria bellidifolia</i>	24 ⁺²	.	.	.	.
<i>Rhamnus saxatilis</i>	32 ⁺¹	.	.	.	.
<i>Stipa capillata</i> *	12 ⁴	.	.	.	13 ⁺
<i>Lino tommasinii-STIPETUM APENNINICOLAE</i> Pirone, Corbetta, Ciaschetti, Frattaroli et Burri 2001					
+ <i>onobrychietosum albae</i> Ballelli, Gatti, Raponi et Catorci 2006**					
<i>Convolvulus elegantissimus</i>	.	.	.	.	63 ⁺³
<i>Linaria purpurea</i>	.	100 ⁺	.	.	50 ⁺²
<i>Linum tommasinii</i>	28 ⁺¹	67 ⁺	.	.	63 ⁺¹
<i>Aethionema saxatile</i>	76 ⁺¹	100 ⁺	.	38 ⁺	50 ⁺²
<i>Thymus striatus</i> subsp. <i>striatus</i> **	96 ⁺²	100 ⁺	36 ⁺¹	.	.
<i>Onobrychis alba</i> subsp. <i>alba</i> **	8 ⁺¹	100 ⁺	27 ⁺	.	.
<i>Fumano procumbentis-STIPETUM APENNINICOLAE</i> Taffetani, Zitti et Giannangeli 2004					
<i>Artemisia alba</i>	28 ⁺²	.	27 ⁺	100 ⁺²	13 ⁺
<i>Thymus longicaulis</i> subsp. <i>longicaulis</i>	4 ⁺	33 ⁺	27 ⁺	88 ⁺¹	.
<i>Globularia bisnagarica</i>	.	33 ⁺	.	88 ⁺¹	25 ⁺¹
<i>Fumana procumbens</i>	32 ⁺¹	.	.	75 ⁺³	25 ⁺¹
<i>Stipo apenninicolae-SESLERIETUM JUNCIFOLIAE seslerietosum juncifolii</i> Catorci, Gatti et Ballelli 2007					
+ <i>onobrychietosum albae</i> Catorci, Gatti et Ballelli 2007***					
<i>Anthyllis vulneraria</i> subsp. <i>polyphylla</i>	.	.	91 ⁺¹	.	.
<i>Sesleria juncifolia</i>	44 ⁺³	.	100 ⁺⁴	.	.
<i>Thliphthisa purpurea</i> subsp. <i>purpurea</i>	28 ⁺¹	.	82 ⁺	.	13 ¹
<i>Centaurea ambigua</i> subsp. <i>ambigua</i>	.	.	64 ⁺¹	.	.
<i>Crepis lacera</i> subsp. <i>lacera</i>	36 ⁺²	100 ⁺	73 ⁺¹	.	.
<i>Takhtajaniantha austriaca</i> ***	.	.	45 ⁺	.	.
<i>Helianthemum nummularium</i> subsp. <i>obscurum</i> ***	.	67 ⁺	36 ¹⁻²	100 ⁺¹	.
<i>Cytiso-Bromopsis erectae</i> Bonin 1978 mut. Terzi, Di Pietro et Theurillat 2021 / <i>Cytiso spinescentis-Saturejion montanae</i> Pirone et Tammaro 1997					
<i>Bromopsis erecta</i>	84 ⁺³	100 ³	100 ⁺²	100 ¹⁻³	63 ¹⁻⁴
<i>Eryngium amethystinum</i>	20 ⁺¹	100 ⁺	91 ⁺¹	.	25 ⁺¹
<i>Phleum hirsutum</i> subsp. <i>ambiguum</i>	12 ⁺²	100 ⁺¹	82 ⁺	13 ¹	65 ¹⁻³
<i>Silene otites</i> subsp. <i>otites</i>	16 ⁺¹	33 ⁺	82 ⁺	.	13 ¹
<i>Erysimum pseudorhaeticum</i>	44 ⁺¹	33 ⁺	100 ⁺¹	.	.
<i>Centaurea rupestris</i>	28 ⁺¹	100 ⁺¹	91 ⁺¹	.	.
<i>Leontodon crispus</i>	72 ⁺¹	33 ⁺	.	38 ⁺	38 ⁺¹
<i>Globularia cordifolia</i> subsp. <i>bellidifolia</i>	100 ⁺³	.	18 ⁺¹	.	13 ¹
<i>Galium lucidum</i> subsp. <i>lucidum</i>	68 ⁺³	.	.	.	25 ⁺¹
<i>Cytisus spinescens</i>	92 ⁺²	.	.	.	.
<i>Muscari neglectum</i>	4 ⁺	100 ⁺	55 ⁺	.	13 ⁺
<i>Festuco laevigatae-Seslerietalia nitidae</i> Ubaldi 2003 nom. corr. Terzi, Di Pietro et Theurillat 2021					
<i>Anthyllis vulneraria</i> subsp. <i>rubriflora</i>	92 ⁺¹	67 ⁺¹	.	63 ⁺¹	.
<i>Allium sphaerocephalon</i> subsp. <i>sphaerocephalon</i>	40 ⁺¹	100 ⁺	64 ⁺¹	.	13 ⁺
<i>Helichrysum italicum</i> subsp. <i>italicum</i>	12 ⁺¹	.	.	63 ⁺³	75 ⁺²
<i>Teucrium chamaedrys</i> subsp. <i>chamaedrys</i>	36 ⁺¹	100 ⁺	73 ⁺	75 ⁺¹	.
<i>Teucrium capitatum</i> subsp. <i>capitatum</i>	4 ¹	67 ⁺	.	75 ⁺¹	25 ¹
<i>Teucrium montanum</i>	52 ⁺¹	67 ⁺	55 ⁺¹	.	.
<i>Argyrolobium zanonii</i> subsp. <i>zanonii</i>	.	.	.	100 ⁺¹	13 ¹

Cluster	A	B	C	D	E
Elevation range (m a.s.l.)	930–1820	1200–1250	1100–1350	580–695	320–880
Mean vegetation cover (%)	54	92	88	84	88
No. Plot	25	3	11	8	8
<i>Convolvulus cantabrica</i>	4 ⁺	.	9 ⁺	100 ⁺¹	25 ¹
<i>Coronilla minima</i> subsp. <i>minima</i>	36 ⁺¹	100 ⁺	.	.	25 ⁺¹
<i>Pentanema montanum</i>	12 ⁺	100 ⁺	27 ⁺²	.	13 ⁺
<i>Scabiosa columbaria</i> subsp. <i>columbaria</i>	12 ⁺	.	.	.	38 ⁺²
<i>Stachys recta</i> subsp. <i>recta</i>	40 ⁺¹	100 ⁺	.	75 ⁺	25 ⁺¹
<i>Odontites luteus</i> subsp. <i>luteus</i>	.	100 ⁺	.	.	38 ⁺¹
<i>Thesium humifusum</i>	20 ¹⁻²	100 ⁺	18 ⁺	.	.
<i>Melica ciliata</i>	48 ⁺²	.	.	.	13 ⁺
<i>Plantago subulata</i>	.	100 ⁺	64 ⁺²	.	.
<i>Helianthemo cani-Seslerietea nitidae</i> Terzi, Di Pietro et Theurillat 2021					
<i>Koeleria splendens</i>	96 ⁺²	100 ¹	100 ⁺¹	13 ⁺	25 ⁺²
<i>Dianthus virgineus</i>	64 ⁺²	67 ⁺	100 ⁺¹	.	13 ⁺
<i>Carex humilis</i>	88 ⁺³	.	82 ¹⁻²	.	.
<i>Sesleria nitida</i>	36 ⁺²	.	.	.	.
<i>Helianthemum oelandicum</i> subsp. <i>incanum</i>	52 ⁺²	.	100 ⁺²	.	13 ⁺
<i>Helianthemum apenninum</i> subsp. <i>apenninum</i>	72 ⁺²	100 ¹	64 ⁺¹	.	13 ⁺
<i>Satureja montana</i> subsp. <i>montana</i>	60 ⁺¹	.	.	.	50 ⁺²
<i>Festuca</i> spp. (<i>F. inops</i> , <i>F. marginata</i> subsp. <i>marginata</i>)	68 ⁺²	100 ¹⁻²	36 ¹⁻²	38 ⁺²	50 ⁺¹
<i>Linum tenuifolium</i>	24 ⁺¹	33 ⁺	.	25 ⁺	38 ⁺¹
<i>Anthericum liliago</i>	36 ⁺²	.	.	.	.
<i>Centaurea triumfettii</i>	28 ⁺²	.	36 ⁺	.	.
<i>Carex liparocarpos</i> subsp. <i>liparocarpos</i>	8 ⁺	100 ⁺²	.	.	.
<i>Ononis pusilla</i> subsp. <i>pusilla</i>	.	67 ⁺	.	13 ²	.
<i>Valeriana tuberosa</i>	4 ⁺	100 ⁺	27 ⁺	.	.
<i>Cerastium arvense</i> subsp. <i>suffruticosum</i>	.	.	64 ⁺¹	.	13 ⁺
Other species					
<i>Petrosedum rupestre</i>	64 ⁺¹	67 ⁺	100 ⁺¹	.	50 ⁺¹
<i>Poterium sanguisorba</i>	48 ⁺	100 ¹⁻²	.	63 ⁺	75 ⁺²
<i>Dactylis glomerata</i> subsp. <i>glomerata</i>	16 ⁺²	.	.	.	75 ⁺³
<i>Petrorhagia saxifraga</i> subsp. <i>saxifraga</i>	16 ⁺	67 ⁺	36 ⁺	88 ⁺¹	50 ⁺¹
<i>Galium corrudifolium</i>	.	100 ⁺¹	64 ⁺¹	100 ⁺²	13 ⁺
<i>Medicago prostrata</i> subsp. <i>prostrata</i>	.	100 ⁺¹	.	.	13 ⁺
<i>Seseli tommasinii</i>	.	100 ²⁻³	.	.	38 ⁺
<i>Arenaria serpyllifolia</i> subsp. <i>serpyllifolia</i>	48 ⁺	33 ⁺	.	.	.
<i>Anthyllis montana</i> subsp. <i>jacquinii</i>	20 ⁺¹	67 ⁺	64 ⁺	.	.
<i>Eryngium campestre</i>	.	.	.	38 ⁺	63 ⁺²
<i>Cephalaria leucantha</i>	28 ⁺¹	100 ¹	.	38 ¹	50 ⁺²
<i>Crupina vulgaris</i>	12 ⁺	33 ⁺	9 ⁺	50 ⁺¹	50 ⁺²
<i>Bupleurum baldense</i>	.	33 ⁺	.	63 ⁺	13 ⁺
<i>Plantago lanceolata</i>	.	100 ⁺	.	50 ⁺	38 ⁺¹
<i>Hypericum perforatum</i> subsp. <i>perforatum</i>	24 ⁺¹	100 ⁺	.	.	75 ⁺¹
<i>Reichardia picroides</i>	.	.	.	75 ⁺	38 ⁺¹
<i>Ornithogalum comosum</i>	.	67 ⁺	9 ⁺	63 ⁺	.

same time, a floristic uniformity at higher ranks becomes evident, due to the ecological constraints of the habitat. Therefore, given the presence of different diagnostic taxa of the class (*Aethionema saxatile*, *Artemisia alba*, *Centaurea ambigua* subsp. *ambigua*, *Crepis lacera* subsp. *lacera*, *Globularia cordifolia* subsp. *bellidifolia*, *Helianthemum nummularium* subsp. *obscurum*, *Leontodon crispus*, *Linum tommasinii*, and *Thymus striatus* subsp. *striatus*) and the ecological characterization of these grasslands, we

interpret all these communities as belonging to the *Helianthemo cani-Seslerietea nitidae* class described by Terzi et al. (2021). This class encompasses sub-Mediterranean and sub-montane dry grasslands on calcareous substrates, spanning from the Balkan Peninsula to Spain, with the Apennines as the core.

The peculiar biogeographical and floristic features of these communities underline the importance of preserving this vegetation, which displays a relictual and

fragmented distribution along the Apennine chain. These considerations offer an opportunity to include these grasslands under the protection of Habitat 6210 of the Habitats Directive 92/43/EEC (Semi-natural dry grasslands and scrubland facies on calcareous substrates; Biondi et al. 2009), reported in Italy in the Alps and throughout the Apennines. It is worth mentioning that, as indicated by our subassociation *Saponario bellidifoliae-Stipetum apenninicolae stipetosum capillatae*, at hilly and lower elevations these grasslands come into contact with steppe grasslands dominated by *Stipa capillata*, which are protected under the priority Habitat 6240 (Sub-Pannonic steppic grasslands; Biondi et al. 2009). This habitat is reported in Italy only in inner alpine valleys and, more recently, on the southeastern side of the Fucino Basin, within a Natura 2000 area managed by the Abruzzo, Lazio and Molise National Park (Filibeck et al. 2022).

Conclusions

The present work provides an overview of the steppic grasslands of the Velino Massif and surrounding areas, investigating the ecology and syntaxonomy of a relict vegetation dominated by the endemic species *Stipa dasyvaginata* subsp. *apenninicola*. The new association here described characterizes continental mountain communities, often localized in conservative primary sites. Thus, despite the continuous landscape transformations caused by millennial climatic and environmental evolutions during the Pliocene-Holocene (Vera-Polo et al. 2024), the variable pressure along time by livestock grazing (Brown et al. 2013) as well as the different anthropogenic impacts over time (Malone 2003; Mercuri et al. 2019), the mountain biotopes facing the Fucino Basin still preserve species and communities that are unique along the Italian peninsula.

Syntaxonomic scheme

***Helianthemo cani-Seslerietea nitidae* Terzi, Di Pietro et Theurillat 2021**

***Festuco laevigatae-Seslerietalia nitidae* Ubaldi 2003 corr. Terzi, Di Pietro et Theurillat 2021**

***Cytiso-Bromopsion erectae* Bonin 1978 mut. Terzi, Di Pietro et Theurillat 2021**

***Saponario bellidifoliae-Stipetum apenninicolae* Cutini, Zitarelli, De Toma et Marzioletti ass. nova**
Holotypus: Relevé n. 3 [Monte Velino, 42°8'46"N, 13°21'21"E, 04/07/2007, 1540 m a.s.l., 100 sq m, aspect 0.93, slope 30°, rockiness 20%, stoniness 40%, vegetation cover 50%], *Stipa dasyvaginata* subsp. *apenninicola* 4; *Saponaria bellidifolia* +;

Rhamnus saxatilis +; *Bromopsis erecta* +; *Cytisus spinescens* 2; *Galium lucidum* subsp. *lucidum* +; *Sesleria juncifolia* 2; *Aethionema saxatile* +; *Leontodon crispus* +; *Brachypodium genuense* +; *Pimpinella tragiunum* 1; *Seseli montanum* subsp. *montanum* +; *Erysimum pseudorhaeticum* 1; *Cerastium tomentosum* +; *Crepis lacera* subsp. *lacera* +; *Centaurea rupestris* 1; *Thliphthisa purpurea* subsp. *purpurea* 1; *Cynanchica aristata* subsp. *aristata* +; *Anthyllis vulneraria* subsp. *rubriflora* +; *Stachys recta* subsp. *recta* 1; *Polygala major* +; *Artemisia alba* 1; *Teucrium chamaedrys* subsp. *chamaedrys* +; *Teucrium montanum* 1; *Pentanema montanum* +; *Globularia cordifolia* subsp. *bellidifolia* 2; *Carex humilis* 1; *Koeleria splendens* +; *Thymus striatus* subsp. *striatus* 1; *Dianthus virgineus* 1; *Sesleria nitida* 2; *Helianthemum oelandicum* subsp. *incanum* 2; *Satureja montana* subsp. *montana* 1; *Anthericum liliago* 1; *Centaurea triumphetti* +; *Plantago argentea* subsp. *argentea* 1; *Petrosedum rupestre* +; *Arenaria serpyllifolia* subsp. *serpyllifolia* +; *Sempervivum tectorum* +; *Juniperus oxycedrus* +; *Sedum dasyphyllum* subsp. *dasyphyllum* +; *Euphorbia cyparissias* +; *Euphorbia myrsinites* subsp. *myrsinites* +; *Amelanchier ovalis* subsp. *ovalis* +; *Siler montanum* subsp. *stebianum* +; *Daphne oleoides* subsp. *oleoides* +.

***Saponario bellidifoliae-Stipetum apenninicolae stipetosum capillatae* Cutini, Zitarelli, De Toma et Marzioletti subass. nova**

Holotypus: Relevé n. 24 [Collarmele, 42°4'39"N, 13°38'39"E, 24/07/23, 930 m a.s.l., 64 sq m, aspect 1.98, slope 60°, rockiness 30%, stoniness 40%, vegetation cover 60%], *Stipa dasyvaginata* subsp. *apenninicola* 3; *Rhamnus saxatilis* +; *Stipa capillata* 3; *Bromopsis erecta* 3; *Cytisus spinescens* 1; *Festuca inops* 2; *Stachys italica* 1; *Galium lucidum* subsp. *lucidum* 3; *Pimpinella tragiunum* +; *Silene otites* subsp. *otites* +; *Eryngium amethystinum* +; *Melica ciliata* 2; *Anthyllis vulneraria* subsp. *rubriflora* 1; *Teucrium chamaedrys* subsp. *chamaedrys* 1; *Teucrium montanum* +; *Scabiosa columbaria* subsp. *columbaria* +; *Globularia cordifolia* subsp. *bellidifolia* 2; *Carex humilis* 2; *Koeleria splendens* 2; *Thymus striatus* subsp. *striatus* 2; *Dianthus virgineus* 1; *Helianthemum apenninum* subsp. *apenninum* +; *Satureja montana* subsp. *montana* 1; *Petrosedum rupestre* 1; *Dactylis glomerata* subsp. *glomerata* 2; *Arenaria serpyllifolia* subsp. *serpyllifolia* +; *Cephalaria leucantha* 1; *Poterium sanguisorba* +; *Petrorhagia saxifraga* subsp. *saxifraga* +; *Allium flavum* subsp. *flavum* +; *Centaurea ceratophylla* subsp. *ceratophylla* 1; *Cuscuta epithymum* subsp. *epithymum* +; *Silene saxifraga* +.

Other syntaxa quoted in text

Globulario meridionalis-Stipetum capillatae Tammaro 1984; *Lino tommasinii-Stipetum apenninicolae* Pirone, Corbetta, Ciaschetti, Frattaroli et Burri 2001; *Fumano procumbentis-Stipetum apenninicolae* Taffetani, Zitti et Giannangeli 2004; *Lino tommasinii-Stipetum apenninicolae onobrychietosum albae* Ballelli, Gatti, Raponi et Catorci 2006; *Stipo apenninicolae-Seslerietum juncifoliae* Catorci, Gatti et Ballelli 2007.

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References

- Adler P, Raff D, Lauenroth W (2001) The effect of grazing on the spatial heterogeneity of vegetation. *Oecologia* 128: 465–479. <https://doi.org/10.1007/s004420100737>
- Ballelli S, Gatti R, Raponi M, Catorci A (2006) Aspetti vegetazionali e floristici del territorio nursino (Umbria-Italia centrale): le serie di vegetazione della roverella (*Quercus pubescens* s.l.). *Webbia* 61(2): 305–323. <https://doi.org/10.1080/00837792.2006.10670808>
- Bartolucci F, Conti F (2016) *Alyssum desertorum* Stapf (Brassicaceae), new for the Italian flora. *Acta Botanica Croatica* 75(1): 149–152. <https://doi.org/10.1515/botcro-2016-0006>
- Bartolucci F, Peruzzi L, Galasso G, Alessandrini A, Ardenghi NMG, ... Conti F (2024) A second update to the checklist of the vascular flora native to Italy. *Plant Biosystems* 158(2): 219–296. <https://doi.org/10.1080/11263504.2024.2320126>
- Becker T (2010) Explaining rarity of the dry grassland perennial *Astragalus exscapus*. *Folia Geobotanica* 45(3): 303–321. <https://doi.org/10.1007/s12224-010-9068-3>
- Biondi E, Allegrezza M, Zuccarello V (2005) Syntaxonomic revision of the Apennine grasslands belonging to *Brometalia erecti*, and an analysis of their relationships with the xerophilous vegetation of *Rosmarineta officinalis* (Italy). *Phytocoenologia* 35(1): 129–163. <https://doi.org/10.1127/0340-269X/2005/0035-0129>
- Biondi E, Blasi C, Burrascano S, Casavecchia S, Copiz R, ... Zivkovic L (2009) Manuale Italiano di interpretazione degli habitat della Direttiva 92/43/CEE. <https://www.vnr.unipg.it/habitat/>
- Braun-Blanquet J (1932) *Plant Sociology. The Study of Plant Communities*. McGraw-Hill.
- Bray JR, Curtis JT (1957) An Ordination of the Upland Forest Communities of Southern Wisconsin. *Ecological Monographs* 27(4): 325–349. <https://doi.org/10.2307/1942268>
- Brown AG, Hatton J, Selby KA, Leng MJ, Christie N (2013) Multi-proxy study of Holocene environmental change and human activity in the Central Apennine Mountains, Italy. *Journal of Quaternary Science* 28(1): 71–82. <https://doi.org/10.1002/jqs.2591>
- Brullo S, Scelsi F, Spampinato G (1998) Considerazioni sintassonomiche sulla vegetazione perenne pioniera dei substrati incoerenti dell'Italia meridionale e Sicilia. *Itinera Geobotanica* 11: 403–424.
- Cancellieri L, Sperandii MG, Filibeck G (2017) First record of the stepic relict *Astragalus exscapus* L. subsp. *exscapus* in the Apennines (Abruzzo, Italy), and biogeographic implications. *Plant Biosystems* 151(6): 944–948. <https://doi.org/10.1080/11263504.2017.1311963>
- Cancellieri L, Rosati L, Brunetti M, Mancini LD, Primi R, ... 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. *Tuxenia* 40: 547–571. <https://doi.org/10.14471/2020.40.019>
- Cancellieri L, Sperandii MG, Rosati L, Bellisario B, Franceschini C, ... Filibeck G (2024) Drivers of vascular plant, bryophyte and lichen richness in grasslands along a precipitation gradient (central Apennines, Italy). *Journal of Vegetation Science* 35(5): e13305. <https://doi.org/10.1111/jvs.13305>
- Catorci A, Gatti R, Ballelli S (2007) Studio fitosociologico della vegetazione delle praterie montane dell'Appennino maceratese (Italia centrale). *Braun-Blanquetia* 42: 101–143.
- Cavinato GP, Carusi C, Dall'Asta M, Miccadei E, Piacentini T (2002) Sedimentary and tectonic evolution of Plio-Pleistocene alluvial and lacustrine deposits of Fucino Basin (central Italy). *Sedimentary Geology* 148(1–2): 29–59. [https://doi.org/10.1016/S0037-0738\(01\)00209-3](https://doi.org/10.1016/S0037-0738(01)00209-3)
- Chytrý K, Willner W, Chytrý M, Divíšek J, Dullinger S (2022) Central European forest–steppe: An ecosystem shaped by climate, topography and disturbances. *Journal of Biogeography* 49: 1006–1020. <https://doi.org/10.1111/jbi.14364>
- Conti F, Tinti D, Scassellati E, Bartolucci F, Di Santo D (2007) Le piante vascolari endemiche dell'Appennino centrale. *Biogeographia* 28: 25–38. <https://doi.org/10.21426/B6110093>
- Conti F, Bartolucci F (2023) Taxonomy and Distribution of *Spiraea hypericifolia* in Italy and Typification of the Name *S. flabellata* (Rosaceae). *Plants* 12(3): 536. <https://doi.org/10.3390/plants12030536>

- Conti F, Oberprieler C, Dorfner M, Schabel E, Nicoară R, Bartolucci F (2023) *Adonis fucensis* (A. sect. *Adonanthe*, Ranunculaceae), a new species from the Central Apennines (Italy). *Biology* 12(1): 118. <https://doi.org/10.3390/biology12010118>
- Corbetta G, Pirone G (1981) La vegetazione di Monte Alpi e zone contermini (Tavoletta “Latronico” della Carta d’Italia). Collana del Programma Finalizzato “Promozione della Qualità dell’Ambiente”, AQ/1/122. CNR: 1–38.
- Crespi A, Brunetti M, Lentini G, Maugeri M (2018) 1961–1990 high-resolution monthly precipitation climatologies for Italy. *International Journal of Climatology* 38(2): 878–895. <https://doi.org/10.1002/joc.5217>
- Cutini M, Stanisci A, Pirone G (2002) L’alleanza *Berberidion vulgaris* in Appennino centrale (Italia centrale). *Fitosociologia* 39(2): 31–50.
- Cutini M, Marzioletti F, Barbato G, Rianna G, Theurillat JP (2021) Bioclimatic pattern in a Mediterranean mountain area: assessment from a classification approach on a regional scale. *International Journal of Biometeorology* 65: 1085–1097. <https://doi.org/10.1007/s00484-021-02089-x>
- Dengler J, Janisövä M, Török P, Wellstein C (2014) Biodiversity of Palaearctic grasslands: a synthesis. *Agriculture, Ecosystems and Environment* 182: 1–14. <https://doi.org/10.1016/j.agee.2013.12.015>
- Di Lena B, Vergni L, Antenucci F, Todisco F, Mannocchi F (2014) Analysis of drought in the region of Abruzzo (Central Italy) by the Standardized Precipitation Index. *Theoretical and Applied Climatology* 115: 41–52. <https://doi.org/10.1007/s00704-013-0876-2>
- Di Pietro R, Catonica C (1999) *Festuca pallens* Host, a new species of the Italian flora in the central Apennines. *Ecological and phytosociological considerations*. *Plant Biosystems* 133(2): 173–183. <https://doi.org/10.1080/11263509909381546>
- Di Pietro R, Theurillat JP, Capelo J, Fernández-González F, Terzi M, ... Mucina L (2015) Nomenclature and syntaxonomic notes on some high-rank syntaxa of the European grassland vegetation. *Lazaroa* 36: 79–106. https://doi.org/10.5209/rev_LAZA.2015.v36.50835
- Di Pietro R, Terzi M, Fortini P (2017) A revision of the high-altitude acidophilous and chionophilous grasslands of the Apennines (Peninsular Italy), a long-lasting intricate syntaxonomic issue. *Phytocoenologia* 47(3): 261–304. <https://doi.org/10.1127/phyto/2017/0162>
- Divišek J, Večeřa M, Welk E, Danihelka J, Chytrý K, ... Chytrý M (2022) Origin of the central European steppe flora: insights from palaeodistribution modelling and migration simulations. *Ecography*: e06293. <https://doi.org/10.1111/ecog.06293>
- Fanelli G, Lucchese F, Paura B (2001) Le praterie a *Stipa austroitalica* di due settori adriatici meridionali (Molise e Gargano). *Fitosociologia* 38(2): 25–36.
- Feurdean A, Ruprecht E, Molnar Z, Hutchinson SM, Hickler T (2018) Biodiversity-rich European grasslands: ancient, forgotten ecosystems. *Biological Conservation* 228: 224–232. <https://doi.org/10.1016/j.biocon.2018.09.022>
- Filibeck G, Cancellieri L, Bartolucci F, Becker U, Conti F, ... Becker T (2020) *Festuca valesiaca* Schleich. ex Gaudin newly discovered in the Central Apennines (Italy): a further example of steppe relict in the Abruzzo “dry valleys”. *Plant Biosystems* 154(5): 593–600. <https://doi.org/10.1080/11263504.2019.1651784>
- Filibeck G, Cancellieri L, Rosati L (2022) Carta dei Tipi di Habitat di Interesse Comunitario (Direttiva 92/43/CEE) del Parco Nazionale d’Abruzzo, Lazio e Molise e dei siti Natura 2000: ZSC IT7110205, ZPS IT7120132, ZSC IT6050018, ZSC IT6050020, ZSC IT7212121 – Note Illustrative. Università degli Studi della Tuscia, Viterbo, 114 pp. [ISBN 978-88-903361-5-7]
- Giaccio B, Leicher N, Mannella G, Monaco L, Regattieri E, ... Tzedakis PC (2019) Extending the tephra and palaeoenvironmental record of the Central Mediterranean back to 430 ka: A new core from Fucino Basin, central Italy. *Quaternary Science Reviews* 225: 106003. <https://doi.org/10.1016/j.quascirev.2019.106003>
- Hejcman M, Hejcmanová P, Pavlů V, Beneš J (2013) Origin and history of grasslands in Central Europe – a review. *Grass and Forage Science* 68(3): 345–363. <https://doi.org/10.1111/gfs.12066>
- Hensen I, Kilian C, Wagner V, Durka W, Pusch J, Wesche K (2010) Low genetic variability and strong differentiation among isolated populations of the rare steppe grass *Stipa capillata* L. in Central Europe. *Plant Biology* 12: 526–536. <https://doi.org/10.1111/j.1438-8677.2009.00227.x>
- Kajtoch Ł, Cieślak E, Varga Z, Paul W, Mazur MA, ... Kubisz D (2016) Phylogeographic patterns of steppe species in Eastern Central Europe: a review and the implications for conservation. *Biodiversity and Conservation* 25(12): 2309–2339. <https://doi.org/10.1007/s10531-016-1065-2>
- Kirschner P, Závěská E, Gamisch A, Hilpold A, Trucchi E, ... Schönswetter P (2020) Long-term isolation of European steppe outposts boosts the biome’s conservation value. *Nature Communications* 11: 1968. <https://doi.org/10.1038/s41467-020-15620-2>
- Malone C (2003) The Italian Neolithic: A Synthesis of Research. *Journal of World Prehistory* 17(3): 235–312. <https://doi.org/10.1023/B:JOWO.0000012729.36053.42>
- Martinovský JO, Moraldo B (1980) *Stipa martinovskii* (Gramineae), nuova specie dell’Appennino centrale. *Webbia* 37(1): 23–28. <https://doi.org/10.1080/00837792.1983.10670261>
- Moraldo B (1986) Il genere *Stipa* L. (Gramineae) in Italia. *Webbia* 40(2): 203–278. <https://doi.org/10.1080/00837792.1986.10670388>
- Mucina L, Bültmann H, Dierßen K, Theurillat JP, Raus T, ... Tichý L (2016) Vegetation of Europe: Hierarchical floristic classification system of vascular plant, bryophyte, lichen, and algal communities. *Applied Vegetation Science* 19(1): 3–264. <https://doi.org/10.1111/avsc.12257>
- Napoleone F, Giarrizzo E, Burrascano S (2021) Habitat conservation state and plant diversity respond to different drivers in semi-natural grasslands. *Journal of Vegetation Science* 32(4): e13055. <https://doi.org/10.1111/jvs.13055>
- Oksanen J, Simpson GL, Blanchet FG, Kindt R, Legendre P, ... Weedon J (2025) *vegan*: Community Ecology Package. R package version 2.7-1. <https://CRAN.R-project.org/package=vegan>
- Pesaresi S, Biondi E, Casavecchia S (2017) Bioclimates of Italy. *Journal of Maps* 13(2): 955–960. <https://doi.org/10.1080/17445647.2017.1413017>
- Petriccione B (1993) Flora e vegetazione del massiccio del Monte Velino (Appennino Centrale), comprendente il territorio della Riserva Naturale Orientata «Monte Velino» e della foresta demaniale «Montagna della Duchessa». Ministero dell’Agricoltura e delle Foreste, Corpo Forestale dello Stato, Collana Verde 92.

- Pezzetta A (2011) La flora endemico-vicariante delle penisole italiana e balcanica: origini e distribuzione geografica. *Annales: Series Historia Naturalis* 21(1): 41–66.
- Pignatti S (2017–2019) Flora d'Italia. Volumi I, II, III, IV. Edagricole.
- Pirone G, Corbetta F, Ciaschetti G, Frattaroli AR, Burri E (2001) Contributo alla conoscenza delle serie di vegetazione del piano collinare della Valle del Tirino (Abruzzo, Italia Centrale). *Fitosociologia* 38(2): 3–23.
- Pirone G, Cutini M (2002) *Juniperus oxycedrus* L. subsp. *oxycedrus* and *Paliurus spina-christi* Miller scrubs in the intermontane areas of the Abruzzo region (Central Apennine, Central Italy). *Fitosociologia* 39(1): [S2:] 81–95.
- Pokorný P, Chytrý M, Juříčková L, Sádlo J, Novák J, Ložek V (2015) Mid-Holocene bottleneck for central European dry grasslands: Did steppe survive the forest optimum in northern Bohemia, Czech Republic? *The Holocene* 25(4): 716–726. <https://doi.org/10.1177/0959683614566218>
- R Core Team (2025) R: A language and environment for statistical computing. R Foundation for Statistical Computing. <http://www.r-project.org/>
- Roberts CA, Zanchetta G, Giaccio B, Nomade S, Mannella G, ... Tzedakis PC (2025) A radiometrically-constrained reference record of Last Interglacial climate and vegetation changes from the Fucino Basin, Central Italy. *Quaternary Science Reviews* 363: 109377. <https://doi.org/10.1016/j.quascirev.2025.109377>
- Sadori L, Giraudi C, Petitti P, Ramrath A (2004) Human impact at Lago di Mezzano (central Italy) during the Bronze Age: a multidisciplinary approach. *Quaternary International* 113(1): 5–17. [https://doi.org/10.1016/S1040-6182\(03\)00077-6](https://doi.org/10.1016/S1040-6182(03)00077-6)
- Spada F, Cutini M, Paura B (2010) Floristic changes along the topographical gradient in montane grasslands in Monti Picentini (Campania, SW Italy). *Annali di Botanica*.
- Spada F, Cutini M, Paura B (2011) Considerazioni fitostoriche sulla zonazione altitudinale della vegetazione di alcuni rilievi dell'Appennino meridionale e della Sicilia. *Biogeographia* 30(1): 95–112. <https://doi.org/10.21426/B630110559>
- Taffetani F, Zitti S, Giannangeli A (2004) Vegetazione e paesaggio vegetale della dorsale di Cingoli (Appennino Centrale, Dorsale Marchigiana). *Fitosociologia* 41(2): [S1:] 83–161.
- Tammaro F (1984) Vegetazione dei pascoli aridi a *Stipa capillata* L. nell'Appennino centrale. *Informatore botanico italiano* 16(2–3): 191–197.
- Terzi M, D'Amico FS (2016) Dry grasslands of *Hippocrepido glaucae-Stipion austroitalicae* in the Pollino Massif (Calabria, Italy). *Acta Botanica Croatica* 75(1): 89–98. <https://doi.org/10.1515/botcro-2016-0013>
- Terzi M, Di Pietro R, Theurillat JP (2021) Nomenclature of Italian syntaxa of the classes *Festuco hystricis-Ononidetia striatae* and *Rumici-Astragaletea siculi*. *Plant Biosystems* 155(6): 1213–1225. <https://doi.org/10.1080/11263504.2021.2013338>
- Török P, Neuffer B, Heilmeyer H, Bernhardt KG, Wesche K (2020) Climate, landscape history and management drive Eurasian steppe biodiversity. *Flora* 271: 151685. <https://doi.org/10.1016/j.flora.2020.151685>
- van der Maarel E (2007) Transformation of cover-abundance values for appropriate numerical treatment – Alternatives to the proposals by Podani. *Journal of Vegetation Science* 18: 767–770. <https://doi.org/10.1111/j.1654-1103.2007.tb02592.x>
- Vera-Polo P, Sadori L, Jiménez-Moreno G, Masi A, Giaccio B, ... Wagner B (2024) Climate, vegetation, and environmental change during the MIS 12–MIS 11 glacial-interglacial transition inferred from a high-resolution pollen record from the Fucino Basin of central Italy. *Palaeogeography, Palaeoclimatology, Palaeoecology* 655: 112486. <https://doi.org/10.1016/j.palaeo.2024.112486>
- Walter H, Breckle SW (2002) *Walter's Vegetation of the Earth. The Ecological Systems of the Geobiosphere.* 4th Edition, Springer-Verlag, Berlin.
- Wesche K, Ambarlı D, Kamp J, Török P, Treiber J, Dengler J (2016) The Palaearctic steppe biome: a new synthesis. *Biodiversity and Conservation* 25: 2197–2231. <https://doi.org/10.1007/s10531-016-1214-7>
- Wickham H (2016) *ggplot2: Elegant Graphics for Data Analysis.* Springer-Verlag New York. [ISBN 978-3-319-24277-4] <https://ggplot2.tidyverse.org>
- Willner W, Moser D, Plenck K, Acic S, Demina ON, ... Kropf M (2021) Long-term continuity of steppe grasslands in eastern Central Europe: Evidence from species distribution patterns and chloroplast haplotypes. *Journal of Biogeography* 48: 3104–3117. <https://doi.org/10.1111/jbi.14269>

Supplementary material 1

Main biological forms and chorotype categories

Authors: Claudia Zitarelli, Andrea De Toma, Flavio Marzialetti, Maurizio Cutini

Data type: docx

Explanation note: The supplementary file includes tables reporting main biological forms and chorotype categories.

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Link: <https://doi.org/10.3897/ved.167266.suppl1>

Supplementary material 2

Main characteristics of the two clusters

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Data type: docx

Explanation note: The supplementary file includes tables reporting main characteristics of the two subclusters from the sampled dataset.

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Supplementary material 3

Phytosociological relevés

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Data type: docx

Explanation note: The supplementary file includes a table reporting full phytosociological relevés, and information about date, site, and list of sporadic species for each relevé.

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Link: <https://doi.org/10.3897/ved.167266.suppl3>

Supplementary material 4

Sporadic species of the synoptic table

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Data type: docx

Explanation note: The supplementary file includes the list of sporadic species of the synoptic table.

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