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The dry grasslands of Abruzzo National Park, the oldest protected area in the Apennines (Central Italy): overview of vegetation composition, syntaxonomy, ecology and diversity

Das trockene Grasland des Abruzzen-Nationalparks, des ältesten Schutzgebiets im Apennin (Mittelitalien): Überblick über Vegetationszusammensetzung, Syntaxonomie, Ökologie und Vielfalt

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Abstract

The Abruzzo, Lazio and Molise National Park was established in 1923 and is considered a flagship conservation area in Italy. It includes large extensions of semi-natural grasslands, maintained by traditional transhumant grazing for centuries. The patterns and drivers of grassland composition within the Park are still poorly investigated, and the scattered phytosociological data available were often based on relevés with varied and not precisely defined sizes.

In order to provide for the first time a general overview of the Park's dry grasslands, we analysed a dataset of 87 relevés with a fixed size of 2 × 2 m, precisely delimited in the field and GPS-located. Specific research aims were: (1) to classify the vegetation plots into floristic-ecological types, supported by an analysis of mean (Italy-specific) Ellenberg Indicator Values (EIVs); (2) to assign the types to up-to-date phytosociological syntaxa; (3) to identify the main environmental drivers for both composition and richness patterns; (4) to test the degree of correlation between (Italy-specific) EIVs and the measured environmental variables.

Environmental predictors included high-resolution climatologies and remote-sensed standing biomass. Main vegetation types were identified using Hierarchical Cluster Analysis (HCA). Distance-based RDA was performed as a constrained ordination method to reveal correlations between floristic composition and environmental variables. Drivers of species richness were explored through partial correlation and Regression Trees.

HCA and NMDS revealed four floristically and ecologically well-interpretable groups, in turn well corresponding to the level of phytosociological class (namely *Molinio-Arrhenatheretea*, *Nardetea strictae*, *Festuco hystricis-Ononidetea striatae* and *Festuco-Brometea*). Constrained ordination showed that most of the floristic variation was explained by biomass, annual precipitation (P_{ann}) and mean annual temperature (T_m). Strong and significant positive correlations were found between biomass and

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EIV for Nitrogen (EIV-N), and between T_m and EIV for Temperature (EIV-T). Strong and significant negative correlations were found between P_{ann} and EIV-T, EIV for Continentality (EIV-C) and EIV for soil Reaction (EIV-R). Species richness was positively correlated with slope inclination and negatively with elevation; richness was higher in sites with a high rock cover, and on limestone or clayey substrata than on siliceous ones.

We conclude that in the study area: a) dry semi-natural grasslands are arranged at least into four distinguishable, high rank floristic-ecological groups; b) a mixture of climatic (especially precipitation) and edaphic (especially bedrock and soil reaction) gradients are the main drivers of such composition patterns; c) species richness is higher in sites more stressed by summer drought and/or nutrient scarcity; d) community-means of Italy's specific EIVs are well correlated with environmental variables in grasslands, including a good correspondence between EIV-T and mean annual temperature.

Keywords: Ellenberg indicator value, environmental variable, EuroVegChecklist, pasture, phytosociology, semi-natural grassland, species richness

Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Knowledge about patterns of floristic composition and biodiversity in grasslands is crucial for applied purposes such as conservation assessment and habitat monitoring (e.g. HABEL et al. 2013, SOPOTLIEVA et al. 2018). Southern-European secondary grasslands are relatively understudied compared to their Central-European counterparts, yet they harbour a rich flora and are placed at a biogeographical and historical crossroad (APOSTOLOVA et al. 2014, PALPURINA et al. 2015, FILIBECK et al. 2019). In the Apennine mountains (Italy), semi-natural grasslands extend over vast areas and are of high conservation and management interest. Transhumant sheep and goat grazing heavily shaped Apennine landscapes already in 6th century BC or earlier (BROWN et al. 2013); nowadays, most of the communities correspond to protected habitat types (EUROPEAN UNION 1992) and play a key role in the conservation of endangered fauna (e.g. PRIMI et al. 2016) and flora (e.g. FILIBECK et al. 2020). However, they are threatened by land abandonment, fast reforestation processes and management changes (e.g. BRACCHETTI et al. 2012, CANCELLIERI et al. 2017a).

The Abruzzo, Lazio & Molise National Park (formerly known as Abruzzo National Park) is one of the oldest protected areas in Europe, established in 1923 to protect two endemic and charismatic mammals (*Ursus arctos* subsp. *marsicanus* and *Rupicapra pyrenaica* subsp. *ornata*); the area also hosts a large population of wolf (*Canis lupus*). In the 1970–80's this Park set the standards for national park zonation and ecotourism in Italy, and at the same time famously resisted to attempts of land development; nowadays it still represents a landmark in the history of nature conservation in Italy, and an extremely important "flagship" conservation area (SIEVERT 1999, PRATESI 2011).

Surprisingly, composition patterns of dry grasslands and their classification are still poorly investigated within the Park, especially in the montane belt. A pioneer work by BAZZICHELLI & FURNARI (1979) addressed some grassland types in the subalpine belt. Later on, BIONDI et al. (1992) published a preliminary study on a small area of the submontane belt; some acidophilous grasslands were surveyed by DI PIETRO et al. (2005); both PETRICCIONE & PERSIA (1995) and D'ANGELI et al. (2011) present, in synoptic tables, some data from the subalpine grasslands of the Park; finally, CIASCHETTI et al. (2016) described the chamaephyte-dominated grasslands of a subalpine sector. A detailed work by PEDROTTI et al. (1992) concerned exclusively wet or meso-hygrophytic meadows.

Unfortunately, even these phytosociological data were often based on relevés with varied (and sometimes undefined) size; the relevés were not delimited in the field and had vague boundaries or irregular shapes. However, quadrat size influences estimates of species richness and other vegetation parameters, as well as floristic composition and species constancy (DENGLER et al. 2008, 2018): vegetation sampling with differently-sized relevés may yield different classifications, and only plots of equal size should be used for rigorous classification purposes (CHYTRÝ & OTÝPKOVÁ 2003).

In this paper, in order to provide for the first time a general overview of the Park's dry grasslands, we analysed a dataset of 87 precisely delimited, fixed-size (4 m^2) and GPS-located relevés – these were originally surveyed to provide data for the management plan of the Park's pastures (see PRIMI et al. 2016) and remained so far unpublished. Our specific research aims were: (1) to classify the vegetation plots into floristic-ecological types, supported by an analysis of mean Ellenberg Indicator Values (EIVs) using the values calibrated for the Italian flora (PIGNATTI et al. 2005); (2) to assign these types to up-to-date phytosociological syntaxa; (3) to identify the main environmental drivers for both composition and richness patterns; (4) to test the degree of correlation between (Italy-specific) EIVs and measured environmental variables.

2. Study area

The study area lies within the Central Apennine mountains (Italy) and includes Abruzzo, Lazio & Molise National Park and the adjoining Natura 2000 sites, with a total area of 79,500 ha (Fig. 1). Elevation ranges between 500 and 2249 m, with most of the area lying between c. 1100 and 1900 m, i.e. within the montane phytoclimatic belt of the Apennines. Prevailing bedrock types are Mesozoic limestones and dolomites; clayey and marly substrates also occur (BIGI et al. 1986). A steep gradient in annual precipitation can be observed from ca. 700–800 mm/yr in the rain-shadow areas bordering the Fucino basin to > 1600 mm/yr in the upper Sangro valley (CRESPI et al. 2018). However, the precipitation regime is Mediterranean, with marked decrease in summer, leading to drought stress and a fall in grassland productivity that takes place already in June at low elevation, and in July–August in the upper-montane and subalpine belts (PRIMI et al. 2016). Mean annual temperatures range from > 10 °C in the colline belt (i.e. below 800 m a.s.l.) to c. 6–8 °C in the montane belt (800–1800 m) and < 4 °C in the subalpine belt (i.e. above 1800 m) (BRUNETTI et al. 2014, FILIBECK et al. 2015).

Forest vegetation is dominated by *Quercus pubescens* and/or *Q. cerris* at low elevation, while above ca. 1100 m a.s.l. and up to the tree-line is made up almost exclusively of *Fagus sylvatica*. The natural tree-line is reached at approx. 1900 m, and is followed by prostrated shrub vegetation dominated by *Juniperus communis* subsp. *nana* (for details on the Park's vegetation belts see BRUNO & BAZZICHELLI 1966). The park's flora comprises > 2100 taxa, including > 30 taxa endemic to the central Apennine mountains (CONTI & BARTOLUCCI 2015).

Transhumant stocking based on mixed grazing of sheep and goat was the main pasture exploitation system in the study area for millennia (LLOYD et al. 1997, BROWN et al. 2013) and was widely practiced until the 1950s, when small ruminant farming started to dramatically decrease (MANZI 2012). Most of the husbandry is now sedentary. Pastureland usually belongs to the municipality and local farmers obtain grazing rights from the mayor. Present-day stocking rate is drastically lower than in the early twentieth century (PRIMI et al. 2016); however, the abandonment of sheep and goat husbandry has been followed by an increase in

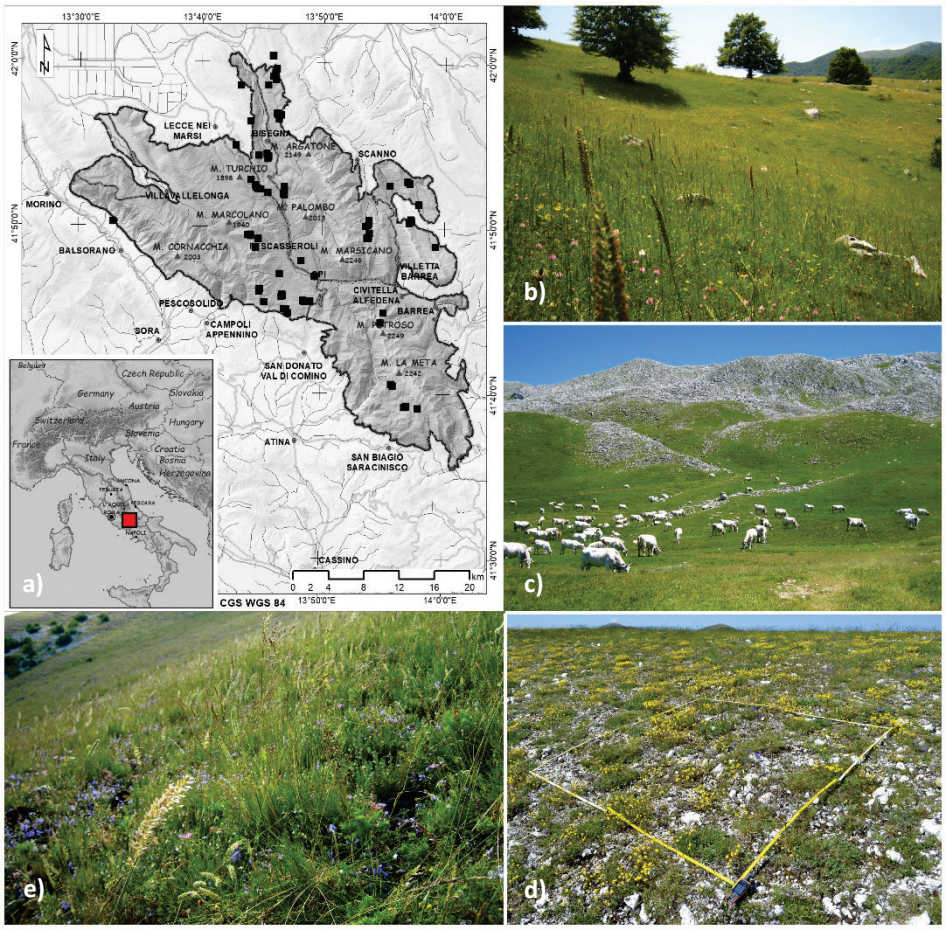


Fig. 1. a) Study area position (red square in the inset) and physiography (main map), with distribution of sampling points (black filled squares). Dashed line: study area boundary (Abruzzo Lazio & Molise National Park, and adjoining Natura 2000 sites). **b–e)** Photos of typical communities of the four main grassland types detected: **b)** cluster 1, with *Cynosurus cristatus* in the foreground; **c)** cluster 2, with free-ranging cattle grazing in a deep-soil karst depression dominated by *Nardus stricta*; **d)** cluster 3, with a vegetation plot delimited on the ground and yellow flowers of *Helianthemum oelandicum*; **e)** cluster 4, with *Koeleria splendens* in the foreground (Map: own elaboration based on publicly available DTM data provided by ISPRA, http://www.sinanet.isprambiente.it/it/sia-ispra/download-mais) (Photos b, c, e: G. Filibeck, d: L. Cancellieri, 2013).

Abb. 1. a) Lage des Untersuchungsgebietes (rotes Quadrat in der kleinen Karte) sowie Geografie und Begrenzung des Untersuchungsgebietes (Abruzzo Lazio & Molise National Park und angrenzende Natura 2000-Flächen; gestrichelte Linie) sowie räumliche Verteilung der Aufnahmenflächen (schwarze Quadrate, beides in der großen Karte). **b–e)** Fotos typischer Bestände der vier unterschiedenen Haupttypen halbnatürlicher Grasländer: **b)** Cluster 1: mit *Cynosurus cristatus* im Vordergrund; **c)** Cluster 2 mit frei weidenden Rindern in einer tiefgründigen Karstdepression, dominiert von *Nardus stricta*; **d)** Cluster 3: mit einer abgegrenzten Aufnahmefläche und den gelben Blüten von *Helianthemum oelandicum*; **e)** Cluster 4 mit *Koeleria splendens* im Vordergrund (Karte: eigene Ausarbeitung basierend auf öffentlich verfügbaren DTM-Daten von ISPRA) (Fotos b, c, e: G. Filibeck, d: L. Cancellieri, 2013).

free-ranging cattle and horses. These animals are farmed for meat production only and are left in the wild with minimum checking for many months (see for details: LLOYD et al. 1997, PRIMI et al. 2016). Red deer (*Cervus elaphus*) was reintroduced in 1970's and is now very abundant. Hay was traditionally necessary only for the small population of livestock not involved in transhumance (MANZI 1990): therefore, mowing has never been a large-scale management option, and hay-meadows were, and still are, restricted to the more productive habitats, such as alluvial plains or karst depressions (cf. PEDROTTI et al. 1992).

3. Material and methods

3.1 Data collection

Sampling took place in June–July 2013. A total of 87 relevés was surveyed. The quadrats were GPS-located, had a fixed size of 2 × 2 m and were precisely delimited on the ground by means of a ruler. They were placed in sites that were considered as representative of each grassland type, within stands of visually homogeneous vegetation. Because of the original purpose of the sampling (assessment of carrying capacity of mountain pastures), the great majority of the relevés was distributed between 1200 and 1800 m a.s.l., i.e. in the montane phytoclimatic belt of the Apennines; a few relevés were surveyed in the colline, submontane and (lower-)subalpine belts. The 4 m^2 size for quadrats was chosen (within the framework of the wider research project: PRIMI et al. 2016) as a trade-off between representativeness of the community's floristic composition, precision of species cover estimates and surveying time. All vascular plant species in the quadrat were recorded following the shoot-presence convention (CANCELLIERI et al. 2017b), and their cover was visually estimated according to the Braun-Blanquet scale; total cover of vegetation was visually estimated on a percentage scale.

A number of environmental variables were associated to each relevé (Table 1). Rock and stone cover values were visually estimated in the field, on a percentage scale (percentage cover of rocks and stones were recorded separately, but were summed up in a joint "rock & stone cover" variable for statistical analyses). Elevation, slope inclination and slope aspect were measured in the field. For statistical analyses, aspect was converted to radians and then to a southing index S with the formula S = -cos(aspect)+1. A heat-load topographical index was calculated using inclination, aspect and

Table 1. Descriptive statistics of the environmental variables, and of above-ground plant biomass, measured for the 87 relevés analyzed in this study. P_{ann} = annual precipitation; I_c = continentality index; T_m = mean annual temperature.

Tabelle 1. Beschreibende Statistik der Umweltvariablen und der oberirdischen Biomasse für die 87 Vegetationsaufnahmen dieser Studie. P_{ann} = mittlerer Jahresniederschlag; I_c = Kontinentalitätsindex T_m = Jahresmitteltemperatur.

	Min–Max	Mean ± standard error
Elevation (m)	576–1940	1549.3 ± 27.3
Slope inclination (°)	0–40	13.1 ± 1.3
Aspect (Southing index)	-1–1	0.22 ± 0.10
Rock & stone cover (%)	0–82	12.0 ± 1.9
Heat-load index	0.5–1	0.8 ± 0.01
P_{ann} (mm)	908–1506	1291.1 ± 18.9
I_c (°C)	15.3–17.8	16.8 ± 0.06
T_m (°C)	4.3–12.7	6.8 ± 0.2
Biomass (kg/ha)	1148–12446	4924± 347
Bedrock (categorical) (number of cases in each category)	Clay (8), Conglomerate (4), Debris (24), Limestone (40), Siliceous (11)	

latitude, following MCCUNE & KEON (2002). Bedrock type was noted in the field, then checked with the Park's geological map (BIGI et al. 1986) and finally grouped into five macro-types: clay, conglomerate, debris, limestone and siliceous. Above-ground biomass was estimated from Normalized Difference Vegetation Index (NDVI), calculated from Landsat 7 images and calibrated with field data (see PRIMI et al. 2016 for the detailed procedure). It is expressed as fresh-weight kg/ha, and is referred to the 30 × 30 m Landsat pixel each quadrat belongs to.

Climate data were obtained from BRUNETTI et al. (2014) and CRESPI et al. (2018), where 1961–1990 high-resolution climatologies of monthly mean temperatures and of total monthly precipitation are presented for the whole Italian territory at 30 arc-second resolution. Following the same technique of BRUNETTI et al. (2014), also 1961–1990 monthly minimum and maximum temperature climatologies were reconstructed for the same grid cells. From the meteorological variables, the following parameters of bioclimatic significance (CANU et al. 2015, FILIBECK et al. 2015) were calculated as means on the time series and used as explanatory variables for species richness and composition, as well as to test the performances of (climatic) EIVs: mean annual temperature (T_m), total annual precipitation (P_{ann}) and continentality index (I_c, that is the difference between mean temperature of the hottest and coldest months of the year: RIVAS-MARTINEZ et al. 2011).

Taxa were identified mainly following PIGNATTI (1982). Given that the genus *Festuca* (one of the dominant taxa in the study vegetation) in C-Italy has a critical taxonomy and a scarcely known distribution of its species (FILIBECK et al. 2020), *Festuca* specimens were carefully collected in each relevé for identification through transverse section of tiller leaves, following FOGGI & ROSSI (1996) and FOGGI et al. (1999). The genus *Stipa* was identified using MORALDO (1986), while *Potentilla* followed TISON & MALÉCOT (2007). Nomenclature was standardized according to PIGNATTI (1982), except the names obtained from the above-mentioned monographs. Life-forms were obtained from PIGNATTI et al. (2005). Syntaxonomical framework and species attribution to syntaxa followed EuroVegChecklist (MUCINA et al. 2016). The Ellenberg Indicator Values (EIVs) specific for the Italian flora were obtained, for each recorded species, from PIGNATTI et al. (2005). The EIVs characterize the adaptation of a plant to edaphic and climatic conditions in comparison with other species (ELLENBERG et al. 1991). A 9- or 12-point ordinal scale for each of the following parameters is used: temperature (T), light (L), continentality (C), soil moisture (U), soil nitrogen status (N), soil pH (R) and salinity – this latter was not used in this study since not informative for Apennines' grasslands. We calculated for each relevé an abundance-weighted mean indicator value (even if differences in effectiveness between simple community means and weighted means are usually negligible: e.g. SCHAFFERS & SÝKORA 2000, FILIBECK et al. 2015).

3.2 Data analysis

3.2.1 Composition patterns and drivers, and EIVs

Main vegetation types were identified through Hierarchical Cluster Analysis (HCA) and NMDS ordination. HCA was performed using the modified TWINSPAN procedure (ROLEČEK et al. 2009) available in JUICE 7.0 (TICHÝ 2002). Four pseudospecies cut levels (0%, 5%, 25%, 50%) and total inertia as a measure of cluster heterogeneity were used. To obtain a significant number of clusters and to determine their characteristic species combination, we calculated the ''phi coefficient'' as a fidelity measure with equalization of cluster sizes. We considered diagnostic a species with $phi > 0.45$ and Fisher's exact test at $p < 0.001$ (ILLYÉS et al. 2009). Constant species were defined as those with a frequency > 50% within each group. Dominant species were defined as those occurring in at least 25% of the relevés of a given group with a cover value > 25%. Classification was stopped at the best judged interpretable level between those indicated by the results of OptimClass analysis performed in JUICE. Ecological interpretation of clusters was supported by EIVs. A permutational multivariate analysis of variance (PERMANOVA: ANDERSON 2005) was used to test the overall significance in EIVs distribution differences among the clusters obtained from HCA (for each indicator, we calculated relevé-by-relevé dissimilarities using Bray–Curtis distance). We then assessed the significance of

differences between clusters for each EIV by means of Mann-Whitney U test, with Bonferroni's correction, computed in PAST 3.12 (HAMMER et al. 2001). Non-metric multidimensional scaling (NMDS), with Bray–Curtis dissimilarity (CLARKE 1993), was used as an exploratory ordination method and to double-check the results of HCA; EIVs were used as (passively plotted) covariates. Distance-based RDA (dbRDA: LEGENDRE & ANDERSON 1999), using Bray–Curtis dissimilarities, was performed as a constrained ordination method to reveal direct correlations between floristic composition and the following environmental variables (after their standardization): aspect (southing index), slope inclination, rock & stone cover, heat-load index, biomass, P_{ann}, T_m, I_c. Elevation was removed from the input variables because of its very high collinearity with T_m (Pearson's r = -0.9). PERMANOVA, NMDS and dbRDA were all performed in PRIMER v. 6.1.11 (Primer-E Ltd., Luton, UK). Finally, the relationship between community weighted-mean EIVs and some measured environmental variables was tested by means of Spearman's r_s correlation coefficient.

3.2.2 Predictors of species richness

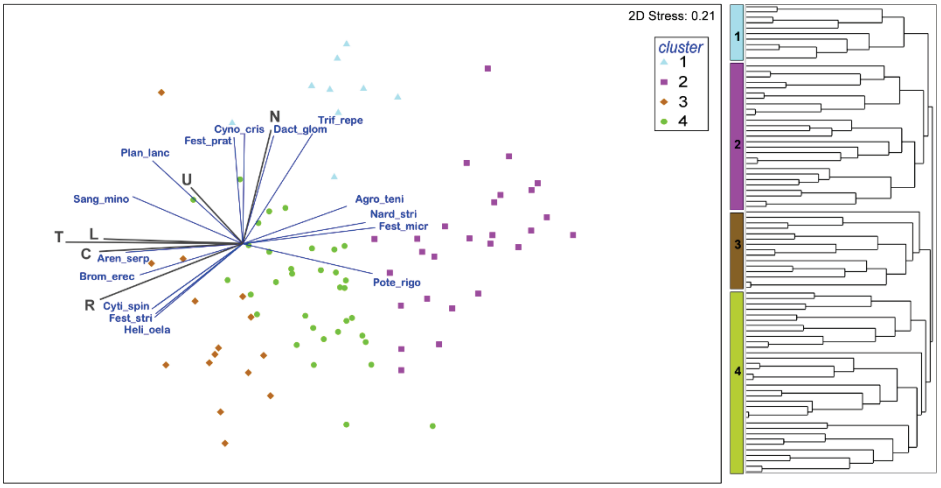
The relationship between species richness and the (numerical) environmental variables was preliminarily screened by means of pair-wise Spearman correlation. Some relationships were further checked by means of first-order partial (Spearman's) correlation analysis (measuring the degree of association between two variables, with the effect of a third variable removed) with the package "ppcor" in R (KIM 2015). Differences in richness between bedrock types were checked by means of Kruskall-Wallis test followed by a pairwise Mann-Whitney test with Bonferroni correction in PAST 3.12. Subsequently, the overall model of the whole set of (continuous and categorical) environmental variables in predicting species richness was explored through Regression Trees (RT), as they are robust to multicollinearity and independent from any assumptions regarding the distribution of errors (DE'ATH & FABRICIUS 2000). We performed RT analysis with package "party" in R (function "ctree"), implementing "conditional inference trees" (STROBL et al. 2009); for the stop criterion, multiplicity adjusted p-values (Bonferroni correction) were used.

4. Results

4.1 Floristic groups and their drivers

HCA revealed four floristically and ecologically well-interpretable groups (Fig. 2, smaller graph). The species with the highest diagnostic values for each cluster were: *Festuca pratensis*, *Cynosurus cristatus* and *Leucanthemum vulgare* (cl. 1), *Festuca microphylla*, *Potentilla rigoana* and *Nardus stricta* (cl. 2), *Helianthemum oelandicum*, *Thymus striatus* and *Chamaecytisus spinescens* (cl. 3), *Thymus longicaulis*, *Pimpinella tragium* and *Euphorbia myrsinites* (cl. 4). See Table 2 for a complete list of diagnostic, frequent and dominant species. See Supplement E1 for a full Synoptic Table of floristic composition across clusters.

In NMDS (Fig. 2), the main four clusters were well separated, with clusters 2–4 ordinated along the first axis and cluster 1 distinguishable along the second one. The two species with the highest positive correlations were: *Festuca microphylla* and *Nardus stricta* (first axis) and *Plantago lanceolata* and *Festuca pratensis* (second axis). The EIVs most correlated with the first NMDS axis were T and R (negatively); while T and N were positively correlated with the second axis. U was the indicator with the worst correlation along the first two axes. Cluster 1 was characterized by higher N and U, whereas cluster 3 by the highest values of T, R and C; on the contrary cluster 2 showed the lowest values for these indicators, with cluster 4 situated in intermediate position.



EIVs	L	T	C	U	R	N
Axis 1	-0.625	-0.805	-0.676	-0.09	-0.795	0.417
Axis 2	0.375	0.457	0.329	0.388	0.107	0.446

Fig. 2. Main graph: Non-Metric Dimensional Scaling (NMDS) of surveyed grasslands in Abruzzo National Park showing vectors of species with correlation with axes > 0.55 and superimposed vectors of Ellenberg Indicator Values (EIVs) calibrated for Italy for light (L), temperature (T), continentality (C), moisture (U), soil pH (R) and soil nitrogen status (N). For EIVs, the relative correlations with the first two ordination axes are also reported. Plot symbols and colours according to Hierarchical clustering in the smaller graph on the right side. Agro_teni: *Agrostis tenuis*; Aren_serp: *Arenaria serpyllifolia*; Brom_erec: *Bromus erectus*; Cyno_cris: *Cynosurus cristatus*; Cyti_spin: *Cytisus spinescens*; Dact_glom: *Dactylis glomerata*; Fest_micr: *Festuca microphylla*; Fest_prat: *Festuca pratensis*; Fest_stri: *Festuca stricta* subsp. *trachyphylla*; Heli_oela: *Helianthemum oelandicum*; Nard_stri: *Nardus stricta*; Plan_lanc: *Plantago lanceolata*; Pote_rigo: *Potentilla rigoana*; Sang_mino: *Sanguisorba minor*; Trif_repe: *Trifolium repens.* Smaller graph: Hierarchical clustering (modified TWINSPAN procedure) showing the four main clusters obtained.

Abb. 2. Hauptabbildung: *Non-Metric Dimensional Scaling* (NMDS) der untersuchten Vegetationsaufnahmen von Grasländern aus dem Abruzzo Nationalpark. Dargestellt sind die Vektoren von Arten mit einer Korrelation mit den Achsen von > 0,55 und Vektoren für die mittleren ökologischen Zeigerwerte (EIVs) für Licht (L), Temperatur (T), Kontinentalität (C), Bodenfeuchte (U), Bodenreaktion (R) und Stickstoffversorgung des Bodens (N). Für die mittleren Zeigerwerte sind unten auch die Korrelationen mit den ersten beiden Ordinationsachsen angegeben. Die Vegetationsaufnahmen sind farblich so dargestellt wie im Ergebnis der hierarchischen Clusteranalyse (mittels modifiziertem TWINSPAN) in der kleinen Abbildung. Für die Bedeutung der Artenkürzel, siehe die englische Bildunterschrift.

These results were confirmed by the between-cluster Mann-Whitney test (Fig. 3): in particular, cluster 1 had significantly higher EIV-U and EIV-N than the remainder of the groups; cluster 2 had significantly lower EIV-T; cluster 3 had significantly higher EIV-T and EIV-R than all other clusters. In addition, PERMANOVA revealed that the four clusters significantly differed for overall EIVs distribution (main test: $df = 3$, *Pseudo-F* = 30.442, $p < 0.001$) and that all the pair-wise comparisons between clusters (again, for the overall EIVs distribution) were significant at $p \leq 0.001$.

Table 2. Diagnostic, constant and dominant species of the clusters resulting from hierarchical cluster analysis (TWINSPAN). Species are listed in alphabetical order within each category. Diagnostic species are those with *phi* > 0.45 and $p < 0.001$. Constant species are defined as frequency > 50%. Dominant species are defined as occurring in at least 25% of the relevés of a given group, with a cover value > 25%.

Tabelle 2. Diagnostische, konstante und dominante Arten der vier Hauptcluster der hierarchischen Clusteranalyse (TWINSPAN). Die Taxa sind alphabetisch in der jeweiligen Kategorie aufgeführt. Diagnostische Arten sind jene mit *phi* > 0,45 and $p < 0{,}001$. Als konstant wurden Arten mit einer Stetigkeit > 50 % definiert. Als dominant wurden Arten definiert, die in mindestens 25 % der Aufnahmen mehr als 25 % Deckung erreichten.

	diagnostic species (Dg)	**constant species (C)**	**dominant species (Dm)**
Cluster 1	*Agrimonia eupatoria*, *Agrostis canina*, *Brachypodium rupestre*, *Cichorium intybus*, *Cirsium tenoreanum*, *Convolvulus arvensis*, *Cynosurus cristatus*, *Dactylis glomerata*, *Daucus carota*, *Dorycnium pentaphyllum*, *Festuca pratensis*, *Lathyrus nissolia*, *Leucanthemum vulgare*, *Lotus corniculatus*, *Medicago lupulina*, *Phleum bertolonii*, *Picris hieracioides*, *Plantago lanceolata*, *Poa pratensis*, *Potentilla reptans*, *Ranunculus bulbosus*, *Trifolium pratense*, *T. repens, Vicia sativa*, *Xeranthemum inapertum*	*Festuca circummediterranea*, *Trifolium campestre*	*Brachypodium rupestre* (Dg), *Cynosurus cristatus* (Dg), *Dorycnium pentaphyllum* (Dg), *Lotus corniculatus* (Dg), *Trifolium repens* (Dg)
Cluster 2	*Agrostis tenuis*, *Alchemilla colorata*, *Crocus napolitanus*, *Dianthus deltoides*, *Festuca microphylla* (Dm), *Luzula multiflora*, *Nardus stricta* (Dm), *Plantago atrata*, *P. holosteum, Potentilla rigoana*, *Ranunculus apenninus*, *R. pollinensis*	*Achillea millefolium*, *Hieracium pilosella*, *Trifolium repens*	*Festuca microphylla (*Dg), *Nardus stricta* (Dg)
Cluster 3	*Alyssum montanum*, *Anthyllis vulneraria*, *Carex macrolepis*, *Chamaecytisus spinescens*, *Coronilla minima*, *Festuca stricta* subsp. *trachyphylla* (Dm), *Helianthemum apenninum*, *H. oelandicum*, *Leontodon crispus*, *Minuartia verna*, *Oxytropis pilosa*, *Sedum rupestre*, *Sesleria tenuifolia*, *Thymus striatus*, *Trinia dalechampii*	*Arenaria serpyllifolia*, *Bromus erectus* (Dm), *Galium corrudifolium*, *Koeleria splendens*	*Bromus erectus* (C), *Festuca stricta* subsp. *trachyphylla* (Dg)
Cluster 4	*Euphorbia myrsinites*, *Pimpinella tragium*, *Sedum acre*, *Thymus longicaulis*	*Acinos alpinus*, *Arenaria serpyllifolia*, *Avenula praetutiana*, *Cerastium tomentosum*, *Hieracium pilosella*, *Koeleria splendens*, *Medicago lupulina*, *Veronica arvensis*	none

In the dbRDA (Supplement E2.1), the first three axes explained 76.5% of constrained variation and 18.4% of total variation. Clusters 1 and 3 were clearly distinguishable; on the contrary, clusters 2 and 4 were weakly differentiated by the available environmental variables. Most of the floristic variation was explained by biomass (first axis), P_{ann} (second axis) and T_m (third axis) (Table 3).

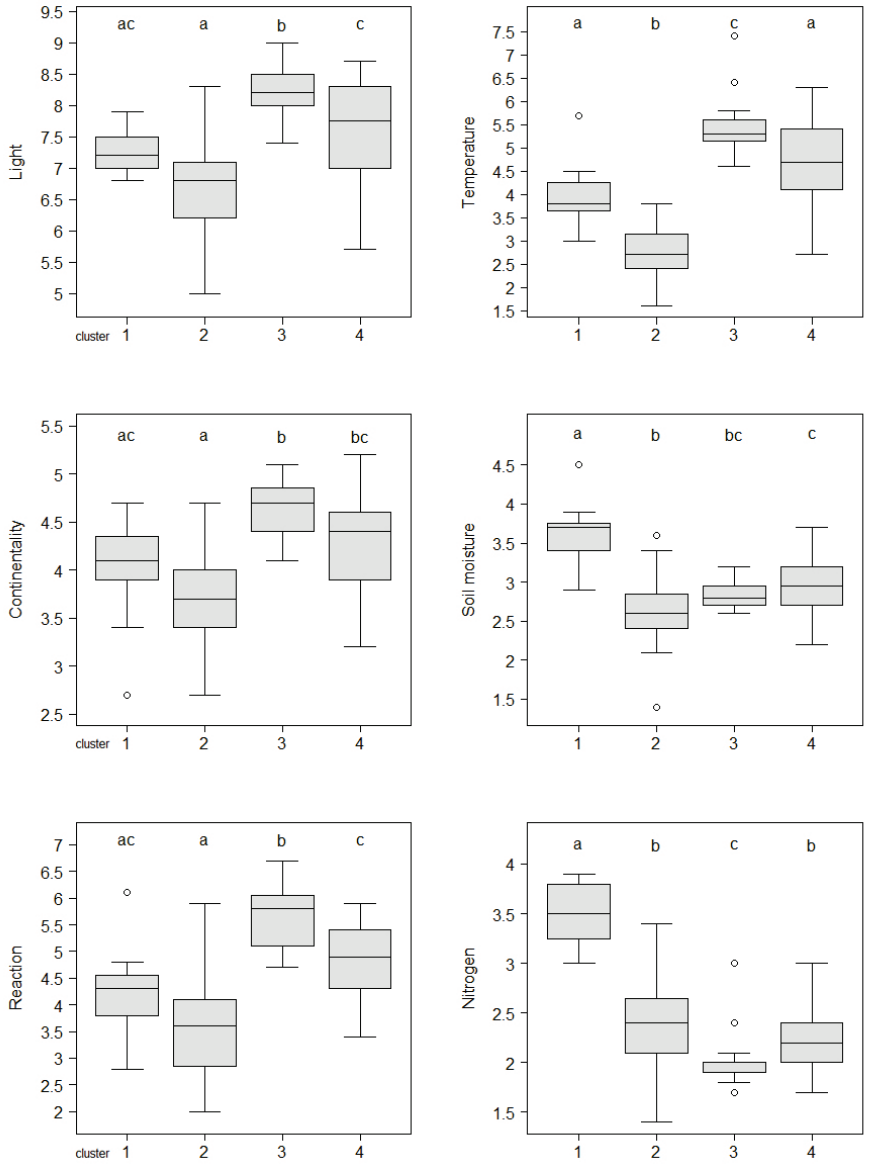


Fig. 3. Between-clusters comparisons of abundance-weighted mean EIVs per relevé. Different letters indicate significance at $p < 0.05$ (Mann-Whitney *U* test after Bonferroni's correction). Cluster numbers as in Figure 2.

Abb. 3. Vergleich der vier Cluster bezüglich der deckungsgewichteten mittleren ökologischen Zeigerwerte der zugehörigen Vegetationsaufnahmen. Dargestellt sind von links oben nach rechts unten die Zeigerwerte für Licht, Temperature, Kontinentalität, Bodenfeuchtigkeit, Bodenreaktion und Stickstoffversorgung des Bodens. Unterschiedliche Buchstaben stehen für signifikante Unterschiede in den Mittelwerten ($p < 0{,}05$; Mann-Whitney *U*-Test mit Bonferroni-Korrektur). Die Clusternummern entsprechen Abbildung 2.

Table 3. Multiple partial correlation values between environmental covariates and dbRDA coordinate axes. P_{ann} = annual precipitation; I_c = continentality index; T_m = mean annual temperature.

Tabelle 3. Multiple partielle Korrelationskoeffizienten zwischen Umwelt-Kovariaten und dbRDA-Koordinatenachsen. P_{ann} = mittlerer Jahresniederschlag; I_c = Kontinentalitätsindex; T_m = Jahresmitteltemperatur.

Variable	dbRDA1	dbRDA2	dbRDA3
Slope inclination	-0.228	-0.431	-0.185
Aspect	-0.241	0.105	-0.422
Rock & stone cover	-0.462	0.007	-0.187
Heat-load	-0.086	0.082	0.134
Biomass	0.678	0.335	0.018
P_{ann}	0.458	-0.607	-0.535
I_c	-0.004	-0.130	0.134
T_m	-0.022	0.547	-0.655

Table 4. Percentage incidence of diagnostic species (according to EuroVegChecklist) of phytosociological classes in the four floristic-ecologic groups.

Tabelle 4. Prozentuales Auftreten diagnostischer Arten von Klassen gemäß EuroVegChecklist in den vier ökologisch-soziologischen Gruppen der Region.

	cluster			
	1	2	3	4
Molinio-Arrhenatheretea	45.4	17.1	2.6	5.0
Nardetea strictae	1.5	21.9	1.0	3.0
Festuco-Brometea	17.7	23.2	43.1	42.5
Festuco-Ononidetea	0.0	0.2	9.1	1.3
Elyno-Seslerietea	0.3	15.0	2.8	9.1
Sedo-Scleranthetea	2.6	2.8	12.4	12.5
other species	25.1	10.1	18.4	16.9

As for the percentage incidence (as for species numbers) of species considered diagnostic of phytosociological classes according to EuroVegChecklist (Table 4), in cluster 1 almost half of the species belonged to *Molinio-Arrhenatheretea* Tx. 1937. In Cluster 2, *Festuco-Brometea* Br.-Bl. et Tx. ex Soò 1947 and *Nardetea strictae* Rivas Goday et Borja Carbonell in Rivas Goday et Mayor Lòpez 1966 accounted for nearly a quarter of the species each. In both cluster 3 and 4, nearly half of the species belonged to *Festuco-Brometea.* Life-form spectra, weighted on cover values, showed that cluster 3 was differentiated from the other groups by a much higher proportion and physiognomic role of chamaephytes (Supplement E2.2).

Overall, as showed in Figure 4 (and Supplement E2.3), cluster 1 was associated to gentle slope inclination, on marly-arenaceous bedrock at lower altitude, and had significantly higher biomass values. Cluster 2 was correlated with mountain slopes with low rock and stone cover, at high altitude with higher precipitation. Cluster 3 had the lowest precipitation and highest rockiness, and it was found only on calcareous substrata. Cluster 4 group had relatively high values of precipitation but higher percentage of rockiness than group 2.

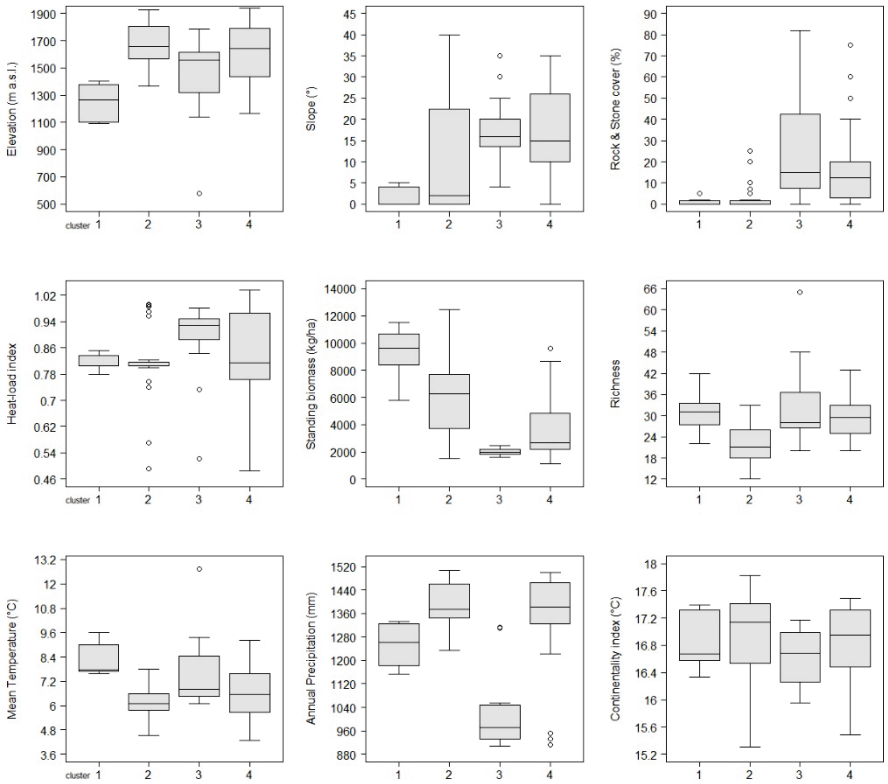


Fig. 4. Boxplots summarizing the main environmental characteristics of the four classification clusters, along with some vegetation parameters (biomass and species richness). Cluster numbers as in Figure 2.

Abb. 4. Boxplots der Verteilung von neun gemessenen Umwelt- und Vegetationsparametern im Vergleich der vier Vegetationscluster (vgl. Abb. 2). Die analysierten Parameter sind von links oben nach rechts unten: Meereshöhe (m ü.M.), Hangneigung (°), Fels- und Steinbedeckung der Bodenoberfläche (%), mikroklimatischer Wärmeindex, oberirdische Biomasse (kg/ha), Gefäßpflanzenartenzahl auf 4 m², mittlere Jahrestemperatur (°C), mittlerer Jahresniederschlag (mm) und Kontinentalitätsindex (°C).

4.2 Correlations between EIVs and environment variables

Pair-wise correlation showed strong and significant ($r_s > 0.4$, $p \leq 0.01$) positive correlations between: slope and EIV-R; aspect and EIV-T, aspect and EIV-C, and aspect and EIV-R; biomass and EIV-N; and finally, T_m and EIV-T. Strong and significant negative correlations were found between biomass and EIV-R, and between P_{ann} and EIV-T, EIV-C and EIV-R (Table 5).

4.3 Predictors of species richness

Across the 87 quadrats, we found a total of 404 vascular plant taxa. Median richness per 4 m^2 relevé was 28 species (min 12, max 65). Pairwise Spearman's correlation (not corrected for multiple testing) found that rock & stone cover, T_m and slope were positively – although weakly – correlated with richness ($r_s = 0.29$, 0.28 and 0.21, respectively); P_{ann}, elevation and

Table 5. Pair-wise correlation coefficients (Spearman's r_s) between environmental variables and EIVs. Significance (not corrected for multiple testing) is coded as follows: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$. P_{ann} = annual precipitation; I_c = continentality index; T_m = mean annual temperature.

Tabelle 5. Paarweise Korrelationskoeffizienten (Spearmans r_s) zwischen Umweltvariablen und ökologischen Zeigerwerten. Signifikanzen (ohne Korrektur für mehrfaches Testen) sind wie folgt angegeben: * $p < 0{,}05$; ** $p < 0{,}01$; *** $p < 0{,}001$. P_{ann} = mittlerer Jahresniederschlag; I_c = Kontinentalitätsindex; T_m = Jahresmitteltemperatur.

EIVs	Elevation	Slope	Aspect	Heat-load	Biomass	P_{ann}	I_c	T_m
L	-0.278**	0.201	0.377***	0.180	-0.334**	-0.356***	-0.042	0.278**
T	-0.374***	0.214*	0.450**	0.187	-0.362***	-0.402***	-0.111	0.455***
C	-0.212*	0.260*	0.459**	0.278**	-0.332**	-0.449***	-0.079	0.239*
U	-0.250*	-0.082	0.002	-0.017	0.187	-0.192	0.035	0.234*
R	0.024	0.438***	0.517***	0.196	-0.525***	-0.518***	-0.268*	-0.001
N	-0.212*	-0.341***	-0.292**	-0.180	0.435***	0.001	0.048	0.136

biomass were negatively, but weakly, correlated with richness (r_s = -0.29, -0.23 and -0.21, respectively). However, elevation and slope inclination were positively correlated (r_s = 0.46), so we can expect that the negative effect of elevation on species richness is counteracted by the positive effect of inclination, and vice versa. This was confirmed by first-order partial correlation, showing that slope inclination, after controlling for elevation, had a more marked positive effect on richness (partial r_s = 0.36, $p < 0.001$), and that elevation had a stronger negative effect on richness after controlling for slope (partial r_s = -0.37, $p < 0.001$).

Kruskall-Wallis test for differences in richness across bedrock types was highly significant ($p < 0.001$); Mann-Whitney (Bonferroni-corrected) post-hoc test highlighted that siliceous bedrock (median richness = 20 species) was significantly species-poorer than limestone (median = 29; p = 0.007) and clay (median = 30.5; p = 0.04); additionally, conglomerate bedrock had a high median richness (31 species), although statistically not significant because of small number of quadrats and high variance (Supplement E2.4). The Regression Tree predicted that relevés with rock & stone cover > 40% were significantly species-richer than the remainder of the dataset. The plots with lower rock & stone cover were further subdivided according to bedrock: siliceous or debris sites were the species-poorest, while those with clayey or calcareous bedrock had intermediate richness levels (Fig. 5). As for vegetation types, species richness had significantly lower mean values in group 2 than in the remainder of the communities (Fig. 4).

5. Discussion

Although based on a relatively small number of relevés, and on a smaller plot size than usually applied in vegetation classification, our data provided for the first time a general overview of Abruzzo National Park's dry grasslands with consistently-sized sampling units. The results clearly highlight the presence of climatic and edaphic gradients that give rise to four broad ecological types, corresponding to different phytosociological classes.

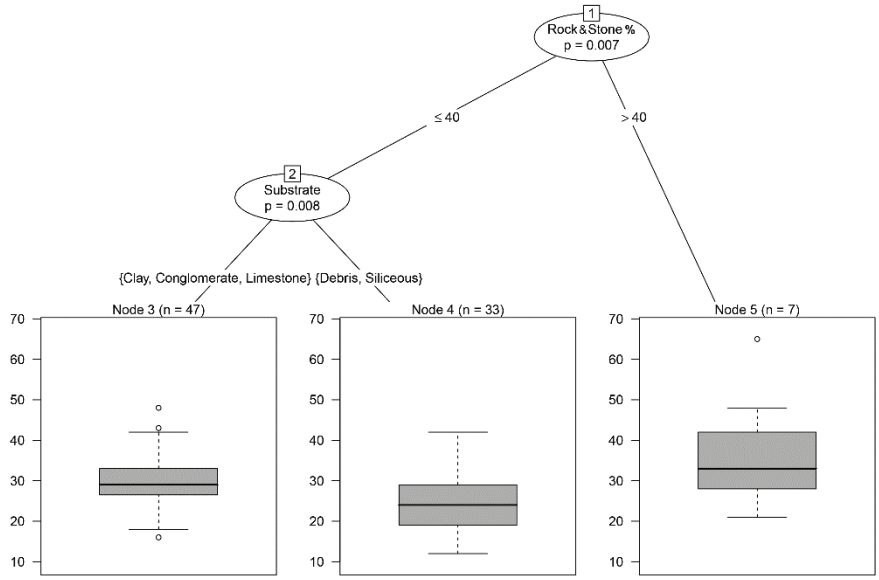


Fig. 5. Conditional-inference regression tree for vascular species richness. All numerical and categorical variables were entered in the model (except elevation, because of very high collinearity with mean annual temperature). The variables responsible for a significant tree splitting are highlighted in the ovals together with their associated (Bonferroni-corrected) *p*-values. The threshold values at which the observations are split into groups are reported on the tree branches. For each terminal node (cluster of observations), the distribution of the response variable is summarized by a boxplot. On top of each boxplot, the number of observations (*n*) in each group is reported.

Abb. 5. Regressionsbaum für die Gefäßpflanzenartenzahl auf 4 m². Alle numerischen und kategorialen Variablen mit Ausnahme der Meereshöhe (wegen hoher Kollinearität mit der Jahresmitteltemperatur) wurden in das Modell eingespeist. Die Variablen, die für eine signifikante Verzweigung des Baumes sorgten, sind in den Ovalen zusammen mit den jeweiligen Bonferroni-korrigierten *p*-Werten dargestellt. Die trennenden Parameterwerte sind auf den Ästen wiedergegeben. An den Astenden visualisiert ein Boxplot die Verteilung der Artenzahl und nennt die Anzahl (*n*) der zugehörigen Vegetationsaufnahmen.

5.1 Ecology, syntaxonomy and composition drivers

Direct gradient analysis (db-RDA) showed two main orthogonal gradients: one can be explained as a gradient in soil fertility, since it resulted from rock & stone cover and aboveground fresh biomass; the other is clearly a climatic gradient, as it is composed by mean temperature and annual precipitation. This is consistent with previous findings in a different sector of the Apennines (CATORCI & GATTI 2010), underlining that the distribution of grassland communities was explained by altitude-driven climatic factors on the one hand and by topography-driven soil properties (especially soil water availability) on the other hand. Moreover, relevés classification (HCA) underlined a clear dichotomy between two contrasting community groups, i.e. acidophytic (and mesic) vs. calciphilous (and xeric), consistently with what was found in other calcareous mountain ranges, such as the Pyrenees (SEBASTIÁ 2004).

Each of the four groups obtained from HCA could be attributed to a different phytosociological class. As for the lower syntaxonomical levels, it is to be underlined that the classification at the association level of the Central Italian grasslands is still largely incomplete

(e.g. BLASI et al. 2010, DI PIETRO 2011). Moreover, the quadrat size used in this study was smaller than the relevés used in most phytosociological studies on Italian dry grasslands (e.g. LUCCHESE et al. 1995, DI PIETRO et al. 2005, CIASCHETTI et al. 2016). For these reasons, we will extend our discussion only to the alliance level.

Cluster 1 was clearly dominated by species of *Molinio-Arrhenatheretea* and can therefore be referred to this class. At alliance level, the whole cluster can be attributed to *Cynosurion cristati* Tx. 1947 (*Arrhenatheretalia elatioris* Tx. 1931, *Molinio-Arrhenatheretea* Tx. 1937), an alliance including anthropogenic mesic pastures, on mineral-rich soils at low to mid-altitudes in temperate Europe (MUCINA et al. 2016). The floristic composition of this cluster resulted to be driven by edaphic factors (flat topographic position and lack of surfacing bedrock – both leading to deep soil), confirmed by higher EIV-N values (Fig. 3 and 4), as observed in other sectors of the Apennines (e.g. CATORCI et al. 2007, CATORCI & GATTI 2010). The occurrence of mineral-rich soils in these relevés is confirmed also by a significant contingent of species (approx. 10%) from ruderal and zoo-anthropogenic classes (i.e. *Artemisietea vulgaris* Lohmeyer et al. in Tx. ex von Rochow 1951, *Chenopodietea* Br.-Bl. in Br.-Bl. et al. 1952 and *Sisymbrietea* Gutte et Hilbig 1975). The high cover values of *Brachypodium rupestre* in some of the relevés included in this group should be considered as an indicator of nitrogen enrichment and of decrease in grazing load (BONANOMI et al. 2006), analogously to what highlighted in C-Europe for *B. pinnatum* (e.g. BUCKLAND et al. 2001). Although at present most of these communities are exploited only for grazing (or even abandoned), in a recent past they may have been ploughed or used as hay meadows and occasionally fertilized (MANZI 1990, PRIMI et al. 2016). The environmental and floristic features (i.e. low incidence of therophytes and the relative importance of *Festuco-Brometea*) point to the sub-alliance *Cerastio arvensis-Cynosurenion* Blasi et al. 2012, described for the central-northern Apennines (BLASI et al. 2012).

Cluster 2 was associated to a mixture of climatic (high precipitation, low temperature) and edaphic drivers; of these latter, one was directly measured (low cover of surfacing bedrock, suggesting that these communities lie on deeper soil compared to cluster 3 and 4), the other (low soil pH) could be inferred from EIV-R values (markedly lower than all other clusters). The soil properties of similar communities were described in detail, just outside the Park's border, by DI PIETRO et al. (2005), who found deep, decarbonated soils, with pH between 5.2 and 6.7 (see also CATORCI & GATTI 2010). In cluster 2, the species of *Nardetea strictae* and *Festuco-Brometea* are in equal number, but the dominant species and those highlighted by HCA as diagnostic for the cluster mostly belong to the former; we thus refer the cluster to *Nardetea strictae*. In the syntaxonomical view proposed by MUCINA et al. (2016), *Nardetea strictae* includes only secondary grasslands, whereas the floristically similar but primary ones are classified in *Juncetea trifidi* Hadac in Klika et Hadac 1944. Although some small extensions of high-elevation, probably primary *Nardus* grasslands (with a rich arctic-alpine flora) do exist in the Park (L. Cancellieri & G. Filibeck, unpubl. data), all the relevés of acidophilous grasslands included in this study lie below the potential treeline. The appropriate syntaxon at alliance level for these pastures is *Nardo strictae-Agrostion caninae* Cortini-Pedrotti et al. 1973 (*Nardetalia strictae* Preising 1950), according to the proposal of DI PIETRO et al. (2017): this is probably the first time that this solution is applied, because usually the C- and S-Apennines *Nardus* grasslands were referred to *Ranunculo-Nardion* Bonin 1972, an alliance now included in the *Juncetea trifidi* (DI PIETRO et al. 2017). The occurrence in cluster 2, as well as in cluster 4 (Table 3), of species from *Elyno-Seslerietea* Br.-Bl. 1948 highlights a gradient of continuous floristic transition towards

the coenoses of *Seslerion apenninae* Furnari in Bruno et Furnari 1966, that are found over limited areas (windy ridges) in the Park's subalpine belt (1900–2200 m) (BAZZICHELLI & FURNARI 1979) and were not surveyed in this study.

The last two clusters (3–4) include grasslands of the colline, submontane and montane belt on steep and stony slopes with limestone bedrock, thus likely featuring shallow and base-rich soils (as confirmed by the high values of EIV-R). The presence of outcropping limestone is underlined by the occurrence of species from *Sedo-Scleranthetea* Br.-Bl. 1955 and *Alysso-Sedetalia* Moravec 1967 (Table 3). Clusters 3 and 4 feature an overall prevalence (as for species number) by *Festuco-Brometea*; however, cluster 3 differs from cluster 4 mainly because of the physiognomy dominated by chamaephytes (Supplement E2.2) (e.g. *Helianthemum oelandicum*, *H. apenninum, Thymus striatus*, *Coronilla minima*). These are mostly characteristic species (MUCINA et al. 2016) of *Festuco hystricis-Ononidetea striatae* and to a lesser extent of *Ononido-Rosmarinetea* Br.-Bl. in A. Bolòs y Vayreda 1950 and *Festuco-Brometea*. Moreover, the communities of cluster 3 were found to be clearly associated with a climatic feature, i.e. with low-precipitation areas.

Indeed, the classification of basiphilous dry grasslands in the C- and S-Apennines is a long-standing and controversial issue, that resulted in quite divergent syntaxonomical proposals (see for details MUCINA et al. 2009, DI PIETRO 2011, BIONDI et al. 2014a). The placement at class level of the communities rich in chamaephytes (i.e. our cluster 3) is particularly critical. The floristic assemblage of the cluster corresponds very well to *Cytiso spinescentis-Saturejion montanae* Pirone et Tammaro 1997, an alliance describing the montane calciphilous grasslands, rich in dwarf shrubs, of the Central Apennines. The Italian syntaxonomical scheme by BIONDI et al. (2014b) assigns this alliance to the class *Cisto-Micromerietea julianae* Oberd. 1954 (i.e. the eastern-Mediterranean garrigues). Instead, EuroVegChecklist (MUCINA et al. 2016) doesn't recognize the existence of *Cisto-Micromerietea* and moves *Cytiso spinescentis-Saturejion montanae* into *Festuco hystricis-Ononidetea striatae*, a class including "Submediterranean submontane-montane and oro-mediterranean dry grasslands and related dwarf scrub on calcareous substrates of the Iberian Peninsula, the Western Alps and the Apennines". For consistency with the most updated classification, we thus refer cluster 3 to *Festuco hystricis-Ononidetea.*

On the other hand, the floristic composition of cluster 4 perfectly matches that of *Phleo ambigui-Bromion erecti* Biondi et al. ex Biondi et Galdenzi 2012 – an alliance endemic to the Apennines, viewed as a geographic vicariant (BIONDI et al. 2005) of the central-European *Xerobromion erecti* (Br.-Bl. et Moor 1938) Zoller 1954. Quite surprisingly, *Phleo-Bromion* [sub *Cytiso spinescentis-Bromion erecti* Bonin 1978, considered as a synonim] is included by MUCINA et al. (2016) in *Festuco hystricis-Ononidetea striatae,* without providing any formalized analysis to support this approach. However, because of the above-mentioned vicariance and the prevalence of *Festuco-Brometea* species, we think *Phleo-Bromion* should remain within the latter class, as proposed by the Italian vegetation Prodrome (BIONDI et al. 2014a), and we thereby refer cluster 4 to it. As for their environmental drivers, the communities of group 4 were found to span over a broad range of environments (see Fig. 4, Supplement E2.1 and E2.3), although precipitation clearly discriminated them from *Festuco-Ononidetea* (group 3) assemblages. Moreover, the latter were associated with low elevation and strictly calcareous, stony substrates – leading to high EIV-T and EIV-R values (see Fig. 3 and 4).

Overall, EIVs proved to be very useful in clarifying the distinctiveness of the four main vegetation groups and the underlying gradients. In NMDS (Fig. 2), EIV-R and EIV-T were clearly correlated with a gradient dividing *Nardetea* (acid soil and cool climate) from *Festuco-Ononidetea* (calcium-rich soil and warm/dry climate); EIV-N (and partly EIV-U) were connected to a second, orthogonal gradient dividing the oligotrophic (and xeric) *Festuco-Ononidetea* and *Festuco-Brometea* from the more eutrophic (and moist) *Molinio-Arrhenateretea.* Similarly, in an analysis of the montane grassland communities of a different sector of the Central Apennines, CATORCI et al. (2007) found that EIV-U and EIV-N well separated different phytosociological classes. These results are consistent with the pivotal role of soil water availability in controlling the spatial distribution of grassland assemblages (both because of direct effects on plants and indirect effects mediated by soil chemical properties), as suggested by recent studies (e.g. ARAYA et al. 2011).

Finally, it is to be underlined that productivity was markedly different between the four phytosociological classes (Fig. 4) and was strongly correlated with the overall gradient of floristic composition in db-RDA (Supplement E2.1): estimates of standing biomass were very low for both *Nardetea* and *Festuco-Ononidetea,* as expected in the former because of the nutrient-poor soils associated with low pH (MUCINA et al. 1993), and in the latter because of climatic aridity and free-draining stony soils (PRIMI et al. 2016). Fresh aboveground biomass was very high for *Molinio-Arrhenateretea*, consistently with the moister soils (GATTI et al. 2007), whereas it was very variable – consistently with the wide habitat range – for *Festuco-Brometea*: within this latter class, a similar variability in productivity (depending on topographical factors) was reported for another sector of the Central Apennines by GRATANI et al. (1999).

5.2 Correlations between EIVs and environment variables

The good correlation between EIVs and measured environmental variables has been widely demonstrated in a number of geographic regions and vegetation types (e.g. DIEKMANN 2003, SCHAFFERS & SYKORA 2000). However, the majority of such works dealt solely with edaphic indicator values, while only a very few studies considered indicator values for temperature (see references in FILIBECK et al. 2015). Our findings, overall, support the reliability of the EIVs (calibrated for the Italian flora) in the grassland communities of the Central Apennines. In particular, EIV-T had a good, although not very strong, correlation with T_m. A very good correlation between (unweighted) EIV-T and annual temperature in Italian forest vegetation has already been showed by FILIBECK et al. (2015); it is thus interesting to confirm this relationship also for the grassland flora. On the contrary, EIV-C was not correlated with the climatic Continentality index, although it was negatively correlated with annual precipitation. A possible explanation is that the continentality gradient in the study area is relatively short, since most of the analyzed grasslands lie within the montane belt, which is relatively oceanic. PIGNATTI et al. (2005) already warned that EIV-C can be scarcely useful in the Italian floras due to the lack of long gradients; see also BERG et al. (2017) who underlined that, even in C-Europe, EIV-C was actually ill-defined in the original Ellenberg's system. The negative relationship between EIV-R and P_{ann} can be partly due to the soil acidification induced in rainier areas, but also by the unbalanced distribution of bedrock types along the precipitation gradient. Finally, it is noteworthy the good positive correlation between EIV-N and (remote-sensed) standing biomass, in turn highlighting the grassland of *Molinio-Arrhenateretea* as those with the highest productivity.

5.3 Predictors of species richness

Species richness decreased with elevation, especially when controlling for slope, similar to what observed in the grasslands of the nearby Velino massif by THEURILLAT et al. (2007), who surveyed an elevation range (1100–2400 m) largely overlapping with ours, although with a much larger sampling grain. Indeed, given that richness usually decreases with latitude (e.g. LYONS & WILLIG 2002), the same pattern can be considered an expected one for elevation gradients, although a number of studies found alternative patterns and/or a sensitivity to sampling grain (see references in BAUMANN et al. 2016). However, in Central Italy the elevation gradient also means a decreasing influx of the Mediterranean biome (e.g. BLASI et al. 2010) and of its very rich species pool, leading, *inter alia*, to a decreasing therophyte component with elevation: the smaller size of Mediterranean annuals can determine higher species density levels per relevé through a purely spatial mechanism (see e.g. references in FILIBECK et al. 2019).

The higher species richness observed in quadrats on limestone compared to acid bedrock types is consistent with a well-known pattern (e.g. CHYTRÝ et al. 2003). However, the high richness levels observed on clayey substrate are interesting; they could possibly be connected to micro-scale natural disturbance connected to soil processes, opening "gaps" for small-sized species.

The positive effect of slope inclination, especially after controlling for elevation as shown by first-order partial correlation, the negative effect of both annual precipitation and biomass in the pairwise correlation analyses, as well as the prominent role of rockiness showed by the RT model, all point to a trend of increasing richness with increasing nutrient/drought stress. A previous study performed in a sector of the Park, using randomized nested plots (FILIBECK et al. 2019), found that slope inclination and rock cover positively influenced plot-scale species richness at 1 m^2 spatial scale. This can be related with the model of humped-back relationship between productivity and richness, often explained assuming that in productive sites a few strong competitors will outcompete slow-growing or small-sized species (e.g. KEDDY 2005). Whatever the causal mechanisms, our results add to a number of studies underlining the importance of the less productive and dryer sites for the conservation of plant diversity in secondary grasslands (e.g. BENNIE et al. 2006, CINGOLANI et al. 2010, KLEINEBECKER et al. 2018, FILIBECK et al. 2019, DEÁK et al. 2020).

Finally, the fact that *Nardetea* quadrats have significantly lower species richness confirms for the Central Apennines, and for the spatial grain used in this study, the well-known pattern of low richness in this class (e.g. MUCINA et al. 1993). In turn, this can be mostly explained by some traits (thick litter, clonal spread etc.) shown by *Nardus stricta* and other mat-forming grasses, that prevent recruitment and establishment of other species (e.g. GRIME et al. 2007).

6. Conclusions

The present work applied a fixed quadrat size to the phytosociological survey of the grasslands in a poorly studied – yet of high value for nature conservancy – region of the Apennines. This is one of the first works in Italy using fixed-size, precisely delimited plots for the purpose of phytosociological classification. The results underlined a clear effect of both climatic and edaphic gradients in structuring four broad types of floristic assemblages, corresponding to the class level in syntaxonomy. The syntaxonomical scheme proposed by EuroVegChecklist was found to be largely applicable to the Central Apennines grasslands,

with the exception of the hemicriptophytic grasslands on base-rich soils (*Phleo ambigui-Bromion*), for which the placement in *Festuco-Ononidetea* proposed by MUCINA et al. (2016) doesn't seem supported by floristic composition (especially because of the lack of diagnostic species at class level).

As for species richness, our results suggested that highest values are attained at sites with relatively dry, nutrient-poor and shallow soils, pointing to the importance of the less productive habitats for the conservation of grassland biodiversity. In addition, we performed a test in grassland communities on the reliability of the EIVs calibrated for Italy, highlighting in particular the good correspondence between EIV-T and mean annual temperature. Finally, it is worth underlining that studies like this one can provide a baseline for diachronic monitoring of secondary grasslands and the connected Natura 2000 habitat types.

Erweiterte deutsche Zusammenfassung

Einleitung – Die anthropogenen Graslandgesellschaften Südeuropas sind verglichen mit jenen Mitteleuropas relativ wenig untersucht, obwohl sie floristisch sehr divers sind und vielfältigen biogeografischen Einflüssen unterliegen (APOSTOLOVA et al. 2014). Der Nationalpark „Abruzzo Lazio e Molise" in Mittelitalien beinhaltet große Flächen halbnatürliche Grasländer, die über Jahrhunderte durch Transhumanz aufrechterhalten wurden. Die Artenzusammensetzung dieser Grasländer und ihre Treiber waren bislang wenig untersucht und die verfügbaren pflanzensozioloigschen Daten beruhten oft auf Vegetationsaufnahmen mit uneinheitlichen oder gar nicht dokumentierten Flächengrößen. Dabei beeinflusst die Flächengröße bekanntermaßen den Artenreichtum, die Stetigkeit von Arten und Muster der Artenzusammensetzung, weswegen nur Aufnahmen gleicher Flächengröße methodisch sauber in einer einzigen Vegetationsklassifikation kombiniert werden können (CHYTRÝ & OTÝPKOVÁ 2003, DENGLER et al. 2008). Um erstmals eine umfassende Übersicht der Grasländer des Parks zu erstellen, haben wir Vegetationsaufnahmen einheitlicher Flächengröße mit genauen Koordinaten erhoben und analysiert. Spezifische Ziele waren dabei, (1) die Aufnahmen in floristisch-ökologische Vegetationstypen zu klassifizieren, unterstützt durch eine Analyse der mittleren, für die italienische Flora kalibrierten Ellenberg-Zeigerwerte (PIGNATTI et al. 2005), (2) diese Vegetationstypen Einheiten des aktuellen syntaxonomischen Systems zuzuordnen, (3) die ökologischen Haupttreiber der Muster von Artenreichtum und Artenzusammensetzung zu identifizieren und (4) den Zusammenhang der mittleren ökologischen Zeigerwerte mit einigen gemessenen Umweltvariablen zu ermitteln.

Untersuchungsgebiet – Das Untersuchungsgebiet umfasst den Nationalpark „Abruzzo Lazio e Molise" und angrenzende Natura 2000-Flächen in den zentralen Apenninen (Italien) mit einer Gesamtfläche von 79.500 ha (Abb. 1). Die Meereshöhe reicht von 500 bis 2200 m ü. NHN, wobei die Mehrheit der Flächen zwischen 1100 und 1900 m ü.NHN. liegt. Kalkgesteine herrschen vor, aber es kommen auch tonige und mergelige Gesteine vor. Die Jahresniederschläge im Gebiet steigen von 700–800 mm im Norden bis auf über 1600 mm im Süden an. Transhumanz mit Schafen und Ziegen war das vorherrschende Landnutzungssystem über Jahrhunderte bis in die 1950er Jahre. Heute ist die Besatzdichte erheblich niedriger als zu Beginn des 20. Jahrhunderts. Allerdings folgte dem Rückgang der Schaf- und Ziegenbeweidung eine Zunahme verwilderter Rinder und Pferde (PRIMI et al. 2016).

Material und Methoden – Es wurden insgesamt 87 Vegetationsaufnahmen auf exakt markierten Probeflächen von 2 × 2 m angefertigt. Sie wurden in repräsentative Gebiete für den jeweiligen Vegetationstyp gelegt (Fig. 1). Da die Datenerhebung ursprünglich der Ermittlung der maximalen nachhaltigen Beweidungsintensität diente, lagen die meisten Aufnahmeflächen zwischen 1200 und 1800 m ü.M. Die Jahresmitteltemperatur (T_m), der mittlere Jahresniederschlag (P_{ann}) sowie der Kontinentalitätsindex (I_c) wurden aus hochauflösenden Klimamodellen (BRUNETTI et al. 2014; CRESPI et al. 2018) berechnet. Die oberirdische Biomasse wurde aus dem *Normalized Difference Vegetation Index* (NDVI) mit Daten von Landsat 7-Bildern und kalibriert mit Felddaten (PRIMI et al. 2016) berechnet. An weiteren Umweltdaten fanden Hangneigung und -exposition, Fels- und Steindeckung sowie Gesteinstyp Verwendung (Tab. 1).

Die folgenden statistischen Verfahren fanden Verwendung: *Non-metric multi-dimensional scaling* (NMDS), hierarchische Clusteranalyse (HCA) mit der modifizierten TWINSPAN-Methode zur Identifizierung der Haupt-Vegetationstypen, distanzbasierte Redundanzanalyse (RDA) als beschränkte (*constrained*) Ordinations-Methode sowie partielle Korrelationen und Regressionsbäume (RT) zur Ermittlung der Treiber des Artenreichtums. Die höheren Syntaxa und die Zuordnung von Arten zu Vegetationsklassen folgte der „EuroVegChecklist" (MUCINA et al. 2016). Die Ellenberg-Zeigerwerte (EIVs) wurden basierend auf PIGNATTI et al. (2005) berechnet.

Ergebnisse – HCA und NMDS ergaben vier floristisch und ökologisch gut interprätierbare Gruppen (Abb. 2; Tab. 2, 4). Die beschränkte Ordination zeigte, dass die Variation in der Artenzusammensetzung hauptsächlich durch Biomasse, P_{ann} und T_m erklärt werden kann (Tab. 3). Starke und signifikante positive Korrelationen bestanden zwischen Biomasse und den mittleren Zeigerwerten für Stickstoff (EIV-N) sowie zwischen T_m und den mittleren Zeigerwerten für Temperatur (EIV-T). Starke und signifikante negative Korrelationen bestanden zwischen P_{ann} auf der einen Seite und EIV-T, mittleren Zeigerwerten für Kontinentalität (EIV-C) und mittleren Zeigerwerten für Bodenreaktion (EIV-R) auf der anderen Seite (Tab. 5). Nach den partiellen Korrelationen war Artenreichtum war positiv mit Hang neigung und negativ mit Meereshöhe korreliert; weiterhin nahm der Artenreichtum mit der Gesteins deckung zu und war auf Kalk- und Tonböden höher als auf silikatischen Böden (Abb. 4, 5; Anhang E2).

Diskussion – In Cluster 1 waren nahezu die Hälfte aller Arten laut der „EuroVegChecklist" (MUCINA et al. 2016) diagnostisch für die Klasse *Molinio-Arrhenatheretea*; im Cluster 2 machten *Festuco-Brometea* und *Nardetea strictae*-Arten jeweils etwa ein Viertel der Artenkombination aus; in den Clustern 3 und 4 schließlich stellten *Festuco-Brometea*-Arten etwa die Hälfte der Artenkombination (Tab. 4). Aufgrund der dominanten Arten, struktureller Merkmale und der diagnostischen Arten, die sich aus der hierarchischen Clusteranalyse ergaben, haben wir letztlich jedes Cluster einer anderen Klasse zugeordnet, nämlich den *Molinio-Arrhenatheretea*, *Nardetea strictae*, *Festuco hystricis-Ononidetea striatae* und *Festuco-Brometea*. Hierin entsprechen sie den Verbänden *Cynosurion cristati*, *Nardo strictae-Agrostion caninae*, *Cytiso spinescentis-Saturejion montanae* and *Phleo ambigui-Bromion erecti*. Die Schätzungen der oberirdischen Biomasse waren für die Bestände der *Nardetea* und *Festuco-Ononidetea* sehr niedrig, wie es aufgrund der nährstoffarmen Böden in der ersten Klasse und der klimatischen Trockenheit und den wasserdurchlässigen Böden in der zweiten Klasse zu erwarten war. In den Beständen der *Molinio-Arrhenatheretea* war die Biomasse entsprechend der fruchtbaren Böden dagegen sehr hoch (GATTI et al. 2007). In der Klasse *Festuco-Brometea* variierte die Biomasse dagegen stark, was der breiten Habitatamplitude entspricht (GRATANI et al. 1999). Unsere Befunde unterstreichen, dass die Ellenberg-Zeigerwerte nach PIGNATTI et al. (2005) in Grasländern der Apenninen aussagekräftig sind; insbesondere besteht ein enger Zusammenhang zwischen EIV-T und T_m (FILIBECK et al. 2015). Der Artenreichtum nahm mit der Meereshöhe ab, insbesondere, wenn man die Hangneigung ebenfalls berücksichtigte, was Befunden aus dem nahe gelegenen Velinomassiv entspricht (THEURILLAT et al. 2007). Auch der höhere Artenreichtung in Probeflächen über Kalk verglichen mit jenen über silikatischen Gesteinen ist ein wohlbekanntes Phänomen (vgl. CHYTRÝ et al. 2003). Die bedeutende Rolle der Felsigkeit im RT-Modell deutet auf eine Zunahme des Artenreichtums bei zunehmendem Nährstoffmangel und Trockenheitsstress hin und unterstreicht, dass die weniger produktiven und trockeneren Standorte unter den sekundären Grasländern besondere Bedeutung für den Schutz der pflanzlichen Biodiversität haben (vgl. BENNIE et al. 2006, CINGOLANI et al. 2010, FILIBECK et al. 2019).

Schlussfolgerungen – Wir schliessen, dass im Untersuchungsgebiet (a) die halb-natürlichen Grasländer zu vier hochrangigen floristisch-ökologischen Gruppen gehören, (b) eine Mischung aus klimatischen (v.a. Niederschlag) und edaphischen (v. a. Gestein und pH) Gradienten maßgeblich die Muster der Artenzusammensetzung bestimmt, (c) kleinskaliger Artenreichtum mit dem Umweltstress zunimmt und (d) gewichtete Zeigerwerte nach PIGNATTI et al. (2005) in italienischen Grasländern gut mit gemessenen Umweltvariablen korrelieren.

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Author contribution

G.F., R.P. and B.R. designed the wider research project from which this work stems. M.B. provided climatic data; R.P. and B.R. provided biomass data. L.C. led the vegetation sampling; A.S., L.D.M. and G.F. participated in field work. L.C. and A.S. identified critical plants. L.R., G.F. and L.C. performed statistical analyses. L.R. led the phytosociological analysis and took the syntaxonomical decisions. L.R. and G.F. conceived and wrote the manuscript. All authors contributed to the final text.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Synoptic table of the four detected clusters within the dry grasslands of Abruzzo National Park (Central Italy).

Anhang E1. Stetigkeitstabelle der vier unterschiedenen Cluster der trockenen Grasländer im Nationalpark Abruzzo (Mittelitalien).

Supplement E2. Supplementary Figures 1–4.

Anhang E2. Ergänzende Abbildungen.

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Supplement E1. Synoptic table of the five detected clusters within the dry grasslands of Abruzzo National Park (Central Italy).

Anhang E1. Stetigkeitstabelle der vier unterschiedenen Cluster der Grasslands in Nationalpark Abruzzo (Mittelitalien).

Cluster number	1		2		3	
Vegetation class	*Molinio-Arrhenatheretea*		*Nardetea strictae*		*Festuco-Obionidetea*	
Number of relevés	11		27		15	
	Rg. %	ø/ø	Rg. %	ø/ø	Rg. %	ø/ø
Festuca pratensis Huds	82	*87.8*	—	—	—	—
Cynosurus cristatus L.	82	*10.7*	—	—	3	1
Leucanthemum vulgare Lam.	73	*11.4*	—	—	—	—
Dactylis glomerata L.	82	*8.8*	—	—	9	1
Dactylis glomerata L.	100	*78.7*	33	—	7	—
Arrhenatherum elatius L.	100	*70.1*	22	—	13	6
Agrimonia eupatoria L.	55	*10.0*	—	—	—	—
Galium verum L. s.l.	55	*10.0*	—	—	—	—
Clinopodium nepeta L.	55	*10.0*	—	—	—	—
Lathyrus nissolia L.	45	*12.0*	—	—	—	—
Dorycnium pentaphyllum Scop.	45	*12.0*	—	—	—	—
Potentilla reptans L.	45	*12.0*	—	—	—	—
Trifolium repens L.	91	*10.9*	52	—	15	—
Brachypodium rupestre (Host) R. et S.	55	*10.0*	—	—	3	—
Trifolium pratense L.	100	*24.5*	48	—	24	—
Xanthoxanum lagurus (L.) Wild.	73	*11.1*	—	—	—	—
Agrostis canina L.	36	*14.8*	—	—	—	—
Cynosurus arvensis L.	36	*14.8*	—	—	—	—
Ranunculus bulbosus L.	36	*14.8*	—	—	—	—
Poa pratensis L.	55	*14.2*	19	—	—	—
Cirsium tenoreanum Petrak	45	*11.9*	11	—	—	—
Poa trivialis L.	36	*14.8*	11	—	—	—
Vicia hirsuta(Koch) L.	73	*17.1*	—	—	—	—
Plantago lanceolata L.	73	*17.1*	—	—	33	—
Festuca ovina(Pseudovina Vest)-Patzke	—	—	74	*10.1*	3	—
Potentilla erguna. Th. Wolf	—	—	81	*15.4*	—	—
Nardus stricta L.	—	—	59	*12.7*	—	—
Plantago atrata Hoppe et Lossel.	—	—	44	*11.1*	—	—
Ranunculus polyboracus (Tom.) Chios.	—	—	48	*14.0*	—	—
Carex ericetorum L.	9	—	37	*11.3*	—	—
Luzula multiflora (Ehrh.) Lej.	—	—	37	*11.3*	—	—
Dianthus deltoides L.	—	—	33	*12.2*	—	—
Alchemilla colonae Buser	—	—	30	*14.6*	—	—
Ranunculus apennuss Chiov.	—	—	30	*19.0*	—	—
Plantago holosteum Scop.	—	—	26	*15.8*	—	—
Agrostis tenuis Sibth.	—	—	22	*12.9*	—	—
Trifolium montanum L.	—	—	11	*12.0*	3	—
Achillea millefolium L.	—	—	56	*12.2*	—	—
Galium verum L.	36	—	44	*28.3*	13	—
Helianthemum velanidicum (L.) DC. s l	—	—	—	—	80	3
Thymus striatus Vahl	—	—	—	—	67	*15.0*
Chamaespartium sparsum (Presl) Rothm.	—	—	—	—	67	*11.7*
Helianthemum apenninum (L.) Miller	—	—	—	—	67	*11.7*
Helianthemum nummularium ssp. tuubspilyllu	—	—	—	—	67	*11.7*
Anthyllis vulneraria L.	—	—	—	—	53	*14.8*
Minuartia verna (L.) Hiern	—	—	—	—	67	*18.3*
Minuartia verna (L.) Hiern	—	—	—	—	*44.4*	3
Sesleria tenuifolia Schrader	—	—	—	—	33	*12.2*
Oxytropis pilosa (L.) DC.	—	—	—	—	33	*12.2*
Sedum rupestre L.	—	—	—	—	*44.4*	*11.8*
Thymus longicaulis (Tm.) Jauchen	—	—	11	—	*44.4*	26
Alyssum montanum L.	—	—	—	—	*44.4*	15
Lonicera etrapae Vill.	—	—	—	—	40	*19.0*
Carex macrolepis DC.	—	—	—	—	*44.4*	—
Sedum acre L.	—	—	—	—	7	—
Thymus longicaulis Presl	—	—	30	—	13	—
Pimpinella tragium Vill.	—	—	4	—	—	—
Ranunculus bulbosus L.	9	—	—	—	—	—
Ranunculus millefoliatus Vahl.	—	—	—	—	7	—
Erysimum pseudorhaetoicum Polatschek	—	—	7	—	13	—
Helianthemum canum L.	—	—	—	—	13	—
Armeria canescens (Host) Boiss.	—	—	19	—	7	—
Astragalus depressus L.	—	—	—	—	7	—
Acinos alpinus (L.) Moench	—	—	15	—	27	—
Alyssum montanum L. s.l. (Pap.	—	—	37	—	53	—
Polygala vulgaris(L.)L.s.l.	27	—	22	—	7	—
Armeria ssp(Vilella L.	11	—	—	—	80	—
Cynosurus echinatus L.	9	—	—	—	13	—
Koeleria splendens Presl	—	—	22	—	80	—
Medicago lupulina L.	100	*67.6*	7	—	42	—
Aquilegia atrata L.	—	—	4	—	—	—
Ranunculus montanus (L.) Vitman	9	—	—	—	—	—
Anthyllis montana L.	—	—	—	—	27	—
Aphanes microcarpa (Boiss. et Reuter) Rothm.	—	—	—	—	7	—
Aceras anthropophorum (L.) R. Br.	—	—	—	—	7	—
Astragalus sempervirens Lam.	—	—	—	—	3	—
Asperula purpurea (L.) Ehrend.	—	—	—	—	20	—
Aster sp.	—	—	—	—	3	—
Astragalus glycyrrhiza L. Fil. + Asperula cynanchica	—	—	26	—	7	—
Bellis perennis L.	27	—	22	—	7	—
Arthanatherum elatius (L.) Presl	18	—	—	—	7	—
Allium sphaerocephalon L.	—	—	11	—	7	—
Astragalus vesicarius L.	—	—	—	—	7	—
Anthoxanthum odoratum (L.) Huysh.	—	—	—	—	7	—
Achillosteuma sacalifi (L.) R. Br.	—	—	—	—	13	—
Ranunculus ficaria L. s.l.	9	—	—	—	—	—
Globularia cordifolia(Pulg.) O.Schwarz	—	—	11	—	13	—
Anthoxanthum odoratum L.	—	—	4	—	—	—
Cerastium liguricum Vv.	9	—	7	—	7	—
Globularia punctata Lapeyr.	—	—	—	—	3	—
Astragalus hamosus L.	—	—	—	—	7	—
Bellis sylvestris Cyr.	—	—	—	—	3	—
Bellis perennis L.	—	—	7	—	3	—
Astragalus danicus Retz.	—	—	—	—	7	—
Cerastium pumilum Curtis	—	—	—	—	13	—
Carlina vulga Hung.	9	—	11	—	13	—
Achillea tenuifi Grande	—	—	—	—	3	—
Buglossoides arvensis (L.) Johnston	—	—	—	—	3	—
Anthis collina Ten.	—	—	4	—	27	—
Aster alpinus L.	—	—	—	—	3	—
Anthemis arvensis L.	9	—	—	—	7	—
Bromus squarrosus L.	9	—	—	—	7	—
Barbarea bracteosa Guss.	—	—	4	—	—	—
Anthemis cretica L.	9	—	—	—	—	—
Anthis arcuifolia Lam.	—	—	—	—	13	—
Bromus tectorum L.	—	—	—	—	7	—
Aster sp.	—	—	—	—	7	—
Botrychium lunaria (L.) Swartz	—	—	7	—	—	—
Bromus hordaceus L.	18	—	—	—	9	—
Bromus mantoanus L.	18	—	—	—	—	—
Cerastium brachypetalum Desportes et Pers.	27	—	—	—	18	—
Carex leporina L.	—	—	7	—	—	—
Centaurea jacea L.	18	—	—	—	—	—
Centaurea nigrescens Willd.	36	—	19	—	73	—
Clinopodium vulgare L.	9	—	11	—	—	—
Carduus crispus L.	—	—	—	—	7	—
Carex kitaibeliana Degen	—	—	19	—	—	—
Campodium vulgare (L.) Hubbard	—	—	—	—	7	—
Centaurea ambigua Guss.	—	—	—	—	20	—
Bromus centenarius Schader	9	—	—	—	—	—
Carex flacca Schreber	—	—	—	—	3	—
Colchicum alpinum Lam. et DC.	—	—	11	—	—	—
Centaurea semidecanden L.	—	—	—	—	3	—
Centaurea arvensis L.	—	—	—	—	7	—
Brachypodium genuense DC.) Rosm. & Schult.	—	—	15	—	—	—
Centaurea nigrescens Willd. ssp. Angel. Hylandat	36	—	7	—	47	—
Chaerophyllum aureum L.	9	—	—	—	—	—
Cerastium arvense L.	27	—	4	—	7	—
Cerastium tomentosum L.	—	—	44	—	40	—
Alyssum minus (L.) Rothm.	—	—	—	—	—	—
Allium vineale L.	9	—	—	—	—	—
Asplenus geraniifolia Roth	—	—	—	—	7	—
Acorus barbata Poiret	—	—	—	—	7	—
Bunium bulbocastanum L.	9	—	37	—	20	—
Bupleurum falcatum L.	—	—	7	—	—	—
Carex vulpina L.	—	—	—	—	3	—
Anagallis arvensis L.	—	—	—	—	7	—
Crocius gulen (L.) Ehrend.	—	—	4	—	—	—
Cupio Sacra Tim.	—	—	—	—	13	—
Cupio angiata L.	—	—	—	—	20	—
Centaurea beaciata Scop.	9	—	—	—	—	—
Cupio Sacra L.	9	—	—	—	7	—
Anagallis foemina Miller	—	—	—	—	7	—
Anthemis tinctoria L.	18	—	—	—	7	—
Alyssum alyssoides (L.) L.	—	—	—	—	—	9
Cupio aurea (L.) Cass.	—	—	11	—	7	—
Consolida ajacis(Gouan) (L.) Koch	—	—	—	—	7	—
Cupio Sunnes L.	9	—	—	—	—	—
Crocius laevigus Opiz	9	—	15	—	—	—
Crocius pedicellatus (Ali.) Ehrend.	—	—	—	—	3	—
Cupio Sacra L.	9	—	—	—	7	—
Dodo mondi L.	—	—	—	—	3	—
Cytisus decumbens (Durande) Spach	—	—	—	—	7	—
Cynoglossum magellanus Tim.	—	—	4	—	—	—
Crocius vulgare Cass.	—	—	—	—	20	—
Cupio Sacra L.	—	—	4	—	7	—
Dodo ovatum L.	9	—	—	—	7	—
Cephala vera (L.) Chevall.	—	—	—	—	—	18
Digitalis oxiensis Roth	—	—	7	—	—	—
Dipsacus fullonum L.	9	—	—	—	—	—
Dianthus longicaulis Ten.	—	—	—	—	3	—
Lactuca virosa (L.) Pred	—	—	7	—	—	—
Knautia calycina (Pred) Guss.	—	—	15	—	13	—
Erysiguim arenifolium L.	—	—	—	—	20	—
Erysimum L.	9	—	—	—	—	—
Edraianthus graminifolius (L.) DC.	—	—	—	—	—	—
Dianthus brachyalyis	—	—	4	—	13	—
Dianthus carthusianorum L.	—	—	—	—	—	—
Cuscuta sp.	18	—	—	—	—	—
Euphorbia cyparissias L.	9	—	4	—	—	—
Erodium cicutarium (L.) L'Her.	—	—	—	—	7	—
Euphorbia dulcis L.	—	—	—	—	7	—
Geranium divaricatum L.	9	—	—	—	—	—
Euphorbia helioscopia L.	—	—	—	—	13	—
Euphorbia peplus L.	—	—	4	—	—	—
Euphorbia salsbugensis Funk	—	—	—	—	—	6
Euphorbia stricta H. Wolff	9	—	—	—	—	3
Euphorbia paniculata (J. Sch. et Th.	—	—	7	—	—	—
Dorycnium villosum (L.) Borbas	9	—	—	—	—	—
Festuca vulgata Gaudin	—	—	—	—	—	—
Galium aparine L.	—	—	15	—	—	6
Galium lucidum All.	—	—	11	—	13	29
Galium vernescens Huds	—	—	—	—	—	—
Festuca inops De Not.	—	—	—	—	27	—
Geranium molle L.	—	—	—	—	—	12
Galium consitilatum Vill.	—	—	4	—	53	24
Geranium cinereum Cav.	—	—	7	—	—	12
Galium corrudifolium Vill.	—	—	—	—	7	—
Hieratrigyloum aldenanum III Baussam	—	—	—	—	—	3
Homcizm cytoneum L.	—	—	4	—	—	—
Gaudinia fragilis (L.) Beauv.	—	—	—	—	—	—
Geranium tuberosum L.	—	—	—	—	—	—
Helianta gilata L.	—	—	15	—	—	—
Hospets laciniata L.	—	—	—	—	7	—
Helianthemum salicifolium (L.) Miller	—	—	—	—	13	—
Hypochoeris ostrenia (L.) Gerath. et Boy	—	—	—	—	—	3
Hypochoeris achyophorus L.	—	—	—	—	7	—
Helianthemum canum (Dun.) Pers.	—	—	—	—	—	—
Homcizm sp.	9	—	—	—	3	—
Hieratrio laevigata L.	—	—	—	—	7	—
Coprio ascitha (L.) Hale.	—	—	—	—	7	—
Hieratrio pilosella L.	—	—	—	—	—	50
Galium aparuchyphyl Vill.	—	—	—	—	—	3
Homcizm pilosella L.	9	—	59	—	33	68
Genista tinctoria L.	—	—	—	—	33	6
Helianthemum nummularium (L.) Miller	—	—	7	—	—	6
Geum molle Vv.	—	—	11	—	—	6
Homungia petraea (L.) Rchb.	—	—	—	—	—	—
Hieratrio pilosella L.	—	—	—	—	—	—
Hypnogeris corona L. = Hypocoeris glauca Tm.	9	—	11	—	27	—
Homcizm villosum L.	—	—	—	—	—	—
Iuda montana L.	—	—	—	—	13	—
Iberis pinnii Tenor	—	—	—	—	7	—
Iberis saxatilis L.	—	—	—	—	13	—
Lathyrus aphacaca Ktze.	—	—	—	—	7	—
Lathyrus cicera L. Gaudon	—	—	—	—	7	—
Lactrolon cichoraceus (Tm.) Sanguin.	—	—	15	—	7	—
Orlaya kochii Heywood	—	—	—	—	7	—
Lathyrus cicera L.	—	—	—	—	—	—
Homcizm sylvatcum (L.) L.	—	—	—	—	—	—
Petrorhagia prolifera (L.) Ball et Heyw.	—	—	—	—	—	—
Geranium sanguineum L.	—	—	—	—	—	—
Lactuca perenis L.	—	—	—	—	7	—
Narcissus poetaxus L.	—	—	—	—	7	—
Orchis tridentata Scop.	—	—	—	—	13	—
Myosotis cylvatica Hoffm.	—	—	4	—	—	—
Lathyrus incarnopsus L.	9	—	—	—	—	—
Omithogalum etscopum Tm.	—	—	—	—	—	—
Lonicera caprifolium L.	—	—	—	—	—	—
Lonicera etrusca Santi	9	—	—	—	20	—
Lonicera xylosteum L.	—	—	—	—	3	—
Muscari neglectum Guss.	—	—	—	—	47	—
Omithogalum umbellatum Tm.	—	—	—	—	13	—
Onobrychis viciifolia Scop.	9	—	—	—	—	—
Ononi spinosa L.	—	—	—	—	—	—
Potentilla pulsina Wild.	45	—	—	—	—	—
Pimpinella saxifraga L.	27	—	—	—	53	—
Prunella laciniata (L.) L.	27	—	—	—	—	—
Onobanche sp.	—	—	—	—	—	—
Trifolium scabrum Hudson	36	—	4	—	—	—
Lotus alpinus (DC.) Schleicher	—	—	—	—	—	—
Tragopogon sanctorum Halácsy et Sart.	—	—	—	—	7	—
Tordylium apulum L.	—	—	—	—	7	—
Trifolium campestre Schreber	9	—	—	—	—	—
Pastinacella latifolia (L.) Crtnof	—	—	—	—	3	—
Lonicera hispidula L.	18	—	7	—	7	—
Pallenis spinosa (L.) Cass.	—	—	—	—	7	—
Lonicera xylosteum L.	—	—	4	—	—	—
Lolium perenne L.	—	—	—	—	—	—
Plantago arenaria Chaix	—	—	—	—	20	—
Lonicera caprifolium Koehl	—	—	—	—	7	18
Odontites rubra (Baming.)Opiz	27	—	—	—	—	—
Trifolium campestre Schreber	55	—	—	—	27	—
Trifolium lacunosum Gmp. ex Gmo.	—	—	—	—	7	—
Trifolium arvense L.	—	—	—	—	—	15
Tamacum laviigatum (Willd.) DC.	—	—	—	—	13	—
Thymus ontopentanus H. Braun	—	—	—	—	13	—
Tragopogon porrifolius ssp. apennisuvia Martin.	—	—	—	—	33	6
Teucrium montanum L.	—	—	—	—	20	6
Stachys salvifolia Ten.	—	—	—	—	7	—
Myosotis arvensis (L.) Hill	—	—	—	—	—	—
Poa bulbosa L.	18	—	11	—	27	—
Polygonum aviculare L.	—	—	—	—	—	—
Pulicaria vulgaris Gaertner	9	—	—	—	—	—
Plantago lag. L.	9	—	—	—	—	—
Prunella vulgaris L.	27	—	—	—	—	—
Trifolium sp.	—	—	—	—	7	—
Tragopogon porrifolius L.	9	—	—	—	—	—
Orchis pauciflora Ten.	—	—	4	—	7	—
Orchis sp.	—	—	—	—	3	—
Orchis morio L.	—	—	—	—	3	—
Trifolium campestre Schreber	—	—	—	—	7	—
Tragopogon dubius Scop.	9	—	—	—	—	—
Polygala angelisii Ten.	—	—	4	—	3	—
Plantago lagopus L.	9	—	—	—	—	—
Plantago major L.	9	—	—	—	7	—
Medicago rigidula (L.) All.	—	—	—	—	—	3
Polygala amarella Crantz	—	—	19	—	—	—
Poa pratensis Gaudin	—	—	15	—	13	—
Poa sylvicola Guss.	18	—	—	—	—	—
Polygala monspeliaca L.	—	—	—	—	7	—
Plantago cynops L.	—	—	—	—	7	—
Pimpinella saxifraga L.	—	—	—	—	20	6
Phytuma orbiculare L.	—	—	7	—	3	—
Minuartia hybrida (Vill.) Schischkin	—	—	—	—	13	—
Pilosa ambigua Tenore	—	—	—	—	40	—
Phleum phleoides (L.) K. Meyer	18	—	—	—	—	29
Pulsatilla alpina (L.) Delarbre	—	—	—	—	13	—
Phleum pratense L.	9	—	—	—	—	—
Poa alpina L.	—	—	48	—	29	—
Poa annua L.	—	—	4	—	—	6
Plantago sarda Pampan.	—	—	—	—	—	—
Sedum sediformi Tm.	—	—	—	—	13	—
Ranunculus granatensis L.	—	—	—	—	20	3
Trifolium thalii Vill.	—	—	7	—	—	—
Melilotus neapolitanus Ten.	—	—	—	—	3	—
Mantha longifolia (L.) Hudson	18	—	—	—	—	—
Linaria purpurea (L.) Miller	—	—	7	—	—	15
Linum tenuifolium L.	—	—	—	—	7	—
Tragopogon pratensis L.	—	—	—	—	—	—
Linum catharticum L.	—	—	7	—	3	—
Trifolium stellatum L.	—	—	7	—	7	—
Linaria vulgaris P. W. Schmidt	—	—	7	—	29	—
Polygala major Jacq.	—	—	4	—	27	—
Mollotus abvesina Thiell.	—	—	—	—	—	—
Linaria simplex (Willd.) DC.	—	—	—	—	13	—
Medicago prostrata Jacq.	—	—	—	—	13	—
Medicago polymorpha (L.) DC.	27	—	—	—	—	—
Medicago sativa L.	—	—	—	—	—	—
Linum capitatum Kit.	—	—	11	—	—	—
Linaria spuria (L.) DC.	—	—	4	—	—	—
Medicago minima (L.) Bartal.	9	—	—	—	27	—
Medicago orbiculata (L.) Bartal.	—	—	—	—	7	—
Mutanoxia gnea (L.) Bentham	—	—	—	—	—	—
Medicago lupulina L.	—	—	7	—	—	3
Silene nutans Ewe.	—	—	7	—	—	6
Silene vulgaris (Moench) Garcke	9	—	—	—	—	3
Silene multicaulis Guss.	—	—	—	—	—	18
Rosa corymbifera Borkh.	9	—	—	—	—	—
Small tetrameria L.	—	—	—	—	—	—
Schanerlus polyspermus L.	—	—	—	—	—	6
Ranunculus ficaria L. s.l.	9	—	—	—	—	—
Carlina acaulis L.	—	—	—	—	7	—
Sedum album L.	—	—	—	—	—	3
Sedoris romanus L.	—	—	—	—	—	—
Rumex acetosa L.	—	—	26	—	—	18
Rhinanthus wettrenius (Stornock) Soo	—	—	19	—	13	18
Silene otites (L.) Wibel	—	—	—	—	—	3
Sedum dasyphyllum	36	—	—	—	—	3
Rumex acetosella L.	—	—	26	—	9	—
Sideritis syriaca L.	—	—	—	—	33	6
Silene conica L.	—	—	—	—	13	6
Silene italica (L.) Pers.	9	—	—	—	—	—
Rumex scutatus L.	—	—	—	—	13	—
Shanaria arvensis L.	9	—	—	—	13	3
Sedum hispanicum L.	—	—	—	—	7	—
Carex flacca Schreber	18	—	7	—	13	—
Paronychia kapela (Hacq.) Kerner	—	—	—	—	13	6
Cardous macrocephalus Desf.	—	—	7	—	7	—
Sedum tenuifolium (w. et S.) Strobl	—	—	—	—	—	6
Campanula glomerata L.	—	—	—	—	—	3
Carex caryophylea La Tour	—	—	11	—	—	3
Sedum ochroleucum	27	—	—	—	—	—
Stuplumum bifurum L.	—	—	—	—	—	6
Bupleurum praealtum L.	9	—	—	—	—	—
Bupleurum baldense Turra	—	—	—	—	—	—
Carex depressa Link	—	—	—	—	—	—
Sesli libanotis (L.) Koch	—	—	—	—	—	3
Campanula rapunculus L.	—	—	—	—	—	6
Carex halleriana Asso	—	—	—	—	27	21
Sempervivum sp.	—	—	—	—	—	—
Veronica praecox All.	—	—	—	—	—	—
Campanula odmedianti Vill.	—	—	4	—	—	—
Carex hirta L.	—	—	15	—	—	—
Calamintha nepeta (L.) Savi	—	—	4	—	7	—
Campanula cochlearifolia Lam.	—	—	—	—	—	3
Campanula trachelium L.	—	—	—	—	—	3
Ranunculus thoratus Tm.	—	—	—	—	—	3
Veronica chamaedrys L.	—	—	4	—	—	6
Vicia lathyroides L.	—	—	—	—	—	3
Xeranthemum cylindraceum S. et S.	9	—	—	—	—	3
Vicia sepium L.	—	—	—	—	—	3
Vicia angustifolia L.	—	—	—	—	—	3
Valerianella dentata(Pulg.) L.Schmidt	—	—	—	—	—	3
Urtica dioica L.	—	—	—	—	—	3
Verbascum longifolium Ten.	—	—	4	—	—	—
Valerianella coronata (L.) DC.	—	—	—	—	13	—
Vicia cerdwyensis L.	—	—	11	—	27	3
Thlaspi perazzi Wettb.	—	—	19	—	7	—
Thymus longicaulis C.	9	—	—	—	7	—
Thymus longifolius L.	—	—	—	—	7	—
Thymus divaricatum Jan	—	—	4	—	13	—
Valerianella carinata Loisel.	—	—	—	—	—	—
Vicia villosa Roth	—	—	—	—	—	3
Veronica orsinana Ten.	—	—	4	—	15	—
Vicia bithynica (L.) L.	—	—	—	—	—	3
Vicia cassubica L.	—	—	—	—	—	—
Viola eugenia Parl.	—	—	15	—	20	32
Valerians tuberosa L.	—	—	4	—	33	24
Sulla hedysa L.	—	—	4	—	7	6
Scandix australis L.	—	—	—	—	—	—
Satureja graniten L.	—	—	—	—	7	—
Scabiosa ranitensis L.	—	—	—	—	—	—
Ranunculus repens L.	9	—	—	—	—	—
Sanguisorba minor Scop.	36	—	—	—	40	—
Scabiosa columbaria Boiss. et Heldr.	—	—	—	—	—	—
Verbascum pseudoleanthus Vill.	—	—	—	—	—	—
Verbascum sp.	36	—	22	—	20	59
Verbascum sp.	—	—	4	—	—	—
Verbena officinalis L.	—	—	—	—	—	—
Sanfrigia patriciana Miller	—	—	—	—	—	—
Sanfrigia bulbifera L.	—	—	4	—	—	21
Sonchi pustum venosum L.	—	—	—	—	—	6
Verbascum simonkeri L.	—	—	—	—	—	—
Sonchus tenerrimus L.	—	—	—	—	27	18

Supplement E2. Supplementary Figures 1–4.

Anhang E2. Ergänzende Abbildungen.

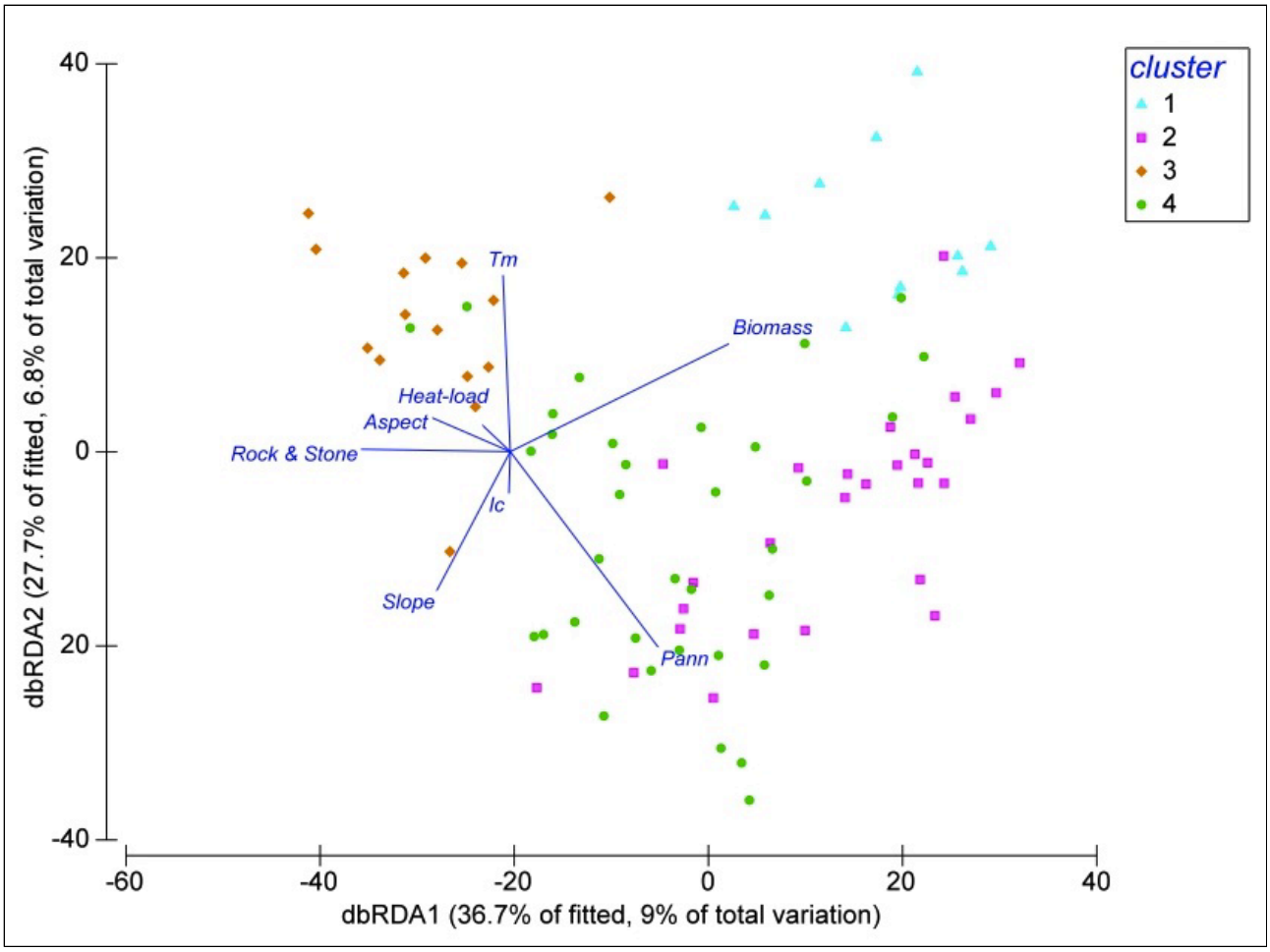

Fig. E2.1. Distance-based redundancy analysis (dbRDA) showing constrained ordination of relevés based on the (standardized) environmental variables. P_{ann} = annual precipitation; I_c = continentality index; T_m = mean annual temperature; Aspect = southing index.

Abb. E2.1. Distanzbasierte Redundanzanalyse (dbRDA) mit der beschränkten Ordination der Vegetationsaufnahmen basierend auf den standardisierten Umweltvariablen. P_{ann} = mittlerer Jahresniederschlag; I_c = Kontinentalitätsindex T_m = Jahresmitteltemperatur, Biomass = oberirdische Biomasse, Slope = Hangneigung, Rock & Stone = Deckung von Steinen und Felsen an der Bodenoberfläche, Aspect = Südkomponente der Exposition, Heat-load = Heat-load Index.

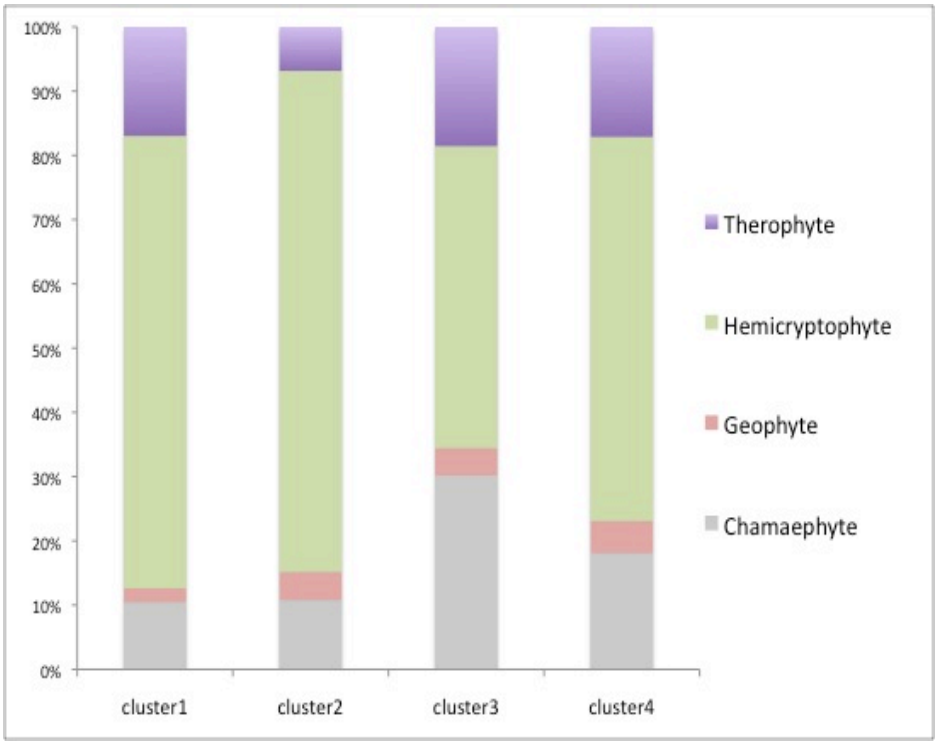

Fig. E2.2. Life-form spectra (weighted on cover data) of the four floristic-ecological groups obtained from hierarchical cluster analysis.

Abb. E2.2. Lebensformspektren (gewichtet mit den Deckungen) der vier floristisch-soziologischen Gruppen, die mittels hierarchischer Clusteranalyse unterschieden wurden.

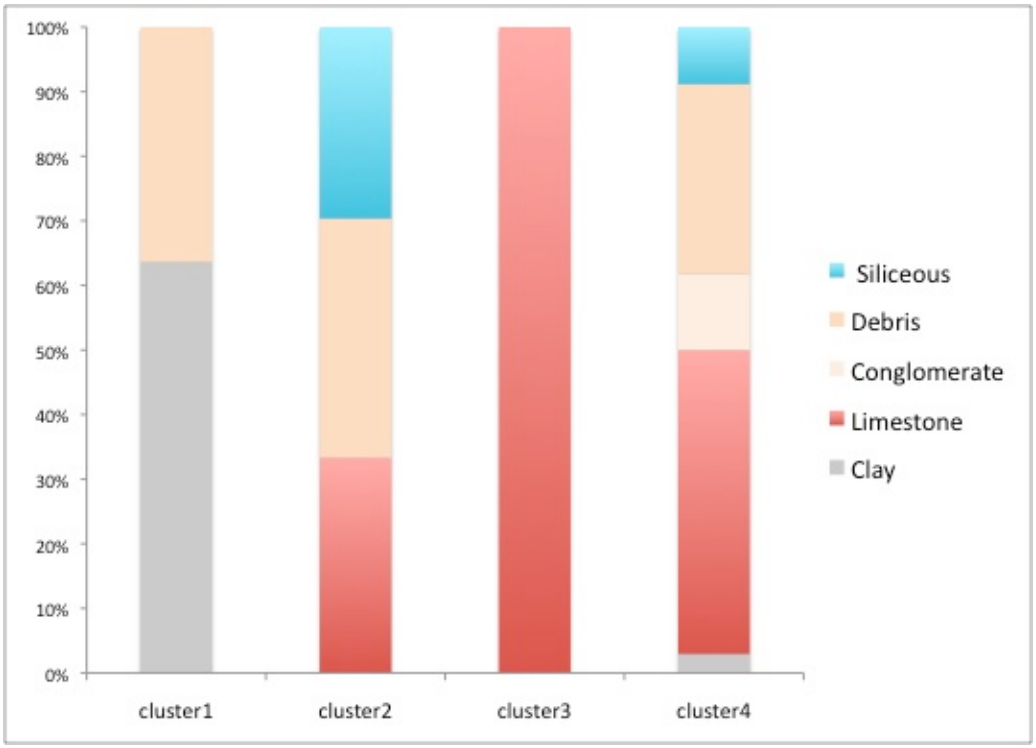

Fig. E2.3. Percentage distribution of the bedrock types out of the total number of relevés across the clusters.

Abb. E2.3. Prozentuale Verteilung von Gesteinstypen in der vier floristisch-soziologischen Gruppen, die mittels hierarchischer Clusteranalyse unterschieden wurden.

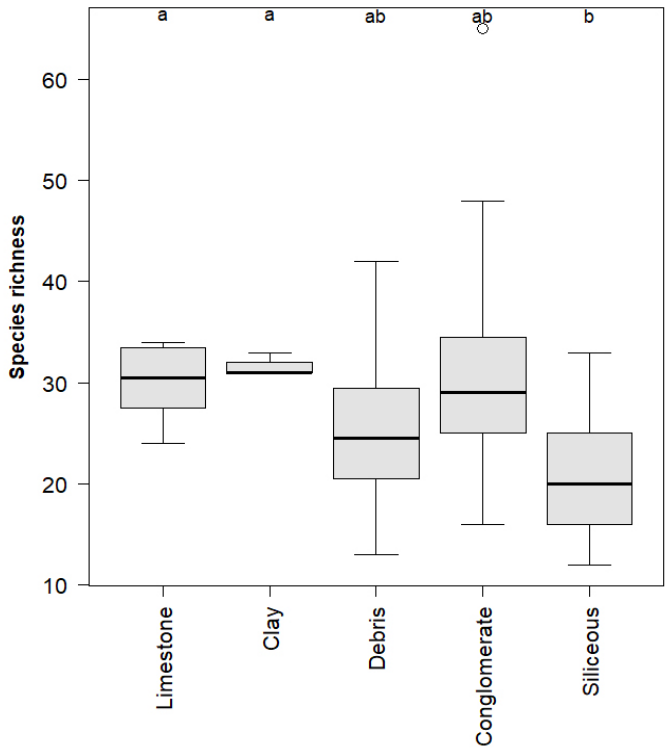

Fig. E2.4. Boxplots of vascular plant species richness on 4 m² across bedrock types. Different letters indicate significance (Mann-Whitney *U* test) at $p < 0.05$ after Bonferroni's correction .

Abb. E2.4. Boxplots des Gefäßpflanzenartenreichtums auf 4 m², abhängig vom geologischen Untergrund (Limestone = Kalkstein; clay = tonige Gesteine; debris = Geröll; conglomerate = Konglomerat; siliceous = silikatisches Festgestein. Verschiedene Buchstaben stehen für Gesteine mit signifikant verschiedenem Artenreichtum (Mann-Whitney *U*-Test mit $p < 0.05$ nach Bonferroni-Korrektur).

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Artikel/Article: The dry grasslands of Abruzzo National Park, the oldest protected area in the Apennines (Central Italy): overview of vegetation composition, syntaxonomy, ecology and diversity Das trockene Grasland des Abruzzen-Nationalparks, des ältesten Schutzgebiets im Apennin (Mittelitalien): Überblick über Vegetationszusammensetzung, Syntaxonomie, Ökologie und Vielfalt 547-571