Received: 16 April 2024 | Revised: 21 August 2024 | Accepted: 22 August 2024

DOI: 10.1111/jvs.13305

Journal of Vegetation Science IAVS

RESEARCH ARTICLE

Drivers of vascular plant, bryophyte and lichen richness in grasslands along a precipitation gradient (central Apennines, Italy)

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Funding information

Global Sponsorship Committee of the International Association for Vegetation Science (IAVS); European Union - NextGenerationEU; Fondazione Anna Maria Catalano (Fiumicino, Italy)

Co-ordinating Editor: Eric Lamb

Abstract

Questions: Semi-natural grasslands in Southern Europe are biodiversity hotspots, yet their patterns of plant species richness are less studied than in Central Europe. In the Central Apennines (Italy), there are large areas of dry calcareous grasslands, across a steep gradient of mean annual precipitation (from 650 to 1350 mm within c. 30 km). We asked: How do these grasslands compare to other Palaearctic grasslands in richness levels? How do the precipitation gradient and other environmental predictors influence species richness? Does this influence differ among taxonomic groups?

Location: Submontane and lower-montane belt of the Central Apennines (Abruzzo and Lazio, Italy).

Methods: We recorded the species richness of vascular plants and (terricolous) bryophytes and lichens in 97 plots of 10 m^2, aligning them with the precipitation gradient while maintaining geological substrate and elevation similar. Mean temperature and precipitation were estimated with a high-resolution regional model. A wide array of environmental variables (including soil properties and grazing load) were measured for each plot. Multivariate relationships within and between response and predictor variables were studied with Canonical Correlation. The relative importance of predictors on response variables was modeled with Boosted Regression Trees.

For affiliations refer to page 10.

Results: The sampled grasslands were very species-rich in the Palaearctic context. Vascular plant richness was negatively influenced by topographic heat load and soil sand content, but we did not detect a relationship with mean annual precipitation. Bryophyte richness was poorly modeled by the measured variables, although it was positively correlated with lichen richness. Lichen richness had a marked negative relationship with soil phosphorus and mean annual precipitation.

Conclusions: In Southern European semi-natural mountain grasslands, vascular plant richness is driven more by fine-scale edaphic factors than by precipitation gradients. In contrast, bryophyte and lichen species richness is predicted by a mixture of climatic and edaphic variables.

KEYWORDS
Apennines, biodiversity, bryophyte, environmental driver, lichen, mean annual precipitation, semi-natural dry grassland, soil property, species richness, vascular plant

1 | INTRODUCTION

Palaearctic grasslands hold some of the world highest values of plant richness at small spatial scales (Wilson et al., 2012; Dengler et al., 2020) and are therefore of outstanding importance in the study of biodiversity patterns and their conservation (Feurdean et al., 2018; Prangel et al., 2023; Staude et al., 2023). Although vascular plants are the most represented component of Palaearctic grasslands, other groups of photosynthetic organisms, namely bryophytes and lichens, play relevant functional roles in these communities (e.g. Boch et al., 2016; Janišová et al., 2022; Jaroszynska et al., 2023); yet, their diversity patterns are less explored—potentially leading to an unaware loss of biodiversity and ecosystem services (Boch et al., 2018; Gheza et al., 2020).

The study of biodiversity patterns along climatic gradients is a fundamental goal in ecology (e.g. Vetaas et al., 2019; Smith et al., 2022). Many studies found a positive relationship between mean annual precipitation and grassland species richness at the plot scale (i.e. the species density within sampling units: e.g. Adler & Levine, 2007; Cleland et al., 2013; Zhang et al., 2014). However, the vast majority of these works were based on gradients ranging from desert-like vegetation to climatic steppe. According to the "humped-back model" of richness–productivity relationship in grasslands (e.g. Grime, 1973; Huston, 2014; Fraser et al., 2015), species richness is expected to peak in systems of intermediate productivity. Smith et al. (2022) found a hump-shaped relationship between richness and mean annual precipitation in grassland ecosystems worldwide. The decline in richness at high precipitation levels might be explained by increased competition and light limitation (Lane et al., 2000).

In Southern Europe, semi-natural dry grasslands (i.e., originating from and maintained by disturbance, on draining bedrock such as limestone) are more widespread than their Central European counterparts (Apostolova et al., 2014; Ambarlı et al., 2018), yet they are much less studied. In the Central Apennines (Italy), secondary grasslands extend over vast areas, under different climatic and edaphic conditions (e.g. Theurillat et al., 2007; Blasi et al., 2012; Cancellieri et al., 2020). Due to the rain shadow effect, some inner valleys have precipitation values (c. 600–700 mm/year) that are half of those recorded, at the same elevation, in surrounding areas exposed to westerly winds (Crespi et al., 2018). This situation is similar to that of the well-known "dry valleys" in the Alps (Filibeck, Cancellieri, et al., 2020), which host outposts of Eastern European steppe species (e.g. Magnes et al., 2021; Bergauer et al., 2022). However, in contrast to the Alps, the Central Apennines are characterized by a Mediterranean-type precipitation pattern, with a minimum in summer (Crespi et al., 2018; Cutini et al., 2021).

Since the "arid" end of the Central Apennine gradient is relatively "humid" on a global scale, a (globally) unimodal response of species richness to precipitation would imply a decrease in richness with increasing precipitation in this region. However, two studies in the Alps, along a precipitation interval very similar to ours, found unimodal (Bergauer et al., 2022) or no effects (Gheza et al., 2018) on grassland richness at the plot scale. Moreover, other drivers are known to shape community-scale richness patterns (e.g. Marini et al., 2007; Polyakova et al., 2016; Talebi et al., 2021). In particular, macro- and meso-scale climatic factors might be overridden by micro-scale climatic, edaphic and topographical factors such as slope aspect or soil depth and texture (Bennie et al., 2006; Moeslund, Arge, Bøcher, Dalgaard, & Svenning, 2013), which have been shown to be particularly relevant in (Mediterranean) mountain grasslands (e.g. Sebastià, 2004; Catorci & Gatti, 2010; Filibeck, Sperandii, et al., 2020; Massaccesi et al., 2023). Such factors can lead to very different levels of actual soil water availability for plants (e.g. Araya et al., 2011; Moeslund, Arge, Bøcher, Dalgaard, Odgaard, et al., 2013). Finally, richness patterns of different taxonomic groups of photosynthetic organisms (vascular plants, bryophytes and lichens) may respond differently to the same gradients and drivers (e.g. Schaffers, 2002; Löbel et al., 2006; Dembicz et al., 2021; Asplund et al., 2022).

We sampled richness patterns of vascular plants and terricolous bryophytes and lichens in grasslands, along a precipitation gradient in the Central Apennines, while keeping geological substrate and altitude similar. Several abiotic and biotic descriptors were obtained at each sampling point. Our research questions were:

(i) What are the (plot-scale) richness levels of the three taxonomic groups in the sampled grasslands, and how do they rank in a Palaearctic context?
(ii) How is (plot-scale) grassland species richness related to the precipitation gradient and the other environmental descriptors?
(iii) Is the effect and the relative importance of the precipitation gradient and the measured environmental predictors different across the taxonomic groups considered?

2 | METHODS

2.1 | Study area

The study area is located in a section of the Central Apennines (Abruzzo and Lazio regions, Italy) (Figure 1). Mean annual precipitation varies from c. 650 mm in the intermontane basins of L'Aquila and Fucino, to c. 1350 mm in the Sangro and Comino valleys. The annual precipitation cycle shows a minimum in summer and a maximum in late autumn (Crespi et al., 2018; Cutini et al., 2021).

Grasslands in the study area are mostly dominated by perennial, relatively xerophytic grasses such as *Bromopsis erecta*, *Festuca circummediterranea*, and *Phleum hirsutum* subsp. *ambiguum* (Filibeck et al., 2019, 2023). At the lower end of the precipitation gradient, grasses are mixed with chamaephytes (*Satureja montana*, *Globularia* spp., *Helianthemum* spp., etc.) (Cancellieri et al., 2020). Most of the studied communities can be assigned to the phytosociological orders *Erysimo-Jurineetalia bocconei* (class *Festuco hystricis-Ononidetea striatae*) and *Brachypodietalia pinnati* (class *Festuco-Brometea*) (syntaxonomy follows Mucina et al., 2016).

Transhumant sheep grazing was the main grassland exploitation system in the area for centuries, until the 1950s; the abandonment of sheep husbandry has been followed by an increase in free-ranging cattle and horse grazing (Primi et al., 2016). Mowing is usually restricted to productive habitats in the valley-bottoms (Filibeck et al., 2023), which are not included in this study.

2.2 | Sampling design and species richness survey

Site selection aimed to cover the precipitation gradient, following a climatic stratification based on Crespi et al. (2018) (Table 1). To reduce the variation range of environmental factors other than precipitation, sampling was performed solely on calcareous bedrocks and was restricted to altitudes between c. 700 and 1300 m a.s.l., corresponding to mean annual temperatures between 13 and 8°C (Brunetti et al., 2014).

Field sampling was conducted in mid-June 2017, i.e. at the phenological peak for the area (Primi et al., 2016). We recorded 97 10-m^2 plots, following the protocol of Dengler et al. (2016). Plots were placed in visually homogeneous stands and their position was recorded with a GPS. A magnet was buried in each plot for future resurveys. For each plot, all species of vascular plants, terricolous bryophytes and terricolous lichens were recorded, following the "shoot presence" convention (Cancellieri et al., 2017). Names were standardized following Bartolucci et al. (2018) for vascular plants, Aleffi et al. (2020) for bryophytes and Nimis (2016) for lichens (see Appendix S1 for details). Together with the species richness of vascular plants, bryophytes and lichens, we determined the "total richness" as the number of all photosynthetic species recorded in a plot.

2.3 | Environmental data collection

At each sampling point we measured environmental variables (Table 1) potentially relevant to grassland richness (see e.g. Kuzemko et al., 2016; Filibeck et al., 2019; Dembicz et al., 2021). Topographical and geomorphological variables, namely *elevation*, *slope inclination*, *slope aspect*, *microrelief*, *soil depth* and *cover of gravel and rocks* were measured in the field, following Dengler et al. (2016). As a proxy for microclimate, we calculated the *heat load index* following equation 2 in McCune and Keon (2002). To obtain *soil chemical and physical variables* (see Table 1 for full list), a mixed soil sample was collected from the upper 10 cm at five pre-defined points within each plot (see Appendix S1 for details). *Normalized Difference Vegetation Index* (*NDVI*) was obtained from Landsat-7 images, while *grazing load* and *prevailing grazing species* were assessed in the surroundings of each plot using the Faecal Standing Crop method (Campbell et al., 2004) (Appendix S1).

2.4 | Climate variables

We exploited the high instrumental data density of Italy (which is much higher than the number of stations contributing to global data sets, such as e.g. those provided by CRUTEM-Climatic Research Unit TEMperature or NOAA-National Oceanic and Atmospheric Administration) to model climate information at a detailed spatial scale. For each sampling site, temporal records of monthly mean temperatures and precipitation for the 30 years preceding the sampling were reconstructed using the anomaly method (details in Appendix S1) (Brunetti et al., 2014; Crespi et al., 2018). This allowed us to obtain a model specific to the study area, and thus to estimate the climatic variables, that is *mean annual temperature* and (mean) *annual precipitation* for the coordinates and elevation of each sampling plot.

2.5 | Statistical analysis

We preliminarily tested for correlation among predictors; if two predictors were highly correlated with each other (i.e. $|r| \geq 0.7$), we

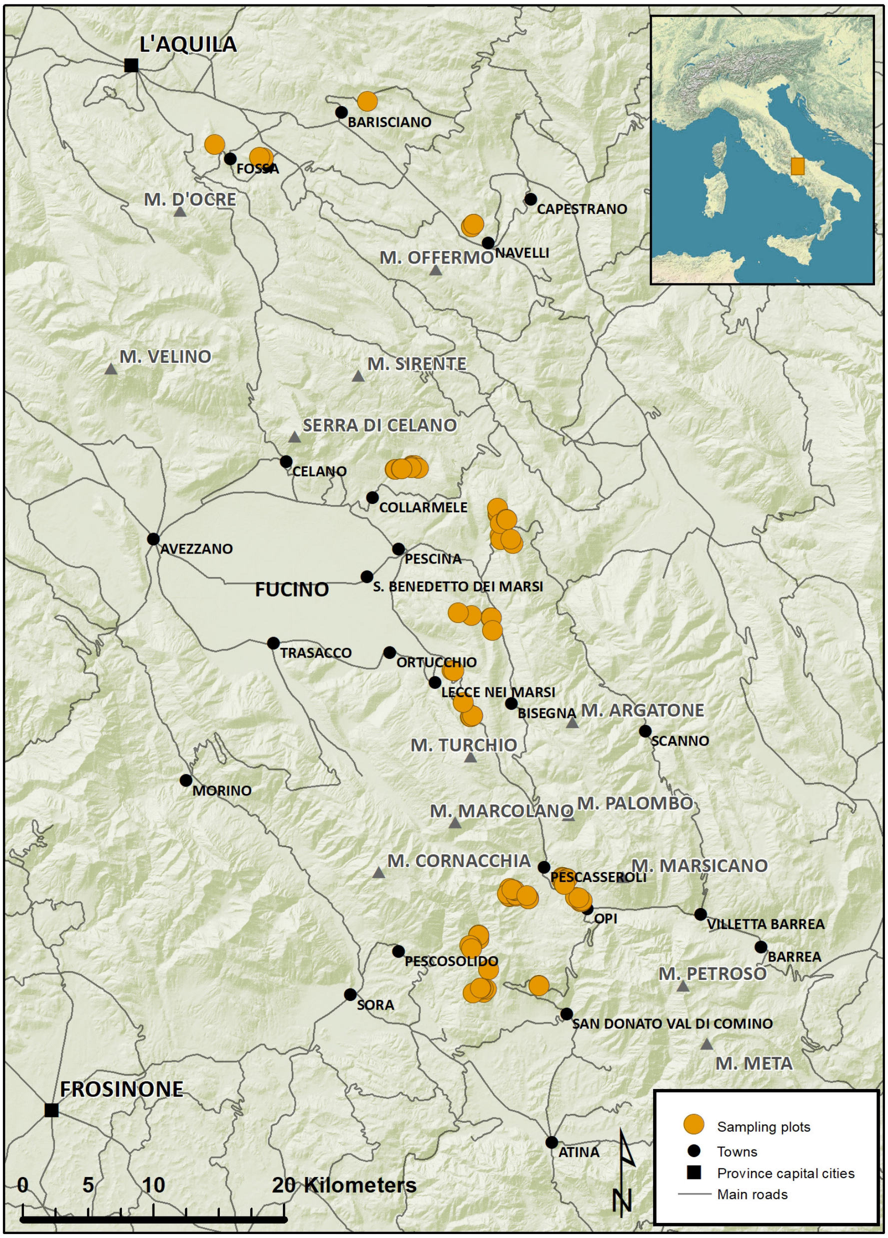

FIGURE 1 Study area location (inset) and distribution of sampling plots (main map).

selected only the more ecologically relevant one, leading to a set of 19 continuous and two categorical predictor variables retained for the analyses (Table 1).

Multivariate patterns within the environmental (continuous) variables and within the response variables (total, vascular, bryophyte and lichen richness), as well as between the two groups, were explored and tested through Canonical Correlation (hereafter CC) (Mardia et al., 1979) (see Appendix S1 for details).

To estimate the relative importance of predictors (both continuous and categorical) in driving the species richness of each taxonomic group, we modeled the response variables using Boosted Regression Trees (BRTs) (Elith et al., 2008). To visualize the shape of the fitted functions, we used partial dependence plots, which show the effect of each variable on richness after accounting for the average effects of all other variables in the model (Elith et al., 2008). All statistical analyses were performed in R (R Core Team, 2020) (see Appendix S1 for details).

3 | RESULTS

3.1 | Plot-scale richness

A total of 517 taxa were recorded, including 444 vascular plants, 40 bryophytes and 33 lichens. The most frequent species were: *Poterium sanguisorba* and *Koeleria splendens* among vascular plants;

Syntrichia ruralis and *Hypnum cupressiforme* among bryophytes; *Cladonia furcata* subsp. *furcata* and *Cladonia foliacea* f. *convoluta* among lichens (Appendix S2). Mean total species richness per plot was 52.8 (max. 85); mean vascular richness was 47.0 (max. 76); mean bryophyte and lichen richness was 3.8 (max. 10) and 1.9 (max. 7) species, respectively (Table 2).

3.2 | Role of environmental descriptors

The overall CC model was highly significant ($p < 0.001$). Bryophyte and lichen richness were weakly positively correlated with each other, while neither variable was correlated with vascular plant richness (Table 3). Vascular richness and total richness were positively correlated with the second canonical dimension ($r = 0.65$ and 0.58, respectively), which was a linear combination of decreasing coarse sand, decreasing gravel and rock cover, decreasing soil pH and, to a lesser extent, decreasing heat load. Bryophyte richness was (weakly) negatively correlated with the third canonical dimension ($r = -0.35$), which, in turn, was characterized by decreasing soil pH and increasing coarse silt and NDVI. Lichen richness was negatively correlated ($r = -0.66$) with the first canonical dimension, which was a linear combination of increasing assimilable P, increasing precipitation and increasing slope inclination; bryophyte richness also had a weak negative correlation ($r = -0.30$) with the same dimension.

3.3 | Relative importance of the environmental predictors across the taxonomic groups

Boosted Regression Trees performed best for vascular plants, as indicated by the highest value of explained variance (Table 4), while they had the poorest performance for bryophytes. For vascular richness, the two most influential predictors were coarse sand and heat load (Figure 2). For bryophyte richness, they were mean annual temperature and heat load; for lichen richness, assimilable P and annual precipitation (Figure 2).

In partial dependence plots, vascular plant richness showed a negative nonlinear relationship with coarse sand, exhibiting a steep decline at low values and no further effects above c. 150 g/kg. Vascular plant richness was also negatively affected by heat load (but only for high values of the predictor), C/N ratio and gravel and rock cover (with practically no effect for values <50%) (Figure 3). Lichen richness was negatively affected by assimilable P (with no effect above c. 40 mg/kg), annual precipitation (strong effect only above c. 1200 mm/year) and slope inclination (but with no effects above c. 25°), while coarse sand had a positive effect (Figure 3). Bryophyte richness increased irregularly with mean annual temperature. Heat load had a negative effect; soil depth had a negative effect, with high species diversity for values below 5 cm; assimilable P had a steep negative relationship, but only for values below c. 40 mg/kg (Figure 3).

4 | DISCUSSION

4.1 | Plot-scale species richness in a Palaearctic context

We found a mean vascular plant richness per 10 m^2 plot (Table 2) of 47.0 species, which is considerably higher than the Palaearctic means for the *Festuco-Brometea* (34.6) and *Festuco-Ononidetea* (35.1) recorded in the GrassPlot Diversity Explorer v. 2.10 (https://edgg.org/databases/GrasslandDiversityExplorer; see Biurrun et al., 2021). For bryophytes and lichens, however, the mean richness in the present dataset is only slightly higher compared to the Palaearctic mean.

Interestingly, the rain-shadowed valleys of the Alps instead show an average plot-scale richness of vascular plants well below the Palaearctic *Festuco-Brometea* mean (Magnes et al., 2021; Bergauer et al., 2022). On the other hand, some plots surveyed in the rain-shadowed valleys of the Armenian Caucasus had a mean value (46.8 vascular plants in 10 m^2; Vynokurov et al., 2024) almost identical to that in the present survey. It has been suggested that, as the Alps were covered by an ice shield during the last glacial, only the species pool of cold-climate grasslands was able to find refugia along the margins of the mountain range, resulting in a smaller pool of xerophytic species compared to other regions (Bergauer et al., 2022). Conversely, the Apennines were never covered by a continuous ice shield (Jaurand, 1999); moreover, they are in direct contact with the rich biota of the Mediterranean floristic region. A similar explanation has been proposed for Armenia (Vynokurov et al., 2024).

The maximum total species richness per 10 m^2 plot in our dataset is 85 species, a very high value in the Italian context (cf. e.g. Baumann et al., 2016; Cerabolini et al., 2016), although lower than some plots surveyed in other sub-Mediterranean regions (e.g. up to 97 species in northern Spain: Biurrun et al., 2014).

4.2 | Predictors of richness

Canonical Correlation showed that vascular plant and lichen richness responded to orthogonal gradients, suggesting that they were explained by independent sets of environmental factors. Consistently, BRTs showed that the most important predictors were different for the two groups. In contrast, bryophyte and lichen richness were moderately correlated with each other in CC, although in BRTs only one of the most important predictors (assimilable P) was shared between the two groups. Total richness was explained by the same factors as vascular richness, because vascular plants constituted the majority of species in each plot.

As already found in studies across the Palaearctic (e.g. Kuzemko et al., 2016; Gheza et al., 2018; Dembicz et al., 2021), vascular plant, bryophyte and lichen diversity respond differently to most environmental gradients. Apart from different ecological preferences (e.g. Asplund et al., 2022), this can be due to the fact that competition between vascular plants and lichens is asymmetric (e.g. Löbel et al., 2006): since vascular plants grow taller than lichens, the former can shade out the latter from light, but not vice versa.

TABLE 1 Descriptive statistics of the environmental (predictor) variables.

Variable (continuous)	Mean	SD	Median	Min	Max
Annual precipitation (mm)	1053	232	1170	656	1304
Assimilable P (mg/kg)	23.5	27.4	11.9	3.5	157.0
*$CaCO_3$ (g/kg)	67	122	19	2	623
Clay (g/kg)	63	48	44	12	281
C/N	10.5	1.9	10.0	8.3	18.5
Coarse sand (g/kg)	80	95	35	5	425
Coarse silt (g/kg)	158	50	156	35	426
*Elevation (m)	1116	211	1176	620	1555
*Exchangeable Ca^{++} (mg/kg)	11,600	2479	12,134	4418	16,440
Exchangeable K^{+} (mg/kg)	201	131	168	48	766
Exchangeable Mg^{++} (mg/kg)	284	186	228	70	1109
Exchangeable Na^{+} (mg/kg)	19.3	10.2	18.6	6.0	50.9
*Fine sand (g/kg)	552	160	583	131	790
*Fine silt (g/kg)	148	67	142	14	319
Gravel and rock cover (%)	42	29	42	0	100
Grazing load (AU/km^2)	75.6	70.5	38.5	0.0	222.3
Heat load	0.9	0.1	0.9	0.5	1.0
Mean temperature (°C)	10.3	1.3	10.0	7.5	13.2
Microrelief (cm)	14	10	10	3	85
NDVI	140	11	137	119	189
Organic carbon (g/kg)	124.2	42.9	123.0	24.6	254.0
*Organic matter (g/kg)	214	74	212	42	437
Slope inclination (°)	21	10	20	1	50
Soil depth (cm)	9	6	8	0	30
Soil pH	7.1	0.4	7.1	5.9	7.8
*Total N (g/kg)	11.8	3.4	12.0	2.5	17.8
Variable (categorical)					**Frequency**
Prevailing grazing species					
Roe deer					5.2%
Red deer					10.3%
Sheep					23.7%
Horse/cattle					60.8%
Bedrock type					
Calcareous conglomerate					12.4%
Calcareous debris					17.5%
Massive limestone					70.1%

Note: Variables not retained for the subsequent analyses because of high collinearity (i.e. with pairwise Pearson's $|r| \geq 0.7$) are marked with an asterisk (*): Namely, "elevation" was excluded because of negative correlation with "mean temperature"; "fine sand" because of negative correlation with "coarse sand"; "fine silt" because of positive correlation with "mean temperature"; "$CaCO_3$" because of positive correlation with "coarse sand"; "total N", "organic matter" and "exchangeable Ca^{++}" because of positive correlation with "organic carbon".

4.2.1 | Predictors of vascular plant richness

In the BRTs, coarse sand, heat load and C/N were the most influential predictors for vascular plants, while mean annual precipitation was not correlated with vascular richness in CC and did not score as an important predictor in BRT. This suggests that fine-scale (edaphic and topographic) habitat factors prevail over climate in controlling vascular richness in our study area. Recent work has emphasized that microhabitat properties, including soil heterogeneity (Fridley et al., 2011) and microclimate (e.g. Mazalla et al., 2022; Meier et al., 2022; Haesen et al., 2023), are more important than macroclimate in predicting plant species assemblages.

In CC, lower vascular richness was associated with free-draining, rocky, calcareous, south-facing habitats — that is, with higher (edaphic)

TABLE 2 Descriptive statistics of richness values (response variables) in 10 m^2, per taxonomic group.

	Total richness	Vascular richness	Bryophyte richness	Lichen richness
Mean	52.8	47.0	3.8	1.9
SD	10.9	10.4	2.0	1.9
Coeff. var.(%)	20.7	22.0	53.2	101.7
Median	52	46	4	1
Min.	33	25	0	0
Max.	85	76	10	7

TABLE 3 Canonical correlation results (canonical loadings for the two sets of variables).

Canonical variates	1	2	3	4
Set of the environmental variables				
Grazing load	0.154	0.180	0.113	0.031
Annual precipitation	0.371	−0.083	−0.101	0.128
Mean temperature	−0.118	−0.228	−0.046	0.018
Slope inclination	0.332	−0.017	−0.123	0.193
Heat load	0.196	−0.293	0.134	−0.170
Microrelief	−0.017	−0.089	−0.120	0.143
Soil depth	−0.009	0.024	0.126	−0.079
Gravel and rock cover	−0.005	−0.363	−0.004	0.069
NDVI	0.144	−0.098	0.207	0.025
Coarse sand	−0.226	−0.555	−0.100	−0.047
Coarse silt	0.020	0.058	0.229	0.099
Clay	−0.053	−0.097	−0.163	−0.198
Soil pH	−0.088	−0.337	−0.260	−0.052
Organic carbon	0.101	0.007	0.034	0.237
C/N	0.029	−0.259	−0.090	0.124
Assimilable P	0.427	−0.049	0.069	−0.061
Exchangeable Mg^{++}	0.210	0.094	−0.186	0.058
Exchangeable Na^+	0.155	0.226	−0.094	0.052
Exchangeable K^+	−0.146	0.076	0.008	−0.077
Set of the richness variables				
Total richness	−0.301	0.583	−0.119	0.049
Vascular richness	−0.135	0.654	−0.063	0.010
Bryophyte richness	−0.298	−0.058	−0.347	0.294
Lichen richness	−0.662	−0.142	0.073	−0.054

TABLE 4 Prediction accuracy estimates for each BRT model.

	Total richness	Vascular plants	Bryophytes	Lichens
Optimal *n* trees	3000	4550	900	2800
Mean total deviance	117.97	106.17	4.12	3.68
Training data correlation	0.82	0.87	0.72	0.79
R^2	0.59	0.70	0.21	0.54
Mean absolute prediction error	5.41	7.18	3.13	1.04

drought stress. BRT models showed that the most important predictors of vascular richness, with a negative effect, were coarse sand and topographic heat load; both factors predict how fast soils drain and heat up (Moeslund, Arge, Bøcher, Dalgaard, & Svenning, 2013). A possible explanation is that at very fine spatial scale, available soil moisture is controlled by microtopographic factors that can override

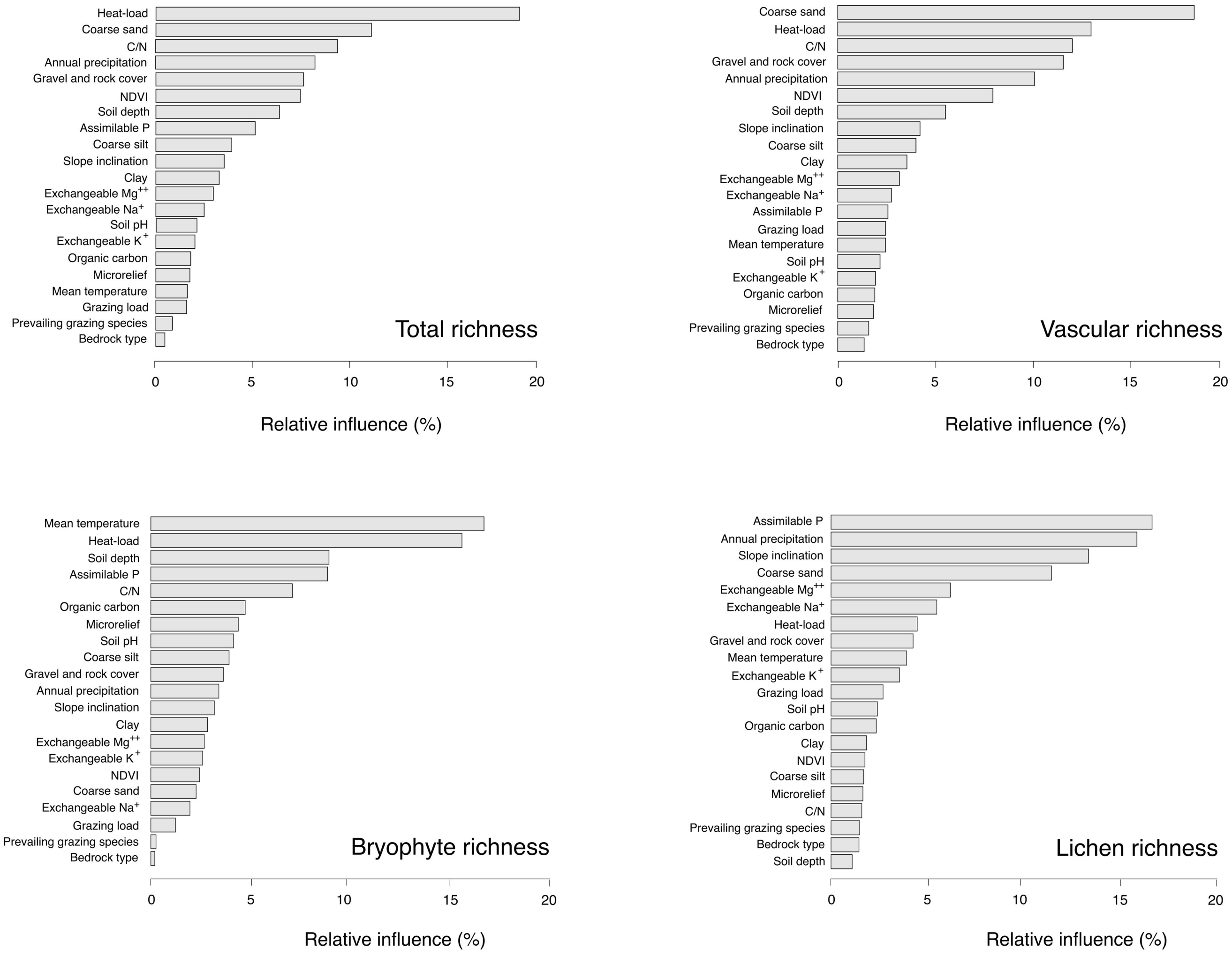

FIGURE 2 Relative influence of each predictor (including both continuous and categorical variables) in explaining variation in species richness for each BRT model.

the effects of precipitation (Araya et al., 2011; Moeslund, Arge, Bøcher, Dalgaard, Odgaard, et al., 2013). Interestingly, only few studies on grassland richness have analyzed soil texture, and even these often failed to find a relationship (e.g. Turtureanu et al., 2014; but see Filibeck et al., 2019).

The observed negative relationships between vascular richness and stress factors may be surprising, because other works from adjacent study areas (albeit with a finer sampling grain; Filibeck et al., 2019; Filibeck, Sperandii, et al., 2020; Cancellieri et al., 2020) showed maximum vascular richness in relatively dry and stony sites. These studies, in turn, were consistent with a number of works on grasslands from different continents, finding higher levels of fine-scale richness in the more stressed, less productive topographical positions (e.g. Cantero et al., 2003; Bennie et al., 2006; Cingolani et al., 2010; Kleinebecker et al., 2018). This is usually explained via the "humped-back model" for the productivity–richness relationship in grasslands (e.g. Grime, 1973; Janssens et al., 1998; Fraser et al., 2015). However, our results can be explained taking into account that the sampling units were placed along a precipitation gradient, while all the other variables were held relatively constant. As a result, the gradients for many edaphic variables were quite short. For example, we excluded from sampling the bottoms of karst depressions, that is, the sites with the deepest soils (cfr. Filibeck et al., 2019; Filibeck, Sperandii, et al., 2020). Furthermore, most of the previous work was carried out in the wetter part of the climatic gradient. Therefore, most of the sampling sites of the present study might lie to the left of the peak of the unimodal productivity–richness curve, leading to a positive relationship between soil moisture (or nutrients) and species diversity.

Finally, it is interesting that grazing load was not related to vascular richness. Grazing has been shown to influence vascular plant richness in some grassland systems, as it prevents competitive plants from limiting light availability in productive communities (e.g. Borer et al., 2014). However, our study area is characterized by a continuous process of variation in grazing species and loads (Primi et al., 2016); perhaps, the past distribution of stocking rates has a greater influence on plant richness than the current patterns.

4.2.2 | Predictors of bryophyte species richness

Our environmental predictors had only a weak explanatory power for bryophyte richness. In contrast to Gheza et al. (2018) and

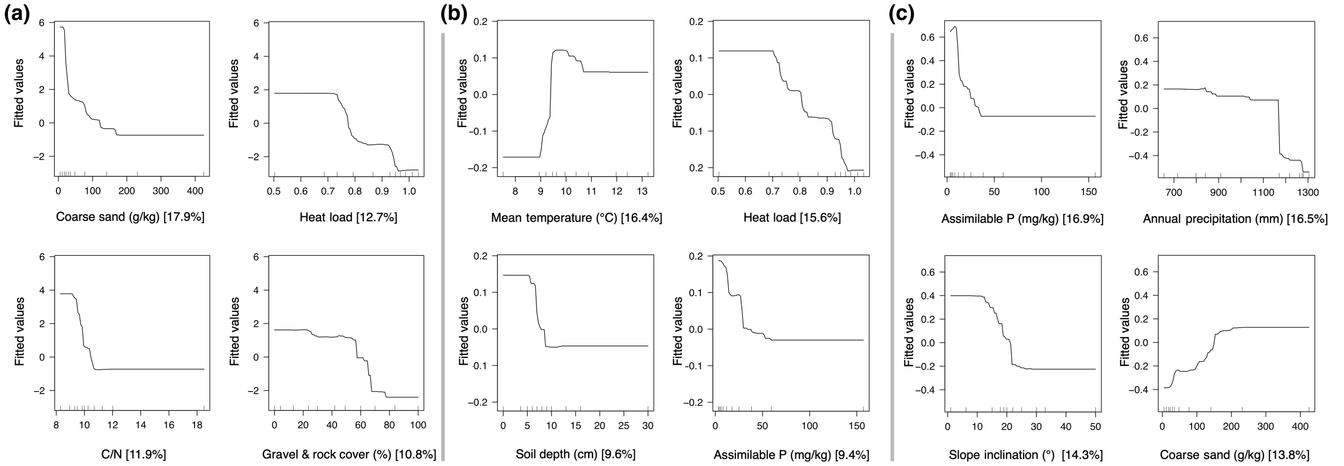

FIGURE 3 Partial dependence plots for the four most influential variables explaining, in the BRT models, the species richness variation of vascular plants (a), bryophytes (b) and lichens (c). The plots show the effect of each predictor variable on richness after accounting for the average effects of all other variables in the model. Y-axes are on logit scale centered to have zero mean over the data distribution. X-axes show the gradient of the predictor variable, while rug plots along the x-axes show distribution of sampling units across that predictor variable, in deciles. The numbers in square brackets show the relative influence (in %) of each variable in the BRT model (average number of times a variable was selected for splitting, weighted by the squared improvement of the model).

Bergauer et al. (2022), we did not find an effect of annual precipitation. CC showed a (moderate) positive correlation of bryophyte richness with soil pH, in accordance with other studies (Löbel et al., 2006; Boch et al., 2018; Gheza et al., 2018), and a positive correlation between bryophyte and lichen richness. Most bryophytes do not require fertile soils (van der Wal et al., 2005), and some are very drought-resistant (Huttunen et al., 2018), being thus able to share the same habitat with lichens (Lakatos, 2011). In grasslands, many bryophytes (especially the xerophytic acrocarpous mosses) are outcompeted by a dense cover of vascular plants (van der Wal et al., 2005; Becker & Brändel, 2007; Boch et al., 2018; Asplund et al., 2022), which, in the sub-Mediterranean climate, is favored by deep soils (Filibeck, Sperandii, et al., 2020). This is consistent with the BRT results, where bryophyte richness was negatively related to assimilable phosphorus and soil depth. On the other hand, some bryophyte species (e.g. pleurocarpous mosses) are bound to moist or shady microclimates (including the "undergrowth" of a closed grassland), and can tolerate competition from vascular plants better than lichens (Schofield, 1985; Löbel et al., 2006); these different strategies can confound the overall effects of the environmental gradients on bryophytes.

However, the two most important factors in BRTs for bryophyte richness were mean annual temperature (unimodal relationship) and heat load (negative relationship). A negative effect of heat load was also found by Turtureanu et al. (2014) and Bergauer et al. (2022); it can be explained by the high moisture requirements of many bryophytes. Regarding temperature, the unimodal shape of the fitted function suggests that at low temperatures the reduced drought stress leads to a continuous canopy of herbs that outcompetes bryophytes; while at very warm sites, the level of drought stress is too high for most bryophyte species. Finally, in contrast to Takala et al. (2014) and Janišová et al. (2022), we did not find a relevant effect of grazing on bryophyte richness; however, these studies were performed in a different macroclimate (temperate summer-rain biome of Central and North Europe).

4.2.3 | Predictors of lichen species richness

Lichen richness was the only dependent variable markedly related to the precipitation gradient. In CC, lichens were negatively correlated with a gradient of increasing available P, precipitation and slope inclination. BRT showed that these were the three most important predictors, with a marked negative relationship. In addition, coarse sand had a positive relationship with lichen diversity.

Most terricolous lichens are typically stress-resistant organisms (sensu Grime, 1977), that is, slow-growing and able to survive on extremely nutrient-poor soils. At the same time, they usually require high light intensities; therefore, they are favored in scarcely productive habitats where they cannot be outcompeted by the vascular plant cover (e.g. Löbel et al., 2006; Boch et al., 2016; Asplund et al., 2022); this can explain the decrease of lichen richness with higher assimilable P, lower coarse sand content and higher annual precipitation. While the negative effects of high soil P on vascular plant richness in grasslands are well known (e.g. Ceulemans et al., 2014), to our knowledge this is the first study to find a clear (negative) relationship between soil P and terricolous lichen richness (but see Arnesen et al., 2007 for the effects on lichen species composition). On the other hand, both Gheza et al. (2018) and Bergauer et al. (2022) found a negative relationship between annual precipitation and grassland lichen richness; higher precipitation levels can limit the light available for lichens (via the development of a closed layer of vascular plants), cause bryophytes to outcompete lichens and even directly damage fruticose thalli (Gheza et al., 2018).

The negative relationship between lichen diversity and slope inclination seems less obvious to explain, as steep slopes are usually dry and nutrient-poor habitats that should prevent competition from vascular plants (e.g. Bennie et al., 2006). However, a similar negative relationship was found by Bergauer et al. (2022); perhaps, on very steep slopes, continuous erosion (Moeslund, Arge, Bøcher, Dalgaard, & Svenning, 2013) may prevent the formation of a slow-growing lichen community.

5 | CONCLUSIONS

Edaphic and microclimatic factors prevailed in controlling vascular plant richness in the study area, while bryophyte species richness was poorly modeled by the available predictors. Instead, mean annual precipitation was the most important predictor of terricolous lichen richness, along with soil phosphorous availability; both factors had a negative effect, probably because of increased competition by vascular plants. These contrasting responses confirm the importance of a multitaxon approach in assessing and monitoring grassland biodiversity.

AUTHOR CONTRIBUTIONS

Goffredo Filibeck planned and coordinated the research and organized the 10th EDGG Field Workshop, during which data were collected; Goffredo Filibeck, Laura Cancellieri, Leonardo Rosati and Marta G. Sperandii guided the Field Workshop; Jürgen Dengler advised on the consistent application of the EDGG methodology; Anna Rita Frattaroli and Fabio Conti advised on site selection; most authors participated in the field sampling; Laura Cancellieri supervised vascular plant identification and taxonomic standardization, and coordinated data processing; Fabrizio Bartolucci, Fabio Conti and Leonardo Rosati contributed to critical vascular plant revision; Michele Aleffi revised bryophytes; Giovanna Potenza revised lichens; Riccardo Primi designed the collection of grazing data; Andrea Vacca and Stefania Fanni performed soil analyses; Michele Brunetti provided the climate data; Bruno Bellisario, Cinzia Franceschini and Marta G. Sperandii performed statistical analyses; Goffredo Filibeck wrote the paper, with major inputs provided by Marta G. Sperandii, Laura Cancellieri and Jürgen Dengler, and with specific sections contributed by Bruno Bellisario, Idoia Biurrun, Michele Brunetti, Cinzia Franceschini, Riccardo Primi and Andrea Vacca; Thomas Becker, Jürgen Dengler and Marta G. Sperandii helped with language editing; Laura Cancellieri and Idoia Biurrun revised the formal editing; Laura Cancellieri prepared figures; all authors discussed the results and commented on the text.

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ACKNOWLEDGEMENTS

We are extremely grateful to Denis Vynokurov, who significantly contributed to field work and data processing, and we respect his decision to decline to appear as an author due to Ukrainian regulations regarding the presence of Russian co-authors. We thank Abruzzo Lazio e Molise National Park, Gran Sasso e Monti della Laga National Park and Sirente-Velino Regional Park for authorizing sampling. Many thanks to: A. Carrara and C. Sulli at PNALM, and the Mayor of Navelli, for their warm welcome and logistic support; V. Di Cecco, M. Di Musciano, G. Ferella and W. De Simone for help during sampling; F. Chaboteaux, I. Collepardi, V. Orazi and J. Palli for grazing survey; S. Fascetti for revising some Orchidaceae; C.M. Rossi for help with NDVI. We commemorate the late Andrea Amici who significantly contributed to the planning of our grazing survey. Open access publishing facilitated by Università degli Studi della Tuscia, as part of the Wiley - CRUI-CARE agreement.

FUNDING INFORMATION

We are grateful for financial support to the Fondazione Anna Maria Catalano (Fiumicino, Italy), the Eurasian Dry Grassland Group and the Global Sponsorship Committee of the International Association for Vegetation Science (IAVS). L. Cancellieri and G. Filibeck were supported during manuscript preparation by the National Biodiversity Future Center (Spoke 4, Activity 4), Project code CN_00000033, funded by the European Union - NextGenerationEU. M. Janišová was supported by the VEGA grant 02/0065/23.

DATA AVAILABILITY STATEMENT

The data used in this study are stored in and available from the GrassPlot database, v. 2.09, 20 Oct 2020 (GIVD ID EU-00-003; https://edgg.org/databases/GrassPlot). Dataset code: IT_L; dataset name: EDGG Apennines.

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SUPPORTING INFORMATION

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

Appendix S1. Supplementary methodological specifications.

Appendix S2. List of all species recorded in the 97 sampling plots.

How to cite this article: Cancellieri, L., Sperandii, M.G., Rosati, L., Bellisario, B., Franceschini, C., Aleffi, M. et al. (2024) Drivers of vascular plant, bryophyte and lichen richness in grasslands along a precipitation gradient (central Apennines, Italy). *Journal of Vegetation Science*, 35, e13305. Available from: https://doi.org/10.1111/jvs.13305