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Environmental and Management Control over the Submontane Grassland Plant Communities in Central Slovakia

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Abstract: In Central Europe, submontane grassland plant biodiversity is currently threatened by management intensification as well as by the cessation and abandonment of management activities (extensive grazing and mowing). Although the vegetation of Central European grasslands has been well described by phytosociological papers, there is still a need to improve our understanding of the effect of both management and environment on species richness and community composition. We studied submontane grassland communities in Central Slovakia. Our study showed that both environmental variables and management were important for shaping the submontane grassland species richness and floristic composition. Plant species richness showed a weak negative relationship with soil pH. When grassland management types were analyzed individually, the amount of phosphorus, nitrogen, pH, and altitude were all found to be significantly correlated with plant species richness or diversity. Management type and local environmental factors (i.e., incoming solar radiation) both determined community composition.

Keywords: diversity; soil chemistry; nutrients; plant community composition; Slovakia

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1. Introduction

Seminatural submontane grasslands are recognized as valuable habitats with extraordinarily high species richness and, despite their relatively small extent, they belong to representative landscape elements in many European countries [1–3]. They often host many characteristic and diagnostic plant species, typical for this type of biotope and provide many important ecological and environmental services (e.g., nutrients cycles, erosion control, provision of habitats, etc.) [4–6]. These features make grasslands important habitats of high conservation value [7,8].

It is generally accepted that high species richness of grasslands has been a result of natural conditions, a plethora of environmental factors, and human activities [9–11].

Management of grasslands seems to be crucial for their persistence and conservation of their biodiversity [12,13]. Studies have shown that extensive grazing or mowing contribute to the maintenance of grassland plant diversity which decreases over time after the abandonment of management activities [12–14]. The abandonment of grazing or mowing followed by progressive succession or afforestation is often considered to be a threat to local or regional biodiversity [15–17].

Each type of management (mowing, grazing, or a combination of both) influences diversity and composition of grassland plant communities. The direction and intensity of management effects depend on the characteristics of specific management and its intensity, and also on geographical or altitudinal position of the grassland ecosystem [18,19]. Several publications have highlighted the positive impacts of certain management practices, or their frequency, on local plant diversity and have emphasized the potentially important role of changing management practices [20–22]. However, studies have differed regarding the identification of the most appropriate management for biodiversity maintenance and debate on this topic is still intensive [23–25].

Among local environmental determinants of grassland diversity and species composition, the role of soil chemical parameters and physical properties is often stressed. One of the key factors influencing both community composition and species richness is soil pH. The relationship between pH and plant species richness has been described as unimodal in some studies [26], but other patterns have been documented in other studies, especially at lower ranges of pH [3,27]. The concentration of soil nutrients, especially phosphorus, is another important environmental factor acting on a local scale. Many studies have documented a negative relationship between species richness and phosphorus supply in grassland soil [28,29], but no relationship or only weak relationships have also been reported [30]. Although local variables often tend to be considered as main environmental drivers of grassland species richness, regional factors such as habitat age, climate, adjacent habitats, or large-scale landscape characteristics may also be important [10,31,32].

Distinct grassland communities differ in their response to environmental variables. Thus, there is no general pattern of species richness and environment relationships. Nevertheless, abiotic conditions may overcome the effect of management activities [19]. In fact, a decision to apply a specific management is, at least partly, dependent on environmental conditions of a specific grassland. This leads to complex simultaneous effects of multiple environmental properties and management and their individual roles are difficult to uncover.

Despite their undeniable importance and high conservation value, large areas of Central European grasslands have been affected by inappropriate human activities, either by intensification or cessation of management, since about the middle of the last century [10,33]. Recently, effective conservation of seminatural grasslands has required a deeper knowledge of the factors and processes that shape their biodiversity and species composition.

Phytosociology of grasslands of Central Europe has been studied frequently [26,34]. Papers describing how the diversity and community composition of European grasslands are shaped by environmental variables and management are also quite numerous (e.g., [3,35–43]). However, a better understanding of the effect of management and environment on grassland community composition and richness is still needed [3].

The objective of this paper is to assess the effects of environmental factors (basic soil chemistry, topography) and management on the diversity and species composition of submontane grassland communities in Slovakia.

We analyzed grassland communities under different management types in two mountain ranges in central Slovakia in order to answer the following questions:

(i) How is plant species richness related to evaluated environmental variables?
(ii) Does management affect species richness of the studied grasslands?
(iii) Does species composition respond to different grassland management?

2. Materials and Methods

2.1. Study Area

The study was conducted in the Štiavnické vrchy Mts. and the Poľana Mts., geomorphologic unit areas of the West Carpathians in the central part of Slovakia (Figure 1).

The volcanic mountain range of the Štiavnické vrchy Mts. (48°12′–48°35′ N, 18°32′–19°05′ E) occupies an area of approximately 776.3 km^2. The bedrock consists mainly of andesites and rhyolites with scattered occurrence of conglomerates and shales. The diverse bedrock is reflected in a range of soil types with prevailing cambisols. A substantial part of the area has moderately warm climate with a mean annual precipitation of 650–800 mm and a mean air temperature of 7–8 °C [44,45]. Štiavnické vrchy Mts. are situated in the contact area of the Carpathian and Pannonian phytogeographic regions and two different climate types. It is reflected in overlapping occurrences of thermophilous flora with Carpathian montane floristic elements. Originally a forested area, the area has been intensively changing due to human activities related to mining and timber production since the 13th century. Nowadays, a large portion of the area is deforested with a mosaic of meadows, pastures, and forested patches.

The Pol'ana Mts. (48°35′–48°44′ N, 19°18′–19°38′ E) is the highest extinct volcano in Central Europe and it covers an area of approximately 450 km^2. Pyroxene and pyroxene-amphibole andesite prevail in the bedrock and andosol and cambisol are dominant soil types of the area. The Pol'ana Mts. are situated in a continental climate with an annual temperature of 2.5–8.0 °C and an average precipitation of 650–1300 mm [44,45], however, the diverse high elevation terrain of the area supports a diversity of climatic conditions. Differences in abiotic conditions of the Pol'ana Mts. make it possible to observe various vegetation types within a relatively small area.

A variety of plant communities are presented in the study areas. The *Arrhenatheretalia elatioris* order (class *Molinio-Arrhenatheretea*) is the dominant grassland community type on both mountain ranges.

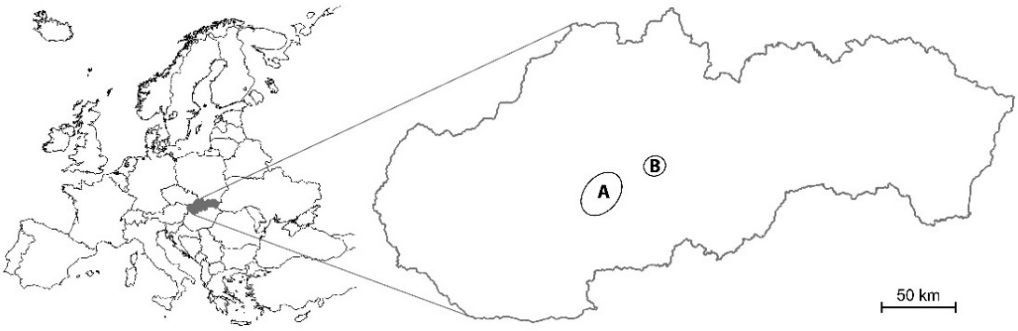

Figure 1. Map showing location of the studied areas. (**A**) Štiavnické vrchy Mts.; (**B**) Pol'ana Mts.

2.2. Field Data Collection

A field vegetation survey was performed during the growing seasons of 2017 and 2018. A total of 30 plots were surveyed (each plot was 16 m^2 large). Individual sites were selected in order to represent the following three management types based on the information available from the landowners for at least the last 5 years: (1) hay meadows (MEADOW hereinafter, mown by mowing machine with mostly two cuts, rarely just one cut, per year, with occasional low-intensity grazing during cattle or sheep passing, and no application of agro-technical mechanical procedures or fertilization); (2) seasonally grazed pastures (PASTURE hereinafter, with extensive sheep and cattle grazing at estimated densities of approximately 0.5 animal/ha grazing, either continuous or rotational, paddock grazing at some places, grazed from May to the end of November, with no application of agro-technical mechanical procedures or fertilization); and (3) recently abandoned grasslands with no management activities (ABANDONED, hereinafter). Each type was represented by 10 sites. Individual sites were selected to represent similar altitude and local climatic conditions among the studied management types (usually three sites close to each other, each representing one of the management types).

All species of vascular plants were recorded, and their cover was estimated according to the principles of the Zürich-Montpellier school [46] using a nine-degree cover-abundance scale [47]. Taxonomy and nomenclature followed Marhold and Hindák [48]. At some sites (ABANDONED), a few individual shrubs or tree species (with low cover) occurred because of progressing succession. These species were not included in further analyses. In phytosociological terms, investigated vegetation was mainly represented by class *Molinio-Arrhenatheretea* Tx. 1937, alliances *Arrhenatherion elatioris*, *Cynosurion cristati*, and *Calthion palustris*.

The altitude was recorded at the time of vegetation sampling using a GPS device. Solar radiation input was calculated from an insolation model (for details see [49]). Data on inclination were excerpted from a publicly accessible database of National Agriculture and Food Centre. The original interval scale was replaced by mid-percentage values for each inclination interval.

2.3. Soil Analyses

To assist with ecological interpretations, selected soil characteristics were evaluated. Three soil samples, from a depth of 10 cm, were taken from randomly selected locations at each plot during the vegetation surveys. Individual samples were pooled to one composite sample prior to analysis. Analyses were performed according to Hrivnáková et al. [50]. All the samples were dried under laboratory conditions (20–30 °C) to a constant weight and crushed to dust (maximum 2 mm). Electrical conductivity ($\mu S \cdot cm^{-1}$) and pH were measured using a multimeter Multi 3402 (Wissenschaftich-Technische Werkstätten GmbH, Weilheim, Germany) with the combined glass electrode SenTix® 940-33 (WTW) and conductometer sonde TetraCon® 925 (WTW). The C, H, N content was characterized using a FLASH 2000 Organic elemental analyzer (ThermoFisher Scientific). Phosphorus content was determined spectrophotometrically in the filtrate of the solution after transfer to phosphomolybdenum blue. The basic characteristics of the studied plots are given in Table 1.

Table 1. Basic characteristics of the studied plots. Average, minimum, and maximum values are shown. Physico-chemical variables refer to soil analyses.

Variable	Abbreviation	MEADOW	PASTURE	ABANDONED
			Average (min., max.)	
Altitude	ALT	626 (490, 765)	626.7 (481, 767)	616 (502, 743)
pH	pH	5.6 (4.9, 6.6)	5.5 (5.0, 6.3)	6.1 (5.3, 7.1)
Electric conductivity ($\mu S \cdot cm^{-1}$)	EC	207 (106, 379)	263 (172, 575)	569 (220, 1110)
Phosphorus ($mg \cdot kg^{-1}$)	P	9.77 (2.9, 24.1)	11.2 (1.8, 32.5)	4.7 (1.5, 11.5)
Nitrogen (% w)	N	0.37 (0.24, 0.53)	0.45 (0.38, 0.56)	0.62 (0.23, 1.17)
Carbon (% w)	C	4.07 (2.60, 6.11)	5.13 (3.86, 6.24)	7.96 (4.00, 15.00)
Slope inclination	INC	8.5 (0.5, 14.5)	12.1 (5.0, 21.0)	2.6 (0.5, 14.5)
Solar radiation input (10^3 $Wh \cdot y^{-1}$)	SR	1033 (917, 1132)	1020 (884, 1135)	1051 (1003, 1173)
N (number of sites)		10	10	10
Species richness		36 (28, 45)	38 (30, 48)	29 (18, 42)
Shannon diversity (H)		2.80 (2.40, 3.22)	3.00 (2.51, 3.62)	2.41 (1.44, 2.91)

2.4. Data Analyses

The differences in plant diversity among the three management types were investigated using the Kruskal–Wallis test since variances were not homogeneous to the Bartlett test performed prior to analysis.

To investigate diversity patterns, we calculated the pairwise Spearman correlation coefficients between environmental characteristics and species richness and the Shannon diversity of studied plots. For better insight, we calculated the Spearman correlation coefficients for overall data and for each management type separately.

To investigate the variation patterns in plant community composition within the studied grasslands, we used nonmetric multidimensional scaling (NMDS) based on Bray–Curtis distance. The relationships among grassland community composition and explanatory variables representing management type and environmental characteristics were summarized using canonical correspondence analysis (CCA). For ordinations, the species cover values recorded on the Braun-Blanquet scale were replaced by mid-percentage values for each degree and square root transformed. According to the results of NMDS, we included only plots of MEADOW and PASTURE management in this step. Species occurring in only one plot were omitted.

Prior to analysis, we initially prescreened all environmental variables with nonparametric correlation analyses using Spearman ρ for possible multicollinearity. Finally, pH, amount of soil phosphorus and nitrogen, altitude, management, inclination, solar radiation, and locations of the sites (Poľana Mts. and Štiavnické vrchy Mts.) as covariables were entered for analysis. The significance of individual variables were tested by permutation test for CCA under reduced model by testing the marginal effects of terms. All analyses were performed in R [51] using library vegan [52]. To help interpret and discuss our results, the Ellenberg indicator values (light, nutrients, continentality, soil moisture, and soil reaction) [53] were calculated as unweighted averages of the values of species present in the plots.

3. Results

3.1. Floristic Diversity of Grasslands

A total of 187 species were recorded at the studied sites. Among those, only a few species included in the Red list of ferns and flowering plants of Slovakia [54] were documented as follows: *Carex flava* (NT), *Carex hartmanii* (NT), *Cephalanthera longifolia* (NT), *Dactylorhiza majalis* (NT), *Lilium martagon* (LC), *Orchis morio* (NT), and *Trollius europaeus* (NT). Four red list species were recorded at ABANDONED sites, three species at MEADOW sites, and two species at PASTURE sites.

The most frequent species with high cover values at MEADOW sites were *Arrhenatherum elatius*, *Dactylis glomerata*, *Avenula pubescens*, and *Alopecurus pratensis*.

Almost all the PASTURE sites were characterized by the presence of *Festuca rubra*, *Agrostis capillaris*, and *Anthoxanthum odoratum*. *Filipendula ulmaria* was the dominant species of the ABANDONED sites. *Lysimachia vulgaris*, *Scirpus sylvaticus*, *Cirsium oleraceum*, *Mentha longifolia*, *Juncus effusus*, and *Galium aparine* also occurred frequently, but their cover values were lower and ranged widely.

The PASTURE sites supported the highest average of species richness, followed by the MEADOW sites. The ABANDONED sites hosted the most species poor communities in our study (Table 1). The differences in plant species richness and Shannon diversity were marginally insignificant (Kruskal–Wallis χ^2 = 6.22, p = 0.07, and Kruskal–Wallis χ^2 = 9.18, p = 0.06, respectively).

3.2. Determinants of Diversity and Community Composition

The relationships among plant species richness and Shannon diversity of studied sites and the environmental variables were evaluated using correlation analysis. Plant species richness showed only a weak negative relationship with pH (Table 2). When analyzed individually for each management type, the amounts of phosphorus, nitrogen, pH, and altitude were found to be significantly correlated with plant species richness or Shannon diversity within the individual management types (Table 2).

Table 2. Spearman correlation coefficients among environmental variables and plant species richness and Shannon diversity (H) assessed at all sites (overall) and separately for each management type. Statistically significant correlations (at $p < 0.05$) are highlighted in bold. For abbreviations see Table 1.

	Overall		**MEADOW**		**PASTURE**		**ABANDONED**	
Variable	**Richness**	**H**	**Richness**	**H**	**Richness**	**H**	**Richness**	**H**
pH	**−0.37**	−0.35	0.16	0.09	−0.08	0.24	**−0.74**	−0.51
P	−0.03	−0.02	**−0.68**	**−0.81**	0.15	0.05	0.02	−0.23
N	−0.08	−0.18	−0.10	−0.29	−0.53	−0.52	**0.91**	**0.73**
ALT	0.16	0.12	−0.05	−0.06	−0.02	−0.18	**0.76**	0.63
INC	0.15	0.20	−0.20	−0.19	−0.67	−0.43	−0.24	−0.07
SR	−0.14	−0.17	−0.41	−0.15	−0.02	−0.15	0.11	−0.03

The NMDS ordination clearly separated all the communities of the ABANDONED sites from the rest of the studied grasslands (Figure 2). The main gradient in species composition estimated from the NMDS plot was presumably associated with soil moisture. Communities of all the ABANDONED grasslands were clearly separated from all the

MEADOW and PASTURE sites (characterized by species of dry and semi-dry soils) on the ordination plot.

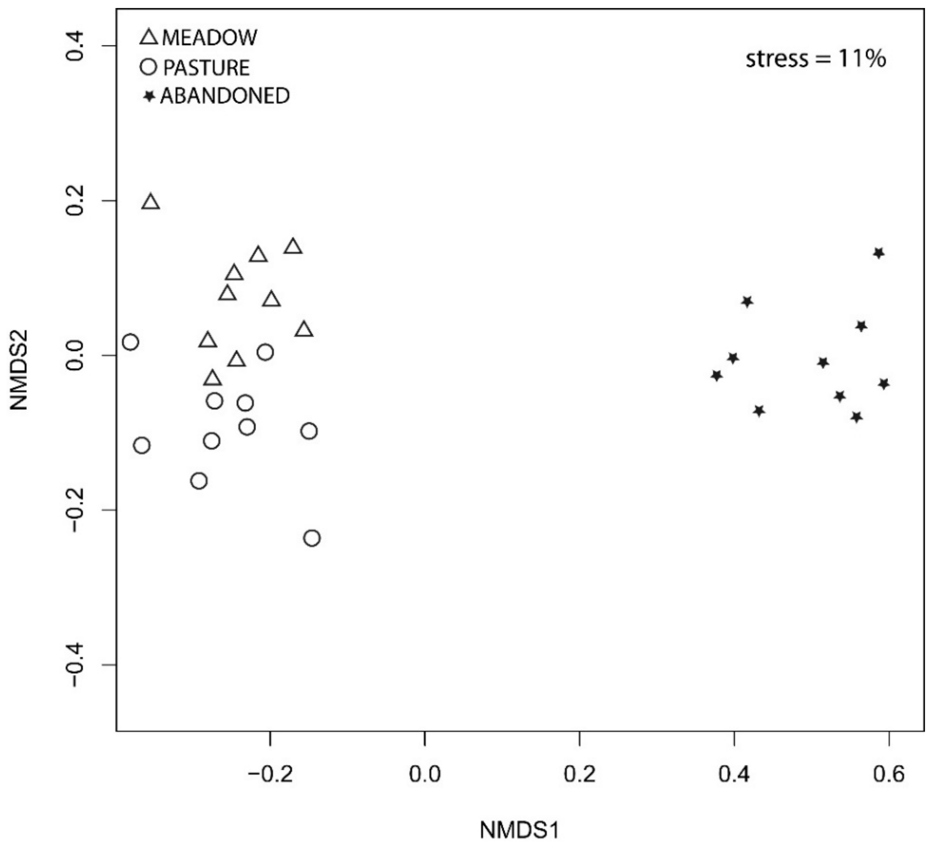

Figure 2. Two-dimensional solution of nonmetric multidimensional scaling of grassland plant communities based on the Bray–Curtis distance. Final stress value is displayed.

Using CCA, we found a significant relationship between plant community composition and the selected explanatory variables and management type (pseudo-F = 1.23, $p = 0.01$), which explained 45% of the total variation in plant community composition. The results of the CCA are summarized in the ordination diagram (Figure 3). The results of the permutation test for CCA under reduced model revealed the management type as the significant term (pseudo-F = 1.55, $p = 0.006$) and solar radiation as the significant variable (pseudo-F = 1.65, $p = 0.04$).

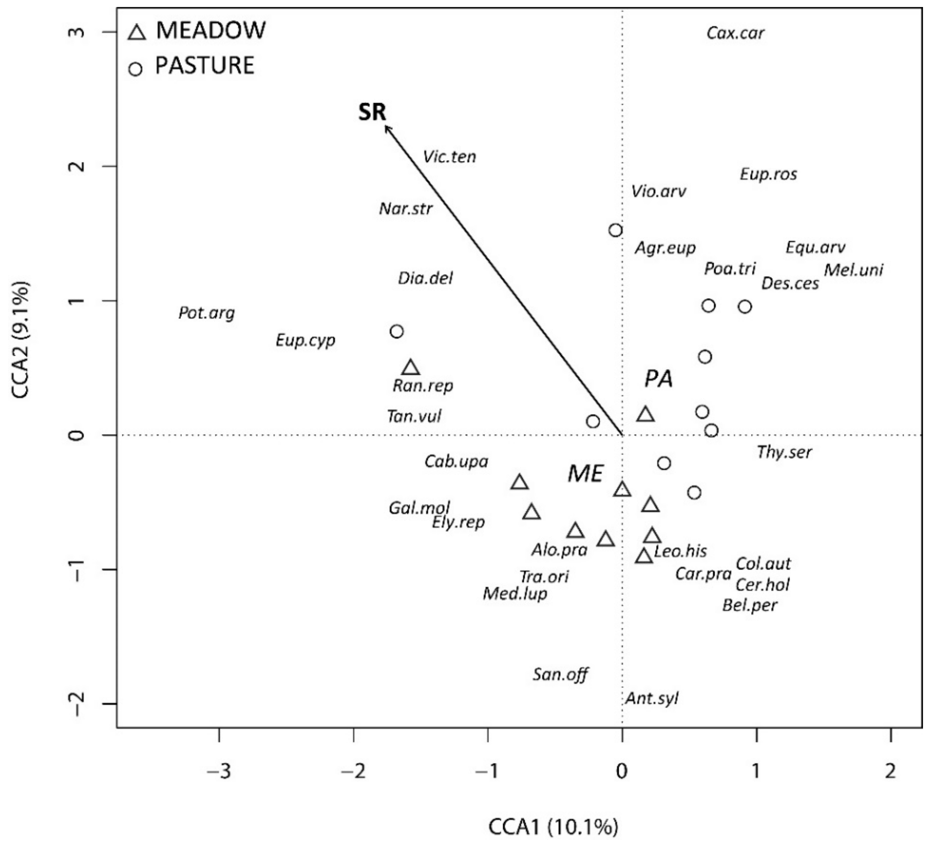

Figure 3. Canonical correspondence analysis (CCA) ordination triplot showing significant variables, sampling sites, and selected species. Only 20% of species best fitted by the ordination space are displayed. Total inertia 1.66; for percentage of explained variance see axes titles. ME, MEADOW; PA, PASTURE; *Agr eup*, *Agrimonia eupatoria*; *Mel uni*, *Melica uniflora*; *Vio arv*, *Viola arvensis*; *Equ arv*, *Equisetum arvense*; *Thy ser*, *Thymus serpyllum*; *Eup off*, *Euphrasia rostkoviana*; *Poa tri*, *Poa trivialis*; *Cax car*, *Carex caryophyllea*; *Des ces*, *Deschampsia cespitosa*; *Vic ten*, *Vicia tenuifolia*; *Nar str*, *Nardus stricta*; *Dia del*, *Dianthus deltoides*; *Eup cyp*, *Euphorbia cyparissias*; *Pot arg*, *Potentilla argentea*; *Tan vul*, *Tanacetum vulgare*; *Ran rep*, *Ranunculus repens*; *Cab upa*, *Capsella bursa-pastoris*; *Tra ori*, *Tragopogon orientalis*; *Med lup*, *Medicago lupulina*; *Alo pra*, *Alopecurus pratensis*; *Leo his*, *Leontodon hispidus*; *Ant syl*, *Anthriscus sylvestris*; *Car pra*, *Cardamine pratensis*; *Col aut*, *Colchicum autumnale*; *Cer hol*, *Cerastium holosteoides*; *Bel per*, *Bellis perennis*; *Gal mol*, *Galium mollugo*; *Ely rep*, *Elymus repens*; *San off*, *Sanguisorba officinalis*.

4. Discussion

4.1. Floristic Diversity of Grasslands

Vegetations surveyed at the study sites were represented by three main types. *Arrhenatheretum elatioris* meadows with high fodder quality, usually with dominant high yielding grass taxa, are the most common type of seminatural grasslands in Slovakia [55]. *Cynosurion cristati (Polygalo-Cynosurenion)* are also widespread communities found across Slovakia except for lowland and alpine areas. The occurrence of wet meadows with a characteristic prevalence of broad-leaved herbs, i.e., *Calthion (Filipendulenion)* is uneven in Slovakia, however, one of our studied mountain ranges, Pol'ana Mts., belongs to those areas with relatively high abundance of this meadow type [56,57].

Seminatural grasslands are sites of great importance for nature conservation because they usually support high species diversity and the occurrence of the red list species. In our study, only seven red list species with sporadic occurrence were recorded, with the highest number of species (four) occurring at the ABANDONED sites and three species occurring exclusively at this type of site. Due to the low number of recorded red list species, we did not relate their diversity to evaluated environmental variables. Nevertheless, relatively higher diversity of red list species has been related to wet conditions by some studies from Central Europe previously [3]. Because they are usually not used for agronomical purposes, wet grasslands are often endangered by succession, and thus rare or threatened grassland species are exposed to the risk of extinction at these sites. Thus, to maintain suitable conditions for endangered or rare species at these sites, occasional management interventions are needed.

In our study, the average species number, considering all the studied sites, was 34. A comparison with published papers from Central Europe in this regard was a difficult task, because studies presenting grassland species richness differ in the size of studied plots, which range from 1–100 m^2. Species numbers similar to ours have been recorded from 16 m^2 plots in a study of upland grasslands of the southern Czech Republic [3], but also from 100 m^2 plots of grassland ecosystems of the Beskidy Mts. (Southern Poland) (35.6 average species) [39], as well as plots with area ranging from 16 to 100 m^2 distributed throughout most of the Slovakia territory [10].

Although species richness and Shannon diversity varied among management types, these differences were marginally not significant. Nevertheless, the PASTURE sites were found to be the most species rich in our study, hosting 38 species on average, and supporting the highest Shannon diversity. Published studies differ in the grassland management type found to support the highest species richness. For example, grassland sites managed by grazing may have more species than mowed [58,59]. Similarly, Gilhaus et al. [24] reported that plant species richness and Shannon diversity were highest in seasonal pastures. Grazing has even documented to be more important for grassland species richness than local soil properties [60]. In addition, Kruse et al. [19] found no differences among species richness of differently managed sites. Identification of the best grassland management practice for maintenance of species rich communities is a complicated issue due to significant variation among and even within management types in individual studies and naturally, different biogeographic or ecological conditions of studied grasslands [12,24].

4.2. Determinants of Diversity and Community Composition

Local environmental factors often strongly influence grassland species richness [61,62]. In our study, we investigated the relationship among species richness and Shannon diversity and basic soil physico-chemical parameters and site aspect, inclination, and altitude. Across all studied sites, pH emerged as the only significant variable, negatively correlated with species richness. The Pol'ana Mts. and the Štiavnické vrchy Mts. are both of volcanic origin, thus, substrates of both mountain ranges should tend to be of lower pH. Soil reaction is one of the key factors controlling plant species richness [26]. The relationship between plant species richness and pH should be negative in regions where the species pool reflects conditions of low pH in an evolutionary past [63]. At our study sites, the pH values ranged from 4.9 to 7.1. In a similar pH range, studies of European temperate grasslands revealed a positive relationship between vascular plant richness and pH [27,64], but also no relationship, for example in [3]. The latter authors argued that pH effects could be overridden by other soil properties, especially by the negative effect of productivity. Because our study sites differed somehow in recorded environmental variables among management type (Table 1), we also investigated particular relationships among species richness and Shannon diversity and environmental properties for each management type. Considering pH, a negative correlation with species richness was found in the ABANDONED sites. This, at least partly, corresponded to the mentioned theory of Pärtel et al. [63].

Phosphorus is a factor of significant importance for species richness of grasslands [3] and grasslands of Europe are considered to be phosphorus limited [39]. We found no overall correlation between phosphorus and species richness and Shannon diversity in our study. However, when the different management groups were analyzed separately, we found negative relationships between phosphorus and species richness in mowed (MEADOW) grasslands. Although grassland plant diversity is usually negatively impacted by nutrient enrichment and an increasing concentration of phosphorus is often considered to be the main cause of species loss [65–68], the relationship between phosphorus and species richness has been described also as curvilinear in several European studies [20,28]. A decrease in grassland species richness on more fertile meadows usually results from an increasing dominance of a few competitors or ruderals, which prevent the establishment of diverse communities of stress-tolerant species [69]. We did not evaluate functional properties of recorded plant species, but our MEADOW sites harbored similar communities with no signs of strong dominance of tall and productive plant species. Thus, the observed negative correlation between phosphorus and species richness on mowed grasslands was probably not a result of outgrowing of specific species over other ones, although the diversity of *Arrhenatheretum elatioris* meadows, the typical community of our MEADOW sites, has been shown to respond more negatively to phosphorus content than other communities [39]. Rather, we would agree that the effect of soil phosphorus is complex because phosphorus often interacts with other nutrients as well as many other factors [3,39]. This could be the reason for the lack of correlation found for in the PASTURE and ABANDONED sites, where phosphorus range was also quite wide.

Some studies have documented negative effects of another important nutrient, i.e., nitrogen, on grassland plant species richness [70–72], mainly due to a decrease in oligotrophic plant species and decreases in light penetration into the plant canopy caused by increases in aboveground net primary productivity. In our study, the only observed relationship was, somehow surprisingly, a positive correlation of soil nitrogen with the species richness and Shannon diversity of ABANDONED sites. These sites also supported the lowest average species richness and diversity as compared with the other management types. However, soil physico-chemical properties that affect availability of soil nutrients are characteristic of high spatial heterogeneity, even within a small area, and individual nutrients interact in their influence. Therefore, generalization of the contribution of individual nutrients to decrease or increase grassland species richness is complicated and still remains unclear [30,70].

Plant species richness of grasslands may also be affected, in different ways, by altitude and topography. The absence of a clear correlation between altitude and species richness in our study could presumably be explained by a narrow altitudinal range in our study. Although relationships among species richness and site topographic attributes (slope inclination or incoming solar radiation) are biologically meaningful, the role of topographic variables has been studied only scarcely, mainly in high altitude regions [73,74], or in considerably wider ranges of altitude and topographic characteristics [75].

Seminatural grassland plant community composition is expected to be determined by local and regional environmental variables and applied management. Among the local factors, moisture, pH, and nutrient availability are recognized as the main determinants of species composition [3,76]. In our study, floristic variation of grasslands was also determined by soil moisture, which was pointed out by distinct separation of the ABANDONED sites from the others in the NMDS. The average Ellenberg indicator value for moisture (not evaluated directly in our study) was 7.1 within this group of sites, while the average for the other sites was 4.9 (Table A1). We somehow expected this clear separation, because (based on the presence of some species) we supposed higher values of soil moisture/higher humidity at the time of the first visit to the localities.

According to the outputs of the NMDS, we applied a direct ordination technique (CCA) to investigate whether different management (mowing vs. grazing) and recorded environmental variables determined community composition only for a subset of MEADOW and PASTURE sites. The CCA outputs showed the importance of both management and site conditions (solar radiation) as determinants of species composition of managed grasslands. Management practices are well known to determine grassland species occurrence [24,58,59,77]. Community composition is dependent on the type of management, and also on the management intensity [58,78]. Due to the overall small variation within management types and the small differences in local conditions among managements in our study, the composition of the vegetation roughly reflected two predefined management schemes (MEADOW vs. PASTURE).

Most of the communities at the MEADOW sites were characterized by tall, high forage quality grass species (*Arrhenatherum elatius*, *Avenula pubescens*, *Festuca rubra*, *Dactylis glomerata*, and *Alopecurus pratensis*). These species limited occurrence of low growing herbs by shading the ground herb layer, and therefore the MEADOWs were less florid. The ground herb layer consisted of legume species and shade-tolerant species (*Cerastium holosteoides*, *Leontodon hispidus*, *Achillea millefolium*, *Veronica chamaedrys*, *Stellaria graminea*, *Lotus corniculatus*, *Medicago lupulina*, *Lathyrus pratensis*, and *Bellis perennis*). The higher herb layer consisted of, for example, *Knautia arvensis*, *Galium mollugo*, and *Tragopogon orientalis*. Patches of higher soil moisture enabled the occurrence of *Ranunculus repens*, *Alopecurus pratensis*, *Colchicum autumnale*, and *Sanguisorba officinalis*. *Salvia pratensis* and *Sanguisorba minor* were present at warmer, less humid patches. Because of the close vicinity of the PASTURE sites, some species typical for grazed grasslands (e.g., *Anthoxanthum odoratum*) pervaded into MEADOW sites.

The PASTURE mesophilous communities were formed by a varied mixture of medium-tall grass species (*Melica uniflora*, *Festuca rubra*, *Festuca pratensis*, *Trisetum flavescens*, *Poa trivialis*, *Agrostis capillaris*, *Anthoxanthum odoratum*, and *Carex caryophyllea*), grassland herbal species (e.g., *Lychnis flos-cuculi*, *Cardamine pratensis*, *Dianthus carthusianorum*, and *Dianthus deltoides*), and clovers. However, most of the communities were characterized by the absence of any dominant grass species. Grazing creates gaps within closed swards and promotes the occurrence of low growing and light demanding species (e.g., *Euphrasia rostkoviana*) [24,79]. At warmer sites, *Festuca rupicola*, *Festuca rubra*, *Luzula campestris*, *Hieracium pilosella*, on more acidophilous sites *Nardus stricta*, and on the more humid sites *Poa trivialis* occurred. Conditions of some sites enabled higher cover of grazing and trample-tolerant species (*Trifolium repens*, *Thymus serpyllum*, *Plantago lanceolata*, *Polygala vulgaris*, and *Lotus corniculatus*). Ruderal or segetal species tolerant to repeated disturbances and deterioration of physico-chemical conditions (e.g., *Capsella bursa pastoris*, *Cirsium arvense*, *Artemisia vulgaris*, *Viola arvensis*, and *Equisetum arvense*) were present at patches of intensively disturbed ground.

Solar radiation input was the only local variable that determined community composition in our study. Topographic site characteristics are often important for the occurrence of grassland species in extreme conditions [69,80]. Topography often shows a joint effect with management, because, for example, steep slopes are differently managed than less steep, more accessible sites. Solar radiation input determines the occurrence of species with different heat tolerances and light requirements. We did not observe marked differences in the Ellenberg light or temperature indicator values among the studied sites (Table A1). However, sites with higher values of solar radiation input were characterized by the occurrence of some species that demand high solar radiation input (e.g., *Dianthus deltoides*, *Euphorbia cyparissias*, and *Potentilla argentea*).

The results presented here should be taken as a contribution to the ongoing discussion on processes and factors that determine species composition and maintain diversity of valuable seminatural grassland plant communities. Our results could also be useful as a comparison study for other parts of Central Europe.

5. Conclusions

We showed, in concordance with previous studies, that seminatural grasslands harbor diverse and species rich plant communities. Surprisingly, we recorded only a few red list species, however, the occurrence of more than half of them was documented at localities that had been recently abandoned and characterized as fen tall herb grasslands.

Our study also documented that soil nutrients and pH are important factors affecting the diversity of Central European submontane grasslands. Although the diversity of grassland communities did not differ among management types, our study demonstrated that both grassland management and local environmental variables, represented here by solar radiation input, were determinants of community composition.

Grassland conditions can differ substantially within relatively small areas or among large regions. Management types applied to various grasslands also differ in their intensity and techniques used. A certain management category can potentially have different effects in different environmental conditions. To allow wider generalization of grassland management effects, we encourage studies considering various management types of different intensities performed on larger spatial scales.

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Appendix A

Table A1. Mean Ellenberg values per management type.

	MEADOW	PASTURE	ABANDONED
Light	7.04	7.03	6.77
Temperature	5.41	5.42	5.20
Continentality	3.71	3.65	3.67
Moisture	4.95	4.92	7.06
Soil reaction	6.12	5.88	6.29
Nutrients	4.76	4.54	5.31

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