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Research Article

Plant functional structure varies across different management regimes in submontane meadows

Andrea Diviaková[1], Hana Ollerová[2], Slavomír Stašiov[1], Darina Veverková[3], Milan Novikmec[1]

1 Department of Biology and General Ecology, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T. G. Masaryka 24, 960 01 Zvolen, Slovakia
2 Department of Environmental Engineering, Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, T. G. Masaryka 24, 960 01 Zvolen, Slovakia
3 Technical University in Zvolen, Institute of Foreign Languages, T. G. Masaryka 24, 960 01 Zvolen, Slovakia
Corresponding author: Milan Novikmec (novikmec@tuzvo.sk)

Abstract

Seminatural grasslands are among the most biodiverse habitats in Europe, and they have great conservation value. However, in recent decades, they have been threatened by either intensive fertilization or afforestation or, conversely, by abandonment due to changes in agricultural practices. The impact of management, its frequency or intensity on seminatural grassland communities is traditionally evaluated through views on the composition of communities and their diversity. A better understanding of the functioning of plants in managed grassland ecosystems could be achieved by considering plant functional traits (PFTs). In this study, we investigated whether sites with different management practices differ from each other in terms of the representation of the main PFTs. We studied a permanent plot series of 30 grassland sites in central Slovakia that had been managed or abandoned for over 10 years. Individual management consisted of low-intensity mowing (MGM), medium-intensity grazing (MGP), and abandonment (MGA). Hemicryptophytes, perennials, and semi-rosette species were dominant under all management regimes. We found significant differences in the coverage of the studied PFTs among the sites managed by phytomass removal (mowing, grazing) and abandoned sites. Compared with the MGA sites, mowed and grazed sites were characterised by high proportional coverages of species with medium plant heights (0.3–0.6 m), rosette species, and graminoids. The MGA sites presented high coverages of species with high plant heights (> 0.6 m), competitors, phanerophytes, forbs, geophytes, species with vegetative and seed reproduction types, species with long flowering periods (3 months or more), and species with summer green leaves. The MGM sites supported species with large seeds (seed mass > 2 mg), reproduction type by seed (seeds), and species with short flowering times (1–2 months), whereas the MGP sites supported species with small plant heights (plant height < 0.3 m) and species with persistent green leaves. The communities of submontane Carpathian meadows with different types of management differ in terms of the representation of selected plant functional traits, especially between managed and abandoned sites. This approach is useful not only for understanding the mechanisms involved in the application of different management methods but also for predicting changes in the responses of the functional properties of plants when abandoning grassland habitats.

Key words: Abandonment, grazing, mowing, plant functional traits, seminatural grasslands

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Introduction

Seminatural grasslands are important types of biotopes with species-rich communities of plants and animals, providing several important functions and ecosystem services (Hájková et al. 2007; Rodwell et al. 2007; Wilson et al. 2012). These grasslands are elements of the landscape structure that were created by humans and used for centuries for agricultural production. Mowed meadows and pastures constitute an important part of the cultural landscape (Hejcman et al. 2013), form its typical character and reflect its history. They occur on relatively fertile soils suitable for hay production or cattle grazing (Rodríguez-Rojo et al. 2017). However, in recent decades, they have often been threatened by agricultural intensification or abandonment in Central Europe due to land-use changes (Poschlod et al. 2005; Stoate et al. 2009; Pavlů et al. 2011). One of the main tasks of nature protection, also within the framework of EU agricultural-environmental schemes, is the maintenance of seminatural meadows by appropriate management (Kahmen and Poschlod 2008).

The preservation of seminatural grassland biotopes is conditioned by continuous human economic activity in the form of mowing or grazing of varying levels of intensity. The combination of management and ecological conditions is reflected in the specific species composition of the grasslands (Ružičková and Kalivoda 2007). Management practices also affect plant residue accumulation, nutrient cycles (Schmitt et al. 2010; Zeeman et al. 2010), and biomass production (Hejcman et al. 2010) in meadow communities. They affect the biological, chemical, and physical properties of soil (Mayel et al. 2021), which affect the composition of communities and the diversity of European managed meadow communities (e.g. Chytrý et al. 2007; Kopeć et al. 2010; Soons et al. 2017).

The impact of different types of management or their intensity on seminatural grassland communities is traditionally evaluated through views of the composition of communities and their diversity (Watkinson and Ormerod 2001; Niedrist et al. 2009; Diviaková et al. 2021). However, studies that have evaluated species richness, as well as functional richness and functional composition, have shown that the degree and extent of ecosystem processes are more consistently associated with functional composition (the presence of certain functional types or traits of plants) and functional richness (the number of different functional types of plants) than with species richness (e.g. Rusch and Oesterheld 1997). Indeed, species diversity reflecting the appropriateness or inadequacy of grassland management practices is not always consistent with functional attributes, i.e. the value and extent of the functional traits of organisms present in a given ecosystem (Díaz and Cabido 2001; Mayfield et al. 2010).

Approaches using plant functional traits (PFTs), which have been developed in recent decades, have great potential for improving the understanding of plant function in managed grassland ecosystems (Schellberg and Pontes 2012). PFTs are biological characteristics of plant species that respond to the dominant processes in an ecosystem (Kelly 1996; Lavorel et al. 1997). PFTs enable us to link morphological, physiological, and phenological plant properties to their functions (Schellberg and Pontes 2012). Knowledge of PFTs allows for a better understanding of plant adaptations to environmental conditions

(Kurtz et al. 2018), which are closely related to grassland management. They are often used as predictors of vegetation changes due to changes in management caused by mowing or grazing (Noble and Gitay 1996; Kleyer 1999), and their advantage is the ability to compare different types of vegetation and reveal general trends (Díaz et al. 2001). PFTs respond to grazing management (e.g. McIntyre et al. 1995; Dupré and Diekmann 2001; Schellberg and Pontes 2012) and to the management of mowing, mulching, burning, ploughing or abandonment (e.g. Kahmen et al. 2002; Kassahun et al. 2021). Some of the mentioned studies suggest that defoliation and soil disturbance are the main processes determining PFT responses to mowing or grazing. Differential defoliation on the vertical gradient implies an increase in small or ground layer species. Short-lived species are encouraged by soil disturbances (Kahmen and Poschlod 2008).

Several studies reported differences in the functional plant composition or various reactions of PFTs to different management practices. For example, disturbances in managed grasslands enhance seedling recruitment in small-seeded species to a greater extent than in large-seeded species (Eriksson and Eriksson 1997), managed grasslands favour graminoids, whereas abandonment encourages forbs (Pavlů et al. 2011), and management practices are known to affect distribution of plant life forms (e.g., Noy-Meir et al. 1989; McIntyre et al. 1995; Pykälä 2004; Prévosto et al. 2011).

However, in different geographical regions and under the same management changes, favoured plants are characterised by different PFTs. Therefore, prediction on a wider geographical scale is difficult (Klimešová et al. 2008). This is caused by the pressure of biotic and abiotic factors on PFTs. Nevertheless, there are several general assumptions about how different management modalities affect the representation of PFTs. On the one hand, the geographical specificities of the PFT assessment make it difficult to generalise the results of the studies. On the other hand, they highlight the need for a thorough knowledge of the impact of the management assessed by PFTs in different geographical areas.

In our study, we studied submontane Carpathian meadows with various types of management that were situated in two mountain ranges in central Slovakia. This study aimed to determine whether communities of submontane Carpathian grasslands under different types of management differ in terms of the representation of the main PFTs (plant lifespan, plant growth forms, life strategy, plant height, forbs/graminoids, reproduction type, leaf persistence, leaf distribution along the stem, duration of flowering, and seed mass). We assumed that hemicryptophytes and perennials would prevail in all the sites of the differently managed grassland biotope. We also hypothesised that grazed and mown meadows would support communities dominated by rosettes and semi-rosettes as adaptations to disturbances. At the same time, we expected that abandoned meadows would allow the occurrence of competitors with greater biomass formation, geophytes preferring sufficient nutrients, humidity, and light and competitively the strongest phanerophytes. We also expected that annuals (therophytes), species capable of spreading rapidly, would be characteristic of pasture sites in response to trampling and biomass removal.

Methods

Study area

The study was conducted in two mountain regions in the Western Carpathians, in the central part of Slovakia: Štiavnické vrchy Mts. and Poľana Mts. (Fig. 1). Štiavnické vrchy Mts. (48°12'–48°35'N, 18°32'–19°05'E) occupy a geographical territory of approximately 776.3 km^2, extending from the hills to the submontane belt. Poľana Mts. (48°35'–48°44'N, 19°18'–19°38'E) represent the highest volcano mountain range in Slovakia, with an area of approximately 183.0 km^2. The study areas are typical volcanic mountains with a uniform geological substrate. Abiotic conditions led to the existence of diverse vegetation on both mountains. The dominant meadow communities include submontane mesophilic mowing meadows (*Arrhenatherion elatioris* union) and pastures (*Cynosurion cristate* union). Wet meadows of submontane and mountain areas (*Calthion palustris* union), which belong to regionally important communities, are also represented. The geological substrate of the studied sites consists of andesites. Soil types are represented by cambizems and ranchers, ranging from weathered acidic to neutral rocks. These study areas are moderately cold and very humid, with air temperatures ranging from 12 to 16 °C in July. The average annual precipitation is 800–900 mm (Landscape Atlas of the Slovak Republic 2002).

Field work

The vegetation survey was carried out during the growing seasons of 2017 and 2018 at 30 sites. The study sites occurred at similar altitudes, ranging from 481 to 767 m a.s.l., with similar local abiotic conditions. The sites represented 3 basic types of management with more than 10 years of history (based on information from landlords), with low and medium intensities: mown meadows (hereinafter MGM, mowed once a year, usually at the end of May), grazing meadows (hereinafter MGP, seasonal pastures, or fences) and abandoned meadows (hereinafter MGA). Most of the sites have been under the same management type even for a longer time (according to historical mapping from 1957–1971). Each type of management was represented by 10 localities. Typically, there were three immediately adjacent sites, each representing one of the types of management. From a phytosociological point of view, the studied communities can be classified into the class *Molinio-Arrhenatheretea* Tx. 1937. The coverage

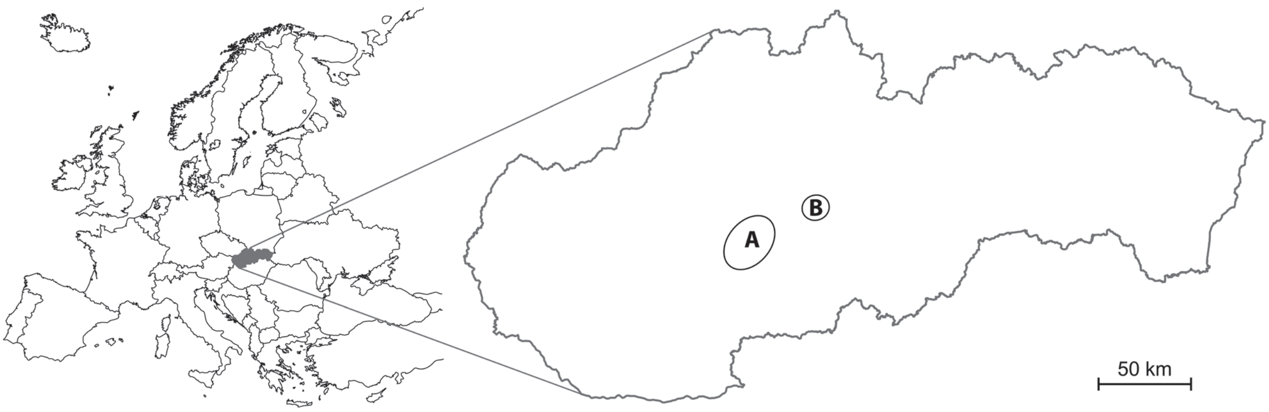

Figure1. Location of study areas **A** Štiavnické vrchy Mts **B** Poľana Mts.

of individual vascular plant species was evaluated following the Zurich-Montpellier School of Phytosociology (Braun-Blanquet 1964), using a nine-point scale of coverage and abundance (Westhoff and van der Maarel 1973), on 30 areas of 16 m^2. The nomenclature of plant taxa is given in the sense of Marhold and Hindák (1998). During the field survey, the altitude was recorded using a GPS device. The slope data were drawn from the publicly accessible database of the National Agricultural and Food Centre. The original interval scale was replaced by mean percentage values for each slope interval.

Laboratory work

To characterise the basic physical and chemical properties of the soil, soil samples were taken to a depth of 10 cm from three randomly selected locations in each area at the time of the vegetation survey. Individual samples were combined into a single sample before analysis. The analyses were carried out according to Hrivnáková et al. (2011). For a detailed description of the methods of analysis, see Diviaková et al. (2021). The basic characteristics of the study sites are listed in Table 1.

Table 1. Basic characteristics of the study sites. The average, minimum and maximum values are shown. Test statistics (χ^2) and associated probabilities (p) of the Kruskal-Wallis test for the differences among management types are displayed. Significant outputs of multiple nonparametric *post hoc* comparisons after Kruskal-Wallis testing are shown in the last column (MGM – meadow, MGP – pasture, MGA – abandoned).

Variable	MGM	MGP	MGA	χ^2	p	*post-hoc* comparison
	Average (min.; max.)					
Altitude	626 (490; 765)	626.7 (481; 767)	616 (502; 743)	0.006	0.99	
pH	5.6 (4.9; 6.6)	5.5 (5.0; 6.3)	6.1 (5.3; 7.1)	5.46	0.07	
Electric conductivity (μS.cm^{-1})	207 (106; 379)	263 (172; 575)	569 (220; 1110)	15.47	**0.0004**	**MGM < MGA, MGP < MGA**
Phosphorus (mg.kg^{-1})	9.77 (2.9; 24.1)	11.2 (1.8; 32.5)	4.7 (1.5; 11.5)	5.14	0.08	
Nitrogen (% w)	0.37 (0.24; 0.53)	0.45 (0.38; 0.56)	0.62 (0.23; 1.17)	6.38	**0.04**	**MGM < MGA**
Carbon (% w)	4.07 (2.60; 6.11)	5.13 (3.86; 6.24)	7.96 (4.00; 15.00)	11.54	**0.003**	**MGM < MGA**
Slope inclination	8.5 (0.5; 14.5)	12.1 (5.0; 21.0)	2.6 (0.5; 14.5)	13.03	**0.001**	**MGP > MGA**
Solar radiation input (10^3Wh.y^{-1})	1033 (917; 1132)	1020 (884; 1135)	1051 (1003; 1173)	0.71	0.70	
Species richness (E3+E2+E1) Σsp.	36 (28; 45)	38 (30; 48)	33 (22; 42)			
Shannon diversity (*H*)	2.80 (2.40; 3.22)	3.00 (2.51; 3.62)	2.41 (1.44; 2.91)			

Data analysis

We selected a set of 10 major PFTs (31 trait attributes) that were supposed to be ecologically meaningful with respect to the studied management types and that we expected to be affected by management. These PFTs included the following PFTs: seed mass, leaf persistence, reproduction type, plant height, duration of flowering, plant lifespan, plant growth form, life strategy, leaf distribution along the stem, and forbs/graminoids. Each plant species was graded for each trait according to the attributes listed in Table 2. The attributes of individual PFTs were evaluated based on 2 databases: the PLADIAS Database of the Czech Flora and Vegetation (Chytrý et al. 2021) and the LEDA Traitbase (Kleyer et al. 2008). All the PFTs monitored attributes were evaluated for each type of management. They were calculated

Table 2. List of the Plant functional traits and their attributes analysed in the study.

Trait	Attribute	Abbreviation	Species example
Seed mass (mg)	< 0.5 (small seed)	ss	*Poa pratensis*
	0.5–2 (medium seed)	ms	*Filipendula ulmaria*
	> 2 (large seed)	ls	*Arrhenatherum elatius*
Leaf persistence	Overwintering green	ovg	*Matricaria chamomilla*
	Persistent green	pg	*Festuca rubra*
	Summer green	sg	*Dactylis glomerata*
Reproduction type	By seed, mainly by seed	s	*Trifolium pratense*
	Vegetative and by seed	sv	*Carex hirta*
	Mainly vegetative	v	*Aegopodium podagraria*
Plant height (m)	< 0.3 (small height)	sh	*Viola arvensis*
	0.3–0.6 (medium height)	mh	*Cardamine pratensis*
	> 0.6 (high height)	hh	*Mentha longifolia*
Duration of flowering	1–2 months (short flowering)	sf	*Galium verum*
	≥ 3 (long flowering)	lf	*Leucanthemum vulgare*
Plant lifespan	Annuals	ann	*Rhinanthus minor*
	Perennials	per	*Ranunculus acris*
	Strict monocarpic bi-annuals and poly-annuals	bie	*Campanula patula*
Plant growth form	Hemicryptophyte	hem	*Plantago lanceolata*
	Chamaephyte	cham	*Cerastium arvense*
	Phanerophyte	pha	*Rosa canina* agg.
	Geophyte	geo	*Lilium martagon*
	Therophyte	the	*Capsella bursa-pastoris*
Life strategy	Competitor	C	*Achillea millefolium*
	Stress-tolerator	S	*Viola canina*
	Ruderal	R	*Poa annua*
Leaf distribution along the stem	Leaves distributed regularly along the stem	ldr	*Lotus corniculatus*
	Rosette	ros	*Leontodon autumnalis*
	Semi-rosette	sro	*Knautia arvensis*
Forbs / Graminoids	Forb	fb	*Cirsium rivulare*
	Graminoid	gr	*Avenula pubescens*
	Wood	ws	*Alnus glutinosa*

from the averages of the values, weighted using the coverage of each species of vascular plant present at the sites where the sum of all categories was 100%. Differences in basic environmental characteristics among the three management types were investigated using the Kruskal-Wallis test, as variances were not homogeneous according to the Bartlett test, which was performed prior to analysis. The relationships between the proportions of functional groups of grassland plants and the management regime were summarised using redundancy analysis (RDA) with centred response data. The functional category proportion data were square-root transformed prior to analysis. The significance of the relationship was tested with a Monte Carlo permutation test (999 permutations). All analyses were performed in R v.4.1.2 (R Core Team 2021) using the libraries vegan (Oksanen et al. 2013) and pgirmess (Giraudoux et al. 2018).

Results

In total, 187 species were recorded at the study sites, of which 7 species are included in the Red List of ferns and flowering plants of Slovakia (Eliáš et al. 2015). The common species with high coverage at the MGM sites were *Arrhenatherum elatius*, *Dactylis glomerata*, and *Avenula pubescens*. *Festuca rubra*, *Agrostis capillaris*, and *Anthoxanthum odoratum* were often present at MGP sites. In addition to the mentioned species, the MGA sites were also characterised by the presence of more hygrophilous species, such as *Filipendula ulmaria*, *Lysimachia vulgaris*, and *Scirpus sylvaticus*. In all the studied areas, the average species richness and the Shannon index were lower at the MGA sites than at the managed MGP and MGM sites. The average number of species at all the sites was 36 in an area of 16 m^2 (Table 1). A more detailed description of the plant communities of the studied sites is presented in Diviaková et al. (2021).

RDA revealed a significant relationship between the proportional coverage of the studied PFTs and management type (F = 18.12, p = 0.001), which explained 25.34% of the total variation in coverage of the studied PFTs. The results of the RDA are summarised in the ordination diagram (Fig. 2). The MGA sites were distinct from the managed MGP and MGM sites; they featured high proportional coverages of geophytes, phanerophytes, forbs, species with reproduction type vegetative and by seed, tall species (plant height > 0.6 m), competitors, species with long flowering times (3 months or more), and species with summer green leaves, while they featured low coverages of species with reproduction by seed, mainly by seed, graminoids, and rosette species (Fig. 3). Differences between managed sites were less pronounced, and mown sites (MGM) differed from pastures (MGP), especially in coverage of persistent green species, small species (plant height < 0.3 m), and species with large seeds (seed mass > 2 mg).

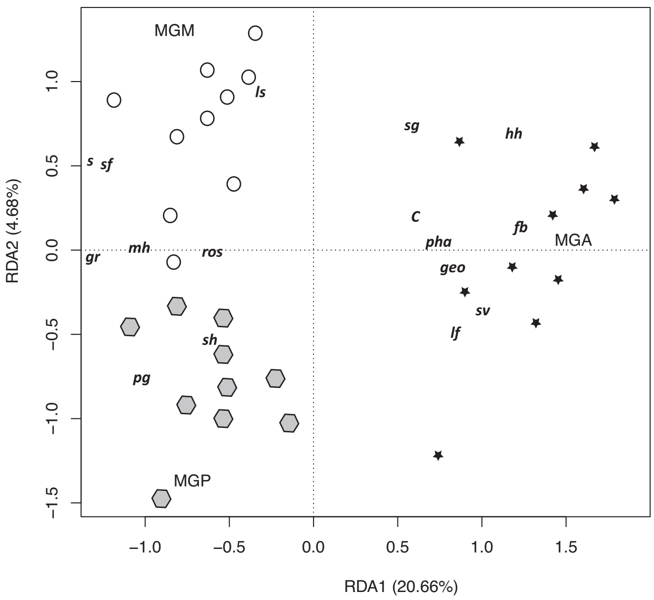

Figure 2. RDA ordination plot showing significant differences in the coverage of the studied PFTs among sites with different management practices. Only 50% of the PFT attributes best fitted by the ordination space are displayed. For the percentage of explained variance, see the axes titles. For abbreviations of PFT attributes, see Table 2. (empty circles – MGM sites, asterisks – MGA sites, filled hexagon – MGP sites).

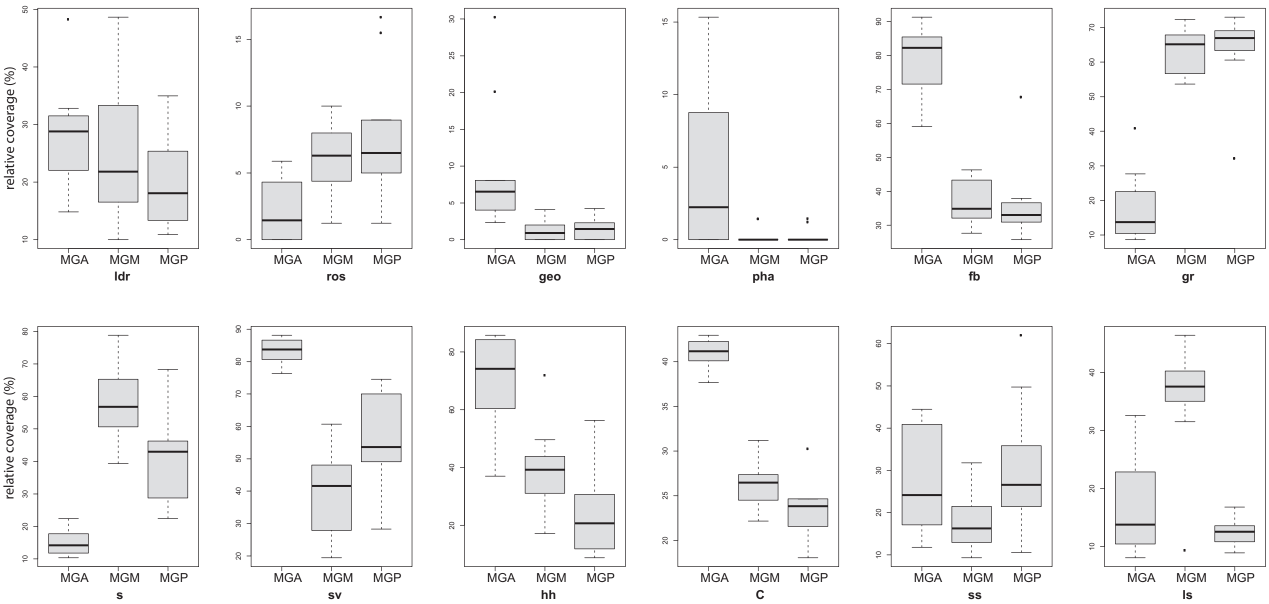

Figure 3. Box plots comparing the coverage of some attributes of selected PFTs in abandoned (MGA), mown (MGM) and pasture (MGP) meadows. For abbreviations of PFT attributes, see Table 2.

Discussion

Grassland management affects not only total species richness but also the relative number and coverage of species with different attributes regarding anatomy, morphology and regeneration (Dupré and Diekmann 2001) and thus different PFTs. We documented significant differences in the coverage of plants with functional traits important for their competitiveness and resistance, reproduction, flowering, morphology, physiology, or plant lifespan among sites managed by phytomass removal (MGM, MGP) and abandoned sites (MGA). The coverages of the selected PFTs differed among the individual managements. Mowing and grazing had similar effects on PFTs in our study, which were different from abandoned sites. In all types of management, the dominant plant growth form was hemicryptophytes, the dominant plant lifespan was perennials, and the dominant PFT leaf distribution along the stem was semi-rosettes.

Mowing (MGM) and Grazing (MGP) vs. Abandonment (MGA)

Compared with abandoned sites, managed sites were characterised by greater coverages of some attributes, e.g., within PFTs leaf distribution along the stem and plant height. Leaf distribution and height are important traits for plant competitive ability and persistence (Drobnik et al. 2011), ergo for plant performance under different management regimes (e.g. Garnier et al. 2007).

We found that rosette species were more successful under the two main management regimes (MGM and MGP). Erect competitor species with leaves distributed regularly along the stem were more likely to occur with higher coverage at abandoned sites (MGA). Similarly, in experimental scenarios of changes in land use, the abandonment or decreasing frequency/intensity of mowing and grazing led to decreases in rosette species and non-branched growth forms, whereas the coverages of taller species and species with leaves distributed regularly along the stem increased (Weiss and Jeltsch 2015), indicating a shift towards stronger above-ground competition (Römermann et al. 2008).

The higher proportion of rosette species, in our study, e.g., *Taraxacum* sect. *Ruderalia*, *Bellis perennis*, *Leontodon hispidus*, *Plantago media*) due to vertical defoliation is the main response to grazing and mowing management (McIntyre et al. 1995; Dupré and Diekmann 2001; Klimešová et al. 2008). These species have lower stature, buds closer to the ground, and horizontal leaf orientation and are able to resist grazers (Noy-Meir et al. 1989; Hadar et al. 1999). The rosette species represent an escape strategy that allows plants to survive disturbances and exploit newly available spatial niches (Grime 2001). However, this issue is complicated because, in addition to the form of leaf distribution, other mechanisms may be involved in greater resistance to defoliation. Among those, e.g., low palatability (Perez-Harguindeguy et al. 2003) depending on chemical composition traits (Pontes et al. 2015), mechanisms related to phenology and dormancy (McIntyre et al. 1999), or physical defence, such as spines (Díaz et al. 2001), may be important.

PFT plant height is the trait most frequently used to assess species response to management (Klimešová et al. 2008). Height is important for competitive performance and the acquisition of carbon and is a fundamental functional trait of plants (Westoby et al. 2002). In our study, tall species (> 0.6 m) prevailed (in terms of coverage) at abandoned sites, whereas at managed sites, species of medium height (0.3–0.6 m) or small species (< 0.3 m) showed higher coverage values (cf. Peco et al. 2005; Rupprecht et al. 2016). This pattern could be explained by the higher concentrations of nitrogen observed at the abandoned sites in our study. At abandoned sites, the proportion of tall species usually tends to increase as litter accumulation increases nutrient availability and hinders seedling recruitment (Huhta et al. 2001; Rosenthal 2010). One of the main environmental filters of most plant communities is light (Crawley 1997), and increased competition for light (i.e. avoiding shade) under abandonment (Lepš1999), especially under dense overgrowth, favours tall plants (Westoby et al. 2002; Neuenkamp et al. 2016), such as light competitors (Prévosto et al. 2011). In contrast, species with shorter heights in abandoned localities are the most susceptible to a lack of suitable microsites (Hautier et al. 2009) because of the absence of grazing animals or mowing.

In our study, the abandoned sites had greater coverage of phanerophytes than did the managed sites. Even grazed (MGP) sites showed greater phanerophyte coverage than mowed (MGM) ones probably because they remained in the area due to selective grazing (Dupré and Diekmann 2001). Phanerophytes are unpalatable to cattle and sheep because of their woody stems and the occurrence of spines (e.g., *Prunus spinosa* and *Rosa canina*). The presence of phanerophyte species and their adequate control by grazing, which prevents reforestation, can lead to greater structural or physiognomic heterogeneity in grasslands (Kun et al. 2024). In abandoned sites, succession leads logically to afforestation. The most visible consequence of land abandonment is the colonisation of previously opened land by phanerophytes, which are often of high biological and aesthetic value (Prévosto et al. 2011). However, in abandoned grasslands, there may not always be significant invasion of shrubs and trees in secondary succession, even after 60 years (Bohner et al. 2019). It is assumed that the germination and establishment of woody plants is impeded by a virtually closed sward and by accumulated necromass, retarding further succession to these communities (Moog et al. 2002; Bohner et al. 2012). Concerning other attributes of plant growth forms, abandoned sites were characterised by greater coverage of geophytes than managed sites. This is probably because the plant storage organs are not damaged by trampling animals or oppressed by heavy mechanisms (e.g. mowing with tractors) at abandoned sites (McIntyre et al. 1995; Lavorel et al. 1999a) or simply because most of the geophytes possess the ability to regenerate vegetatively (Dupré and Diekmann 2001); i.e., they can use nutrients stored in rhizomes or bulbs to grow in the spring through the thick litter layer (Bobbink and Willems 1987).

With respect to life strategy, in our study, competitors prevailed at abandoned sites (see Rupprecht et al. 2016). Weiss and Jeltsch (2015) reported a strong increase in competitor plant types under resource (nutrient, water, and light)-rich conditions where the intensity of stress from their lack was minimal. The abandoned sites in our study were characterised by relatively high soil humidity (although not assessed exactly) and, at the same time, by the absence of disturbances, which favour long-lived plants.

Another evaluated functional trait was the reproduction type. Compared with those in the MGA, the average coverages of the species reproducing by seeds at the managed sites (MGM and MGP) were greater. Similarly, Rysiak et al. (2021) found an increasing number of species reproducing by seed on the managed plots. Seeds of numerous species can survive herbivore consumption or attach to fur, making herbivores vectors for plant dispersal (Malo and Suarez 1995; Cosyns et al. 2005). Also, increased light availability in managed sites can lead to better germination and seedling establishment (Jutila and Grace 2002).

Species reproducing by seeds possess persistent seed banks and their occurrence depends on the formation of bare ground and thus are expected to prefer grazed or mowed sites (e.g. Lavorel et al. 1999b). At the abandoned sites, species with the ability to reproduce vegetatively showed greater coverage values (cf. Pettit et al. 1995). The vegetative spread by rhizomes depends on a low frequency of disturbance (McIntyre and Lavorel 1994).

The results of our study showed that the managed sites allow the preservation of specific vegetation compositions with high coverage of graminoids. In contrast, abandoned sites are colonised primarily by perennial forbs (cf. Vannucchi et al. 2022). The high coverage values of short graminoids in managed grasslands were probably caused by better light conditions, with more opportunities to colonize the open space. Tall forbs increased their cover in abandoned meadows because, as strong competitors, they do not tolerate disturbance (Pavlů et al. 2011).

The effects of abandonment on soil properties, i.e., soil nitrogen and organic contents, confirm the key role of soil chemical properties in influencing vegetation in managed grasslands (Grime et al.,1997; White et al. 2004). Vegetation affects soil properties through a feedback mechanism (Petermann and Buzhdygan 2021). Some functional types, such as forbs, effectively increase nitrogen and carbon contents in grassland soils (Knops and Tilman 2000; De Deyn et al. 2009). Increased amounts of nitrogen and carbon in abandoned sites in comparison with managed sites (Vannucchi et al. 2022), which were also confirmed in our study, may be related to higher aboveground phytomass and increased plant litter decomposition (Gabarrón-Galeote et al. 2015; Bohner et al. 2019). Higher aboveground plant biomass and a denser surface layer of necromass at abandoned sites can also reduce the average soil temperature and increase soil moisture (Facelli and Pickett 1991).

Our study confirmed the differences in leaf persistence between abandoned and managed sites. Summer green species prevailed in coverage at the abandoned sites, whereas persistent green species prevailed at the grazing-managed sites. Rysiak et al. (2021) reported significantly greater coverage of summer green species at mowed sites. Leaf persistence is a functional trait that is important for plant competitiveness. It depends on the climate in the distribution range of the taxon and microclimate, as well as nutrient and light availability in typical habitats of the taxon.

We also observed differences in the PFT duration of flowering between abandoned and managed sites. Long-flowering species were characterised by great coverages at abandoned sites, whereas short-flowering species were dominant at mowed sites. At managed sites, this difference can be due to management timing (as well as intensity and frequency), which is important for the phenology of seed production (Poschlod et al. 2000). Plants in managed grassland biotopes are adapted to disturbances, e.g., by mechanisms related to palatability and mechanical defence (Callaway et al. 2000), growth form (Noy-Meir et al. 1989), and reproductive phenology (Lennartsson et al. 1998). Phenology can be considered particularly important in grazing, mown, and other managed biotopes because it determines whether a plant can produce seeds before the vegetation is disturbed (Akhalkatsi and Wagner 1996). However, in abandoned meadows, some species may experience longer or delayed development due to undecomposed litter, which acts as an insulating layer and fundamentally affects the physical and chemical properties of the soil (Janišová et al. 2007).

Mowing (MGM) vs. Grazing (MGP)

The similarities in the proportional coverage of the studied PFTs between the managed sites (MGM and MGP) were not surprising, as in both cases, applied management represents a disturbance to grassland habitats. In both types of management, mowing and grazing, aboveground vegetation is more or less regularly removed, but at least part of the phytomass is left (Kahmen and Poschlod 2008). This suggests that the effects of management on PFTs may operate mainly through the intensity of biomass loss or the biomass recovery rate, factors that were similar for both management practices in our study. Similar effects of mowing and grazing on PFTs indicate that different management practices may maintain communities with similar functional trait compositions and coverages, even though species compositions may differ (Moog et al. 2002; Garnier et al. 2007; Volf et al. 2016).

The grazed sites that we studied differed from the mowed ones mainly in terms of PFT plant height and seed mass. Small-height and small-seed species prevailed in the grazed sites and mowed sites hosted higher coverages of high-height and large-seed species. In contrast to mowing, grazing, as mentioned above, leads to the formation of gaps, as livestock trample and wallow within pastures (Gilhaus et al. 2017). Consequently, grazing promotes the establishment and maintenance of low-growth plants (Fleischer et al. 2013). Rysiak et al. (2021) noted that mowed and grazed sites are habitats rich in plants with relatively large seeds. Eriksson and Eriksson (1997) or Kahmen and Poschlod (2008) reported an increase in the number and coverage of species with small seeds caused by grazing. Seed mass is a functional trait related to plant dispersal and regeneration ability. Although heavier seeds may be dispersed over shorter distances than lighter seeds, heavier seeds may enhance seedling establishment, especially when light or nutrients are in short supply (Leishman et al. 2000). In terms of seed mass, seedlings from large seed species tend to survive better under a closed canopy (Grime et al. 1997), and an increase in the mean individual seed mass was reported (Westoby et al. 2002) to be a response trait associated with an increase in canopy height (Louault et al. 2005). Plants with large and heavy seeds have difficulty colonising isolated patches (Helsen et al. 2013), and their populations may become locally extinct unless they have good vegetative propagation ability or a long lifespan (Lindborg and Eriksson 2004; Bossuyt and Honnay 2006). In contrast, isolated patches may be more easily reached by plants with low seed mass (Westoby et al. 1996). A decline in the mean seed size in response to grazing was also reported by McIntyre and Lavorel (2001) for both perennial grasses and forbs. In our study, mowed meadows were characterized by greater canopy heights without isolated patches, especially in the time before mowing.

Conclusions

Our study aimed to determine whether the representation of plant functional groups differed among sites with different types of applied management. We identified significant differences in the coverage of some plant functional traits among sites with different management practices. Managed sites differed from abandoned sites in terms of coverage of the PFT height of the plant, the distribution of leaves on stems, the length of the flowering period, the method of reproduction, and the representation of grasses/herbs. We focused on one type of vegetation, the *Arrhenatherion* meadows. This approach allowed for sufficient clarification of the differences between management strategies in a particular place but also for generalisation for predictive purposes. *Arrhenatherion* meadows are the most widespread type of seminatural meadow in Central Europe. In this meadow ecosystem, plants are exposed to regular disturbances and, owing to their abilities, are well adapted for economic use. Currently, many grassland biotopes (especially those at relatively high altitudes, far from economic centres or in steep and sloping locations with shallow soil) are no longer managed. Here, we showed that the abandonment of the management of these valuable grasslands caused important changes in the functional structure of the communities. Several studies have assessed the impact of management on other PFTs or other types of grasslands, on which the research presented in this paper was focused. Nevertheless, many questions regarding the impact of management on grassland biodiversity, ecological stability or adaptability to climate change remain unanswered. Further research broadly focused on different types of grasslands and their management, employing detailed analysis methods, is needed to reveal general patterns of the influence of grassland management on their properties and to select optimal forms of management based on the specific identified natural conditions. This would help to preserve the natural value of these rare and currently endangered habitats.

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Additional information

Conflict of interest

The authors have declared that no competing interests exist.

Ethical statement

No ethical statement was reported.

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Author contributions

Conceptualization: AD, SS. Data curation: HO, AD, MN. Formal analysis: AD, MN. Funding acquisition: SS. Investigation: AD, SS. Methodology: AD, MN. Project administration: AD. Writing - original draft: AD, MN, HO. Writing - review and editing: DV, SS, MN, AD, HO.

Author ORCIDs

Andrea Diviaková https://orcid.org/0000-0002-3062-3976
Hana Ollerová https://orcid.org/0000-0002-7415-2192
Slavomír Stašiov https://orcid.org/0000-0002-4914-4465
Darina Veverková https://orcid.org/0000-0002-3421-1514
Milan Novikmec https://orcid.org/0000-0002-5192-4575

Data availability

All of the data that support the findings of this study are available by authors upon request.

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