



Simplicity or complexity? Important aspects of high nature value grassland management in nature conservation

Róbert Kun¹ · Dániel Babai² · András István Csathó³ · Csaba Vadász⁴ ·
Nikoletta Kálmán⁵ · András Máté⁶ · Ákos Malatinszky¹

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Abstract

Local, adaptive traditional grassland management systems have played a fundamental role in the creation, maintenance and conservation of high nature value (HNV) grasslands. The state of diverse HNV grasslands has deteriorated across Europe in conjunction with changes in various management factors, such as management type and management intensity. To conserve the species-rich vegetation of HNV grasslands and to avoid undesirable shifts in plant functional type dominance, it is important to explore the effects of management factors crucial for nature conservation and to adapt them to local circumstances. In our study, we focus on three of the main factors in the management of valuable meadow steppes in the Great Hungarian Plain region (Central Hungary). We studied management types (mowing, grazing and combined), different levels of herbage removal intensity (low, medium, high) and spatio-temporal complexity (low, medium and high) of grassland management. Altogether 172 plots (1 m × 1 m) were designated in 17 sites. Plant diversity indexes and plant functional types were calculated according to the presence and percentage cover of plant species in the plots. Regarding plant diversity and the dominance of plant functional types, herbage removal intensity and spatio-temporal complexity of management had, for the most part, stronger effects than the type of management. Higher spatio-temporal complexity of management resulted in higher plant diversity, while higher intensity of management led to significantly lower diversity. Proper application of type, intensity and spatio-temporal complexity of management practices (separately and in combination) proved to be determining factors in the long-term maintenance and conservation of diversity and species composition of HNV grasslands.

Keywords Complex management systems · Different management factors · Nature conservation value · High nature value (HNV) grasslands

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✉ Róbert Kun
rbert.kun@gmail.com

Extended author information available on the last page of the article

Introduction

High nature value (HNV) natural and semi-natural grasslands are organic and important elements of European natural and cultural landscapes which have usually been maintained by extensive (traditional) management systems (Plieninger et al. 2006; Söderström et al. 2001). Grassland ecosystems host 18.1% of the more than 6000 European endemic vascular plant taxa (Hobohm and Bruchmann 2009). This is nearly twice as many as in forests, despite the latter covering much more land area (Habel et al. 2013). Dry and steppe grasslands in areas with relatively low altitudes in the continental climatic zone in Central and Eastern European countries can host extremely high species diversity with high conservation value as well (e.g., 79 species per square meter in Romania as the record for East-Central Europe—Dengler et al. 2014; Wilson et al. 2012). In Hungary, among others, meadow-steppes are extremely species-rich habitats (38 plant species in 1 m² and 46 species in 4 m² were the maximum in extensively managed grasslands (Kun et al. unpubl. 2021)).

Extensive (traditional) farming practices, adapted to local ecological circumstances, played a crucial role in the formation and maintenance of HNV grasslands all over Europe over the past centuries (Babai and Molnár 2014; Dahlström et al. 2013; Fischer and Wipf 2002; Kun et al. 2007; Plieninger et al. 2006). Not only extensive management practices but also the micro (parcel)-scale land-use diversity of these systems has a positive effect on plant species diversity and on the proportion of different plant functional types (PFTs—e.g., forbs, Poaceae or Fabaceae species) (Kun et al. 2019). Populations of numerous specialist plant species (e.g., *Blackstonia acuminata*, *Iris spuria*), as well as animals (e.g., red-listed butterflies such as *Maculinea* spp.) have adapted to these extensive management practices and patterns on HNV grasslands (Habel et al. 2013; Öckinger et al. 2006; Schmitz and Isselstein 2020). Determining factors are the spatially and temporally diverse combinations of several management elements with various levels of management intensity (e.g., hayseed sowing, manual control of undesirable species, livestock grazing, etc.) (Babai et al. 2014; Kun et al. 2019).

Nevertheless, extensive, traditional grassland management systems have undergone drastic changes all over Europe since the second half of the twentieth century (MacDonald et al. 2000; Plieninger et al. 2006). Shifting from the extensive (traditional) land-use systems towards less complex and more intensive agricultural practices or towards abandonment has led to severe changes (degradation) in the composition of cultural landscapes with HNV grasslands (e.g., increasing fragmentation, disappearing grasslands, decreasing biodiversity) (Bakker and Berendse 1999; Galvánek and Lepš 2008; Házi et al. 2011; Öckinger et al. 2006; Öckinger and Smith 2006; Poschlod et al. 2005; Ruprecht et al. 2010). Accordingly, the disappearance of once widespread extensive land-use systems has resulted in a decline of the area of the grasslands, of the species diversity, drastic changes in species composition and a homogenisation of the vegetation of HNV grasslands across Europe, even despite nature conservation efforts and financial initiatives (see e.g. CAP subsidies) (Austrheim and Eriksson 2001; Csörgő et al. 2013; Burton and Paragahawewa 2011; MacDonald et al. 2000; Ruprecht et al. 2010; Spiegelberger et al. 2010). Additional indicators of degradation are changes in functional diversity and dominance among different PFTs (e.g., increasing abundance of generalist, disturbance-tolerant or even invasive alien species) (de Bello et al. 2006). PFTs as indicators create a bridge between plants' physiological characteristics and phytosociological behaviour (Diaz and Cabido 1997), and their relative dominance may differ depending on the type and intensity of grassland management (Austrheim and Eriksson 2001; Duru et al. 2005; Házi et al. 2011; Imrichova and

Vrahnakis 2005), affecting the quality of harvestable fodder (e.g., hay) (Babai et al. 2015; Duru et al. 2005).

Previous studies have primarily focused on the effects of a single factor (e.g., type or intensity of management) of HNV grasslands' management on biodiversity or on the compositional or dominance relations of the vegetation (de Bello et al. 2006; Fischer and Wipf 2002; Házi et al. 2011; Tälle et al. 2016). Vadász et al. (2016) suggested for consideration of the spatio-temporal complexity of management (i.e., how the sequence of application of particular management units varies within a year and from year to year), which is a potential factor maintaining plant diversity of HNV grasslands as well.

It follows from all this that studies on grassland management need to focus on three key management factors simultaneously, namely (1) type of management (mowing, grazing and their combination); (2) herbage removal intensity (expressed in Standard Livestock Unit, see Table 1 and Allen et al. 2011); and (3) spatio-temporal complexity of management (different timing and applied rates of herbage removal intensity levels and management types—for more details see Table 1). Modelling the specific and combined effects of various grassland management factors on plant diversity enables us to identify the key factors (and their linear combinations) which are most relevant for successful nature conservation management.

We aimed to explore the following questions:

- Which management factors and combinations of them have a significant effect on plant diversity?
- Do these management factors separately and in combination significantly affect dominance relations (species number and total cover) among PFT groups?
- What priority do management factors have in how they affect diversity indices, PFT group covers and PFT species numbers, and how do they apply to conservation?

Table 1 List and short introduction of explanatory variables, the analysed management factors

Management factors	Meanings and scales of management factors
Type of grassland management (<i>T</i>)	Mowing (<i>M</i>) Grazing (<i>G</i>) Combined (mowing and grazing combined within a year or between years, <i>C</i>)
Herbage removal intensity (<i>I</i>)	Low: 0.5 standard livestock unit (SLU) per hectare grazing, or mowed once a year Medium: 0.5–0.8 SLU/ha grazing, or mowed once a year with subsequent grazing in the same year High: > 0.8 SLU/ha grazing livestock
Spatio-temporal complexity of management (<i>C</i>)	Low: permanent grazing in a single grazing unit (no variance in grazing pressure within and between years) Medium: grazing with standard within-year sequence of two grazing units, or one mowing with 10% left uncut, or mowing once a year combined with subsequent grazing High: mowing and grazing combined between years, or grazing with a varying sequence of four grazing units between years

Herbage removal intensity of management was expressed by Standard Livestock Unit (SLU), which is a non-lactating bovine weighing 500 kg (= 1 SLU, see Allen et al. 2011) and by mowing frequency per year

Materials and methods

Study area

The study area is located in the Turján region of the Great Hungarian Plain (Central Hungary) (coordinates: 47.04023°N; 19.15289°E). This region belongs to the continental forest-steppe zone, with a slight sub-Mediterranean climatic effect. Annual mean temperature is 10.4 °C (Tölgyesi et al. 2016), while annual average rainfall is 520 mm. At the regional level (Turján region), sandy and loamy soils are dominant (Karátson 2002), while in the study area the sandy soils are dominant (Vadász et al. 2016). Potential vegetation of the study area is the Pannonian sandy forest steppe community, but two thirds of the area is covered by the rich mosaic of primary and secondary, semi-natural grasslands grazed by cattle (Hungarian Grey Cattle and Charolais breeds). Our aim was to study spatially scattered primary, ancient grassland sites (or, on the rare occasion, oldfields, abandoned very long ago). This sandy, xero-mesic meadow-steppe habitat is one the dominant grassland types in the study area, being a transitional, species-rich ecotone between *Molinia* fen meadows (Molinion caeruleae, Natura 2000 code: 6410) and Pannonic sand steppes (*Galio veri-Holoschoenetum vulgaris*, Natura 2000 code: 6260). Although extensively managed xero-mesic meadow steppes are one of the most species-rich habitat types in Hungary, management-vegetation interactions in this habitat type are understudied from the perspective of nature conservation (Vadász et al. 2016). Adventive and invasive species are rare in the managed grasslands. Dominant, frequent and characteristic species of this habitat are *Chrysopogon gryllus* (Poaceae), *Molinia caerulea* (Poaceae), *Serratula tinctoria* (Asteraceae), *Sanguisorba officinalis* (Rosaceae) and *Betonica officinalis* (Lamiaceae), while many protected species, such as *Ophrys scolopax* (Orchidaceae) and *Iris spuria* (Iridaceae), are also present.

Sampling protocol

This study considers three management factors: (1) type of management (*T*), (2) intensity of management (*I*), and (3) spatio-temporal complexity of management (*C*). Management types considered are mowing, grazing and the combination of them; furthermore, three categories of herbage removal intensity (low, medium and high intensity) and three spatio-temporal complexity categories (low, medium and high complexity) were investigated. The sample arrangement, in addition to the mentioned categories, was determined by following the method of Vadász et al. (2016) (Table 1). We aimed to sample consantly managed meadow steppe habitats in the study area. Every sampled grassland site exceeded at least 5 ha in size, in order to exclude sources of variance that emerge from diversity of management and neighbouring or edge effects. Investigations were undertaken in the summer of 2015, on 17 grassland sites, which were ordered by the three management factors (*T*, *I*, *C*) (for more details, see Table 1, Appendix Table 12). 10 plots were designated on 15 grassland sites and 11 were designated on two sites, because of the greater extent of the meadow-steppe patches to ensure the proper sampling and interpretation required. Thus, in the end, data gathered in $N=172$ plots (1 m × 1 m each) were evaluated (for more details, see Appendix Fig. 3). Because of the indistinct shape and variable extent of the sampling sites, it was not possible to use a previously determined random protocol in the arrangement of the plots. Therefore we applied linear sampling, where we placed each plot per

site along transects fitted to special forms of every sites. The location of the first plot of the transect in a given site was determined randomly, while further plots were designated at a minimum of four meters along the transects (for more details, see Appendix Fig. 3). Recorded data at every plot included the name and visually estimated percentage cover of each vascular plant species, and the coordinates of the plots were registered using GPS.

Applied terms and data analysis

In this paper, we refer to management as all human activities attempting to serve nature conservation or economic purposes in grasslands. Herbage removal intensity and spatio-temporal complexity levels were determined by local farmers and by the local national park ranger with expertise in this area (Csaba Vadász and András Máté—authors of the paper, Kiskunság National Park) (see also Vadász et al. 2016). All the studied management factors (type of management (T), herbage removal intensity (I) and spatio-temporal complexity (C) of management), as explanatory variables, have different technical parameters (e.g., timing, frequency and level of intensity) (Table 1), which are referred to as ‘management details’ and ‘levels’ below in the text.

We categorized all observed plant species into eight predefined PFTs, based on habitat requirement, life-history traits, and growth form (Table 2, Borhidi 1995). We used species number and total cover of each PFT, as well as total species number, Shannon diversity and Simpson diversity, as response variables (Table 2, Borhidi 1995). In our analyses, we used percentage cover of all PFTs as like species numbers of them. In case of life history trait classifications, we also used the list of protected species in Hungary (see <http#1>). In the life history trait category selection we used only those PFTs, which had hypothetically strongest explanatory and indication power of naturalness and conservation value of the sampled meadow steppe communities (see Borhidi 1996; Hargitai 1940).

Linear mixed models, namely LMER and GLMER were used to evaluate the explanatory power and informativity of the three, studied management factors and their combination on response variables. First, to investigate main effects of management factors (type, intensity, and spatio-temporal complexity) vegetation, we ran three separate models for each response variable: as a function of management type (1: T), as a function of herbage removal intensity (2: I), and as a function of spatio-temporal complexity (3: C). Site was included as a random factor to account for non-independence of plots. Second, to investigate combined effect of management factors, we ran four additional models for each response variable: 4: $T+I$; 5: $T+C$; 6: $I+C$; and 7: $T+I+C$. Normality of residuals were checked with the Shapiro–Wilk normality test. In case of non-normally distributed residuals, GLMER models were applied with Gamma family. In some cases, where convergence problem occurred, “log” link was applied in models. After simple model evaluations (T , I and C), Tukey post hoc tests were applied with “glht” function to evaluate significant differences between levels of different management factors. Bonferroni adjustment method was applied in the post hoc tests to counteract the problem of multiple comparisons. In the models, AICc (corrected Akaike information criterion) values were used to determine model parsimony. Application of AICc values was important and adequate for estimating the relatively few real combinations of the explanatory variables (Burnham and Anderson 2002). Candidate models with strong explanatory power ($\Delta AICc \leq 4$) were used for model averaging and model selection. Unadjusted beta R^2 values (with ‘r2beta’ function) of models were used to evaluate the amount of explained variance and fit, following the recommendations of Posada and Buckley (2004). Analyses were run with R 3.5.1 (R Core Team

Table 2 Attributes of the measured plant functional types (PFTs)

Plant functional type	Trait category	Attributes of variables	Species number in different categories from the total (176)	Optimal percentage cover intervals in plots (2 m×2 m)	Optimal species number interval in plots (2 m×2 m)
Forb species	Growth form	Non-grassy herbs	126	20–40%	20–25
Grass species	Growth form	Species only from the Poaceae family	23	60–70%	7–8
Disturbance-tolerant species	Life history	Plants native to the Hungarian flora with a wide range of perturbation tolerance	49	0–5%	7–8
Generalist species	Life history	Plants native to the Hungarian flora with great area and relatively great spreading capacity	73	25–30%	10–15
Natural competitor species	Life history	Plants native to the Hungarian flora with great competitive abilities in plant communities	18	0–10%	4–5
Ruderal competitor species	Life history	Plants native to the Hungarian flora with great competitive abilities in ruderal plant communities	5	0–3%	0–2
Specialist species	Life history	Plants native to the Hungarian flora with special habitat needs and a narrow range of tolerance	6	1–20%	1–6
Protected species	Life history	Rare plants native to the Hungarian flora with mostly very special habitat needs, protected by Hungarian law	10	1–20%	1–10

Life history trait categories derives from plant Social behaviour type (SBT) categories of Borhidi (1995). Species in forb and grass growth form categories are also included in different life history trait categories and vice versa, but none of the two growth form trait categories overlap with the other growth form trait category and similarly, different life history trait categories don't overlap with other life history trait category. Protected species category doesn't included in Borhidi's SBT category, this plant group based on the protection of Hungarian Law and species in this group have different, extra special needs. This group overlaps mostly with forb and specialist species. Optimal percentage cover and species number intervals of each PFTs were determined by the optimal proportion of species in the studied plant community among natural circumstances (see Borhidi 1996 and Hargitai 1940)

2018) software environment and by ‘MuMIn’, ‘lme4’, ‘gofr’, ‘r2glmm’, ‘multcomp’ and the ‘vegan’ packages.

Results

During the field work, 4780 records of 176 plant species were collected in a total of 172 plots.

Management factors with strong explanatory power on the dependent variables

Management type (*T*) as fixed factor, didn’t affected strongly plant diversity and most of the PFT covers and numbers. Only generalist species number and disturbance tolerant species cover had relatively strong relationship with *T* (Tables 4, 5), but significant differences between different management types wasn’t experienced (Appendix Table 6). Herbage removal intensity (*I*) had much more stronger effects on diversity, mainly on Shannon diversity and species number and had significant effect on grass, generalist and forbs species coverages (Tables 3, 4). Parallely, spatio-temporal complexity of management (*C*) had the strongest relationships with diversity indices and species number. *C* had powerful impact on generalist species cover and number as like forb, specialist and disturbance tolerant species numbers (Tables 4, 5). In several cases, simple, univariate models were most parsimonious and had best fits. In case of Shannon and Simpson diversity, simple *C* model was the most parsimonious. Forb, generalist and disturbance tolerant species coverage had most parsimonious models in relation with single management factors. Similarly, simple models were most parsimonious in case of grass, disturbance tolerant, natural competitor, ruderal competitor, specialist and protected species numbers. On the other hand, in case of species number, grass, natural and ruderal competitor and protected species cover, complex models were more parsimonious (Tables 3, 4, 5). Regarding the aforementioned dependent

Table 3 Simple and complex effects of different management factors on plant diversity

	Estima- tors	<i>T</i>	<i>I</i>	<i>C</i>	<i>T+I</i>	<i>T+C</i>	<i>I+C</i>	<i>T+I+C</i>
Species num- ber	AICc	968.047	951.616	950.913	942.692	949.420	942.945	938.220*
	R ²	0.125	0.488	0.492	0.547	0.498	0.541	0.554
Shannon diver- sity	AICc	73.029	71.761	66.891*	72.150	70.899	71.208	74.672
	R ²	0.160	0.225	0.380	0.352	0.383	0.377	0.392
Simpson diver- sity	AICc	- 383.977	- 383.636	- 387.509*	- 382.706	- 383.648	- 383.277	- 380.258
	R ²	0.147	0.128	0.272	0.255	0.280	0.271	0.301

Effects of explanatory variables—type of grassland management (*T*), herbage removal intensity (*I*) and spatio-temporal complexity of management (*C*)—were measured by using beta R² values and parsimony by AICc in LMER and GLMER models

*The best model (lowest AICc)

AICc values of candidate models with significant explanatory power (with $\Delta AICc \leq 4$) are written in bold

Table 4 Simple and complex effects of different management factors on cover of different plant functional types (PFTs)

	Estimators	<i>T</i>	<i>I</i>	<i>C</i>	<i>T+I</i>	<i>T+C</i>	<i>I+C</i>	<i>T+I+C</i>
Forb species cover (%)	AICc	1385.231	1380.966*	1384.790	1384.894	1388.249	1384.251	1385.187
	R ²	0.065	0.165	0.079	0.171	0.099	0.182	0.223
Grass species cover (%)	AICc	1467.300	1454.464	1463.378	1447.514	1454.573	1446.584*	1458.212
	R ²	0.116	0.341	0.207	0.349	0.245	0.350	0.438
Disturbance-tolerant species cover (%)	AICc	1301.421*	1305.392	1305.446	1305.481	1305.599	1308.373	1308.558
	R ²	0.199	0.052	0.033	0.206	0.205	0.115	0.244
Generalist species cover (%)	AICc	1296.816	1293.951	1289.503*	1290.848	1291.935	1293.646	1291.994
	R ²	0.128	0.233	0.348	0.392	0.379	0.347	0.425
Natural competitor species cover (%)	AICc	1492.611	1490.755	1490.782	1481.689	1482.978	1481.190	1470.438*
	R ²	0.087	0.121	0.115	0.163	0.136	0.158	0.189
Ruderal competitor species cover (%)	AICc	1237.739	1232.633	1235.012	1228.457	1229.791	1227.951	1220.754*
	R ²	0.025	0.149	0.090	0.152	0.117	0.147	0.165
Specialist species cover (%)	AICc	624.490	622.625*	623.085	622.966	624.113	623.490	622.875
	R ²	0.035	0.085	0.064	0.149	0.118	0.119	0.152
Protected species cover (%)	AICc	814.417	815.161	818.860	812.873	813.342	814.167	810.384*
	R ²	0.168	0.146	0.012	0.210	0.197	0.162	0.212

Effects of explanatory variables—type of grassland management (*T*), herbage removal intensity (*I*) and spatio-temporal complexity of management (*C*)—were measured by using beta R² values and parsimony by AICc in LMER and GLMER models

*The best model (lowest AICc)

AICc values of candidate models with potentially significant explanatory power (with ΔAICc ≤ 4) are written in bold

Table 5 Simple and complex effects of different management factors on plant functional type (PFT) species numbers

	Estimators	<i>T</i>	<i>I</i>	<i>C</i>	<i>T+I</i>	<i>T+C</i>	<i>I+C</i>	<i>T+I+C</i>
Forb species number	AICc	894.622	881.691	886.801	881.213*	890.020	883.727	884.911
	R ²	0.084	0.486	0.410	0.524	0.425	0.505	0.523
Grass species number	AICc	644.068	643.017	642.585*	646.095	646.695	645.810	648.362
	R ²	0.015	0.071	0.094	0.121	0.102	0.135	0.187
Disturbance-tolerant species number	AICc	771.976	766.332*	766.359	768.323	769.468	768.201	772.074
	R ²	0.083	0.237	0.245	0.266	0.262	0.279	0.279
Generalist species number	AICc	810.551	803.455	780.598	777.411	780.935	777.034	773.002*
	R ²	0.260	0.568	0.503	0.545	0.503	0.540	0.562
Natural competitor species number	AICc	598.535	597.091*	598.422	601.337	602.691	600.888	604.408
	R ²	0.002	0.057	0.008	0.058	0.010	0.072	0.092
Ruderal competitor species number	AICc	407.871	404.273*	406.821	408.322	410.863	408.067	406.300
	R ²	0.019	0.151	0.046	0.175	0.073	0.160	0.282
Specialist species number	AICc	349.383	345.074	340.268*	342.316	345.085	343.524	344.688
	R ²	0.029	0.241	0.366	0.428	0.377	0.398	0.431
Protected species number	AICc	358.211	356.379*	356.919	360.516	360.628	359.659	363.446
	R ²	0.036	0.084	0.061	0.132	0.127	0.136	0.139

Effects of explanatory variables—type of grassland management (*T*), herbage removal intensity (*I*) and spatio-temporal complexity of management (*C*)—were measured by using beta R² values and parsimony by AICc in LMER and GLMER models

*The best model (lowest AICc)

AICc values of candidate models with potentially significant explanatory power (with ΔAICc ≤ 4) are written in bold

variables, R^2 values of complex models with the best fit increased by $\Delta R^2 = 0.006\text{--}0.131$ when compared to the best fitting single-variable models (Tables 3, 4).

For five of the 19 dependent variables, the most complex model ($T+I+C$) was the best: species number, and the cover of natural competitors, ruderal competitors, and protected species as like generalist species number (Tables 3, 4, 5). For the dependent variables forb species number and grass species cover, explanatory power increased by applying a combination of T , I and/or C (Tables 4, 5).

The effect of management types, herbage removal intensity and spatio-temporal complexity levels on plant diversity as well as on coverages and numbers of different plant functional types

In our study, none of the studied response variables differed significantly by effect of mowing, grazing or combined management based on LMER and GLMER post hoc tests. On the other hand, different levels of I had a strongly negative differential effect on the total number of species, as like on forb species cover. Parallely, factor I had negative effect on forb, generalist disturbance tolerant species numbers. In contrast, high level of I had strong, positive effect on grass and ruderal competitor species coverages (Appendix Tables 7, 10).

High or medium level of C had strong, positive effect on grassland diversity (Fig. 1, Appendix Tables 8, 11) and on the generalist PFT group coverage (Appendix Table 8). Parallely, higher levels of factor C had strong, positive effects on forb, disturbance tolerant, generalist and specialist species numbers. In contrast, C had strong, negative effect on grass species cover (Fig. 1, Appendix Table 11).

Increasing or decreasing level of I and C were the two, most powerfully forming management factors with mostly opposite effects on plant diversity and PFTs. This phenomenon in details is pictured in Fig. 2 below.

Discussion

Effect of different management factors and their importance in conservation

Among the considered management factors, the low and/or medium herbage removal intensity, in line with high spatio-temporal complexity of management resulted in a significantly higher plant species number on the studied grasslands (Appendix Tables 7, 8).

Different management intensity levels affect plant diversity patterns and PFTs' relations (de Bello et al. 2006; Diaz and Cabido 1997; Imrichova and Vrahnakis 2005). Low or medium herbage removal intensity gives room for (1) greater plant heterogeneity (e.g., different reproduction phases or variable height on a management-unit scale) (Austrheim and Eriksson 2001), and (2) increased diversity of plant species. In contrast, high herbage removal intensity can lead to functional and compositional homogenisation, and reduces diversity of grasslands especially in drier grasslands with relatively lower productivity (as our study area as well) (Fedrigo et al. 2018). In our study, high herbage removal intensity alone negatively affected the species number and cover of forbs, while positively affected grass species' cover (Fig. 1, Tables 3, 4 and Appendix Table 7). For example, clonal grasses with great competitive power (e.g. *Calamagrostis epigeios* and *Botriochloa ischaemum*) are favoured by high herbage removal intensity (see Öckinger et al. 2006; Malatinszky 2016; Ruprecht et al. 2010),

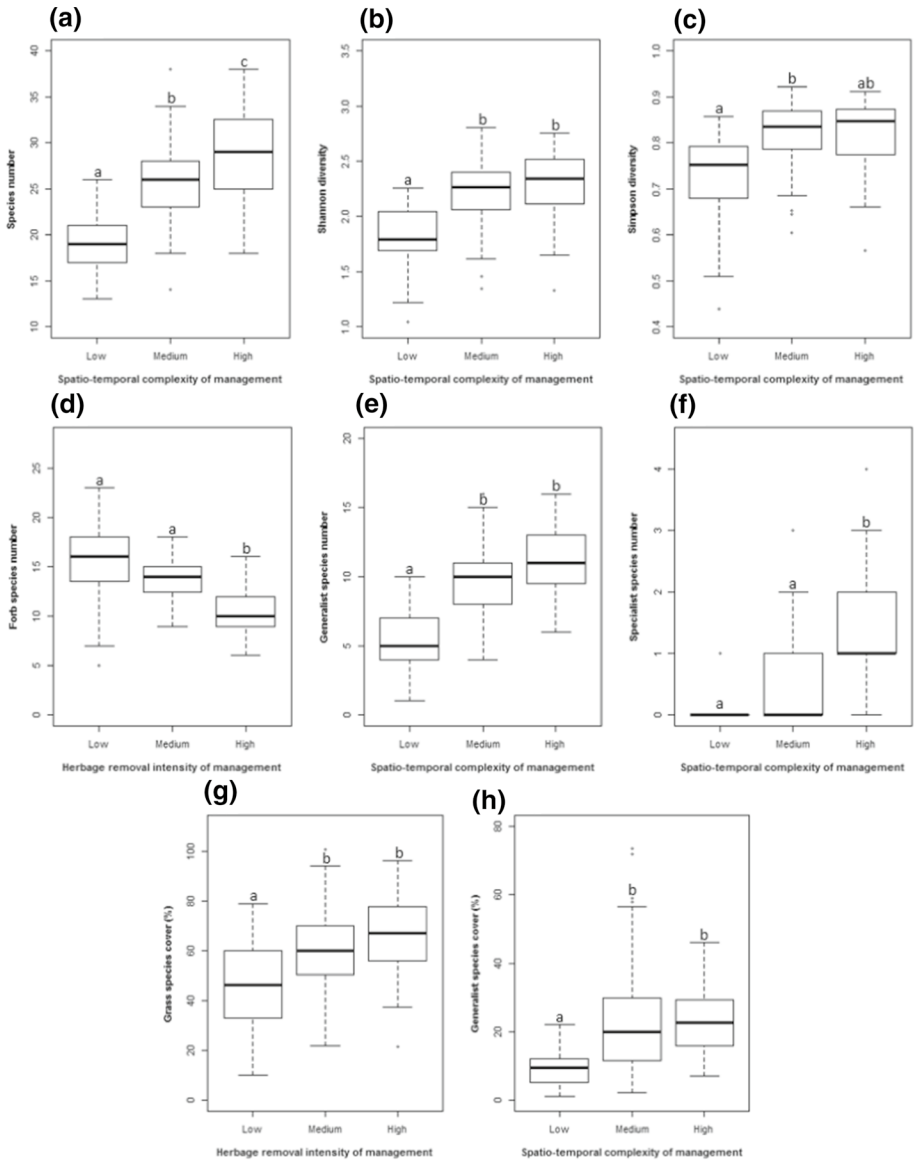


Fig. 1 Significant differences among different levels of particular management factors on dependent variables. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$. Significant differences between management factor levels are signed with different letters ('a', 'b' and 'c') above each boxplots. If there is not any difference, letters aren't different from each other. Letters from **a.)–h.)** mean subsections of Fig. 1. Most parsimonious, simplex (univariate) models were selected for this analysis, where the fit of models were relatively high, $R^2 \geq 0.250$

are able to completely dominate grassland stands (Szentes et al. 2012) and parallelly, reducing the species diversity and leading to a degraded state of grassland composition (Házi et al. 2011; Szentes et al. 2012). Lower level of herbage removal intensity has a

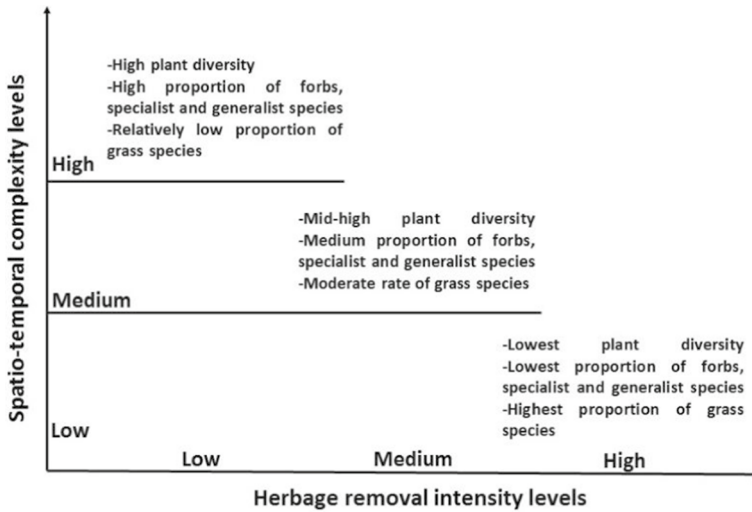


Fig. 2 Overall effects of herbage removal intensity and spatio-temporal complexity of management on plant diversity and plant functional types

positive effect on the proportion between grass and forb species coverage supporting the preservation of the optimal plant composition and diversity (Appendix Tables 7, 10, Fig. 1).

Spatio-temporal complexity of management, namely the application of diverse combinations of mowing and grazing with changing herbage removal intensities between years and within a year can influence the physiognomy, phenology and generative relationships of the grassland vegetation (Kelemen et al. 2017; Szépligeti et al. 2018), and positively affect the diversity and PFTs' dominance relations to a considerable extent (e.g. forb, generalist and specialist species numbers, see Table 5 and Appendix Table 11). This variance in management affects the inter-specific competition by creating temporal reproductive niches (niche partitioning and segregation) (Catorci et al. 2014; Marini et al. 2007). A few years with more intensive herbage removal intensity in a spatio-temporally complex grassland management can create a reduced height of the vegetation, resulting in a sunnier and drier microclimate (benefits light-preferring and drought tolerant species) (Wan et al. 2002). Periods with less intensive management (e.g., one mowing per year) favours species that prefer a milder microclimate, are taller and grow faster (Steen 1980). Thus, higher spatio-temporal complexity of grassland management (e.g., leaving unmown refuge strips with location varying from year to year; or grazing with changing regimes and starting time year by year) coupled with lower herbage removal intensity provides a great opportunity for more plant species with various competitive strategies to coexist (see Tables 3 and 4, Appendix Tables 7, 8, Fig. 1) (Austrheim and Eriksson 2001; Duru et al. 2005). Based on other studies, these abovementioned, positive effects also can be helped by the plant structure providing effect of extensive grazing (Kelemen et al. 2017). In summary, herbage removal intensity and spatio-temporal complexity had stronger effects on grassland diversity and on PFT groups than management type (Figs. 1, 2), furthermore their importance is greater in effective conservation practice and planning than management types only.

Complex effects and hierarchy of different management factors in conservation

Studied management factors and their parameters (different levels of intensity and spatio-temporal complexity) can be combined in several ways (theoretically $3^3 = 27$ ways). At the studied sites 7 combinations were realized (for more detailed information, see Table 1, Appendix Fig. 3, Appendix Table 12). The combination of low herbage removal intensity and high spatio-temporal complexity resulted in the highest number of species by far, positively affecting the cover of forbs and number of specialist species. This combination has the greatest relevance in conservation management practice. Furthermore, based on model selection, a definite hierarchy can be established among the three management factors based on their overall conservation relevance: (1) spatio-temporal complexity of management had the strongest explanatory power on most of the response variables (especially on plant diversity, generalist species cover and species number of forbs and specialists); (2) herbage removal intensity had less, but similarly great importance in conservation, and (3) management type was the third factor in the hierarchical order of the management factors' importance (Table 3). Based on this relevance, grassland conservation planning should take different levels of spatio-temporal complexity of grassland management into consideration to develop more comprehensive management systems. We recommend to investigate the effects of spatio-temporal complexity, herbage removal intensity of management and different management types in different grassland habitats to develop more effective nature conservation grassland management. Considering the significance of the relevance of management factors, a more comprehensive and detailed conservation planning and management would be achieved and oversimplifying models and approaches would be avoided in conservation studies and practice.

Conclusions

In our study we showed that spatio-temporal complexity, herbage removal intensity and management type have a significant role in affecting species composition and diversity of managed grasslands. Thus, conservation management considering only one or two management factors (e.g. only effects of mowing and/or management intensity in a specific region) can be recognised only with limitations regarding conservation planning and management. Complexity levels of applied management factors in space and time together with other technical details (several types and levels of management intensity and management complexity) are highly important in nature conservation management, however, these aspects are definitely understudied. Determining the applicable management factors, and their adequate combinations in accordance with local circumstances on a system level is an urgent need in nature conservation. Thus, resource managers should be very careful in management planning to avoid the potentially false application of oversimplified models and knowledge acquired by them in other regions. The results of this study hopefully shed light on the importance more complex, system-level models in effective conservation management planning of High Nature Value grasslands.

Appendix

See Tables 6, 7, 8, 9, 10, 11 and 12, Fig. 3.

Table 6 Effects of different management types on grassland diversity and coverages of different functional types

Dependent variables	Mown	Combined	Grazed
Species number	26.32 ± 4.177 a	26.220 ± 4.542 a	23.790 ± 5.171 a
Shannon diversity	2.221 ± 0.295 a	2.275 ± 0.246 a	2.058 ± 0.355 a
Simpson diversity	0.826 ± 0.062 a	0.828 ± 0.057 a	0.778 ± 0.096 a
Forb species cover (%)	33.874 ± 15.255 a	31.501 ± 17.454 a	27.019 ± 13.338 a
Grass species cover (%)	47.548 ± 14.514 a	53.169 ± 21.616 a	59.385 ± 19.643 a
Disturbance-tolerant species cover (%)	31.852 ± 17.027 a	18.688 ± 8.163 a	20.607 ± 13.384 a
Generalist species cover (%)	19.036 ± 10.232 a	27.478 ± 17.998 a	18.547 ± 13.365 a
Natural competitor species cover (%)	40.485 ± 15.948 a	39.104 ± 18.590 a	49.049 ± 21.534 a
Ruderal competitor species cover (%)	2.771 ± 5.183 a	5.685 ± 11.988 a	4.945 ± 9.829 a
Specialist species cover (%)	0.282 ± 0.921 a	0.501 ± 1.173 a	0.778 ± 1.928 a
Protected species cover (%)	2.592 ± 4.246 a	0.282 ± 0.830 a	0.853 ± 1.870 a

Significant differences among different type of management in every cases are signed with different letters ('a', 'b' and 'c') next to each management type averages and standard deviations (MEAN ± SD in the table, under every column of management types, namely mown, combined and grazed). If there is not any difference between management types, letters aren't different from each other. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$

Table 7 Effects of different levels of herbage removal intensity on grassland diversity and coverages of different functional types

Dependent variables	Low	Medium	High
Species number	27.549 ± 4.473 a	24.968 ± 2.787 a	20.74 ± 3.361 b
Shannon diversity	2.236 ± 0.298 a	2.214 ± 0.297 a	1.979 ± 0.334 a
Simpson diversity	0.819 ± 0.069 a	0.814 ± 0.08 a	0.770 ± 0.097 a
Forb species cover (%)	34.514 ± 15.386 a	27.703 ± 14.281 ab	23.484 ± 12.632 b
Grass species cover (%)	45.663 ± 17.583 a	60.750 ± 16.338 b	66.579 ± 16.198 b
Disturbance-tolerant species cover (%)	26.127 ± 15.917 a	19.472 ± 10.822 a	20.937 ± 13.207 a
Generalist species cover (%)	23.348 ± 13.82 a	24.447 ± 15.504 a	13.962 ± 11.98 a
Natural competitor species cover (%)	39.056 ± 17.472 a	48.359 ± 16.548 a	50.945 ± 23.094 a
Ruderal competitor species cover (%)	2.253 ± 6.639 a	3.967 ± 7.222 ab	8.881 ± 12.823 b
Specialist species cover (%)	0.672 ± 1.265 a	1.049 ± 2.758 a	0.08 ± 0.444 a
Protected species cover (%)	1.996 ± 3.573 a	0.115 ± 0.281 a	0.501 ± 1.125 a

Significant differences among different herbage removal intensity levels are signed with different letters ('a', 'b' and 'c') next to each herbage removal intensity level averages and standard deviations (MEAN ± SD in the table, under every column of levels, namely low, medium and high). If there is not any difference between levels, letters aren't different from each other. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$

Table 8 Effects of different levels of spatio-temporal complexity of management on grassland diversity and coverages of different functional types

Dependent variables	Low	Medium	High
Species number	19.267 ± 2.803 a	25.604 ± 3.883 b	28.968 ± 4.778 c
Shannon diversity	1.821 ± 0.284 a	2.217 ± 0.275 b	2.271 ± 0.342 b
Simpson diversity	0.730 ± 0.097 a	0.820 ± 0.066 b	0.817 ± 0.085 ab
Forb species cover (%)	23.203 ± 13.429 a	31.857 ± 16.353 a	30.374 ± 9.943 a
Grass species cover (%)	69.243 ± 16.415 a	52.274 ± 18.299 b	47.994 ± 19.383 b
Disturbance-tolerant species cover (%)	22.335 ± 15.728 a	24.467 ± 14.969 a	20.716 ± 11.708 a
Generalist species cover (%)	9.521 ± 4.969 a	23.220 ± 15.426 b	23.148 ± 10.399 b
Natural competitor species cover (%)	55.740 ± 25.553 a	41.982 ± 17.364 a	40.910 ± 18.317 a
Ruderal competitor species cover (%)	9.002 ± 13.410 a	3.924 ± 7.627 a	2.145 ± 9.284 a
Specialist species cover (%)	0.133 ± 0.571 a	0.533 ± 1.684 a	1.115 ± 1.475 a
Protected species cover (%)	0.785 ± 1.375 a	1.267 ± 3.120 a	1.485 ± 2.572 a

Significant differences among different spatio-temporal complexity levels are signed with different letters ('a', 'b' and 'c') next to each spatio-temporal complexity level averages and standard deviations (MEAN ± SD in the table, under every column of levels, namely low, medium and high). If there is not any difference between levels, letters aren't different from each other. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$

Table 9 Effects of management types on species numbers of different plant functional type groups

Dependent variables	Mown	Combined	Grazed
Forb species number	14.900 ± 3.477 a	14.463 ± 4.130 a	13.284 ± 3.887 a
Grass species number	7.420 ± 1.592 a	7.780 ± 1.681 a	7.420 ± 1.672 a
Disturbance-tolerant species number	9.780 ± 2.477 a	9.683 ± 2.115 a	8.704 ± 2.487 a
Generalist species number	10.060 ± 2.551 a	10.000 ± 2.729 a	8.346 ± 3.298 a
Natural competitor species number	4.640 ± 1.274 a	4.561 ± 1.550 a	4.580 ± 1.322 a
Ruderal competitor species number	0.880 ± 0.746 a	1.122 ± 0.980 a	1.000 ± 0.837 a
Specialist species number	0.400 ± 0.495 a	0.463 ± 0.840 a	0.593 ± 0.877 a
Protected species number	0.660 ± 0.688 a	0.390 ± 0.666 a	0.555 ± 0.707 a

Significant differences among different types of management are signed with different letters ('a', 'b' and 'c') next to each management type averages and standard deviations (MEAN ± SD in the table, under every column of management types, namely mown, combined and grazed). If there is not any difference between management types, letters aren't different from each other. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$

Table 10 Effects of herbage removal intensity on species number of different plant functional types

Dependent variables	Low	Medium	High
Forb species number	15.934 ± 3.777 a	13.742 ± 2.081 a	10.760 ± 2.446 b
Grass species number	7.495 ± 1.779 a	8.161 ± 1.485 a	7.120 ± 1.380 a
Disturbance-tolerant species number	10.066 ± 2.666 a	8.935 ± 1.340 ab	7.960 ± 1.916 b
Generalist species number	10.703 ± 2.601 a	9.290 ± 2.383 a	6.540 ± 2.349 b
Natural competitor species number	4.725 ± 1.430 a	4.839 ± 1.293 a	4.200 ± 1.195 a
Ruderal competitor species number	0.780 ± 0.814 a	1.032 ± 0.752 a	1.360 ± 0.851 a
Specialist species number	0.758 ± 0.835 a	0.419 ± 0.848 a	0.100 ± 0.303 a
Protected species number	0.692 ± 0.756 a	0.323 ± 0.541 a	0.420 ± 0.609 a

Significant differences among different herbage removal intensity levels are signed with different letters ('a', 'b' and 'c') next to each herbage removal intensity level averages and standard deviations (MEAN ± SD in the table, under every column of levels, namely low, medium and high). If there is not any difference between levels, letters aren't different from each other. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$

Table 11 Effects of spatio-temporal complexity of management on species number of different plant functional types

Dependent variables	Low	Medium	High
Forb species number	10.333 ± 2.426 a	14.234 ± 3.368 b	16.903 ± 4.020 b
Grass species number	6.700 ± 1.291 a	7.622 ± 1.526 a	7.871 ± 2.125 a
Disturbance-tolerant species number	7.500 ± 1.757 a	9.396 ± 2.103 b	10.419 ± 3.202 b
Generalist species number	5.400 ± 1.958 a	9.748 ± 2.567 b	11.129 ± 2.526 b
Natural competitor species number	4.367 ± 1.129 a	4.631 ± 1.307 a	4.677 ± 1.720 a
Ruderal competitor species number	1.267 ± 0.907 a	0.955 ± 0.802 a	0.871 ± 0.922 a
Specialist species number	0.167 ± 0.379 a	0.378 ± 0.633 a	1.290 ± 1.006 b
Protected species number	0.600 ± 0.675 a	0.459 ± 0.629 a	0.806 ± 0.873 a

Significant differences among different spatio-temporal complexity levels are signed with different letters ('a', 'b' and 'c') next to each spatio-temporal complexity level averages and standard deviations (MEAN ± SD in the table, under every column of levels, namely low, medium and high). If there is not any difference between levels, letters aren't different from each other. Probability level of LMER and GLMER Tukey post hoc tests was $p < 0.05$

Table 12 Sampling design of the study with the sampled sites, applied management factors, factor combinations and factor combination varieties on sites and the number of plots per sites

	Name of sites	Management type	Level of herbage removal intensity	Level of spatio-temporal complexity of management	Factor combination varieties	Number of plots per site
1	Felső	Mown	Low	Medium	1	10
2	Középső	Mown	Low	Medium	1	10
3	Temető	Mown	Low	Medium	1	10
4	Baracs	Mown	Low	Medium	1	10
5	Műtrágy, ősgyep	Mown	Low	Medium	1	10
6	Kunpesztülleg	Grazed	Medium	Medium	2	11
7	Alsópeszéri	Grazed	Medium	Medium	2	10
8	Tengelyúti díflő	Grazed	Medium	Medium	2	10
9	Ordító bejárat	Grazed	High	Low	3	10
10	Égett tüllegelt	Grazed	High	Low	3	10
11	Birkalegelő	Grazed	High	Low	3	10
12	Nagyfaluapós	Grazed	Low	High	4	10
13	Kovács-rét	Grazed	Low	High	4	10
14	Szalai-erdő	Combined	Low	Medium	5	10
15	Égett tanya	Combined	Low	High	6	11
16	Surman tanya	Combined	High	Medium	7	10
17	Libás-erdő	Combined	High	Medium	7	10

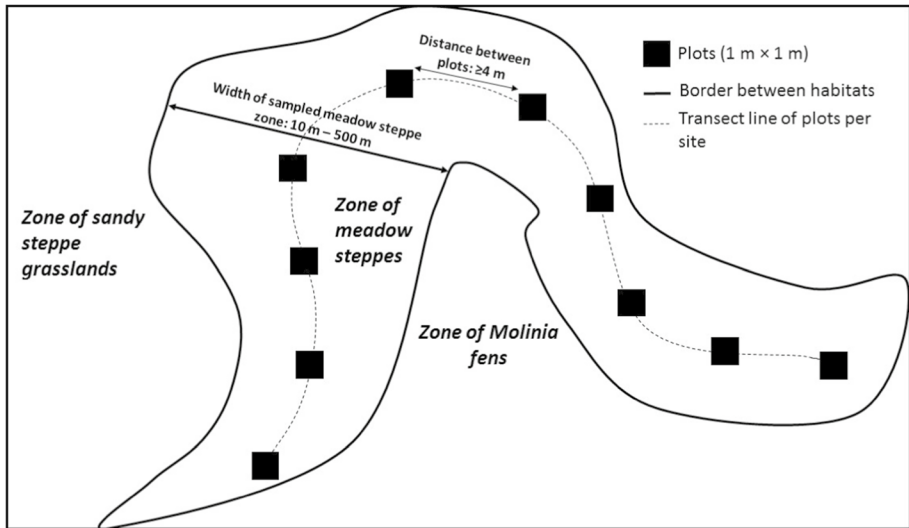


Fig. 3 Sampling protocol of every studied grassland site with the schematic form of transitional meadow steppe zone between *Molinia fens* and sandy steppe grasslands. Form of transect line with 1 m × 1 m plots was fitted to the specific forms of each meadow steppe sites

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Authors and Affiliations

Róbert Kun¹  · Dániel Babai² · András István Csathó³ · Csaba Vadász⁴ · Nikoletta Kálmán⁵ · András Máté⁶ · Ákos Malatinszky¹

¹ Department of Nature Conservation and Landscape Management, Hungarian University of Agriculture and Life Sciences, Páter Károly u. 1, Gödöllő 2100, Hungary

² Research Centre for the Humanities, Institute of Ethnology, Tóth Kálmán u. 4, Budapest 1097, Hungary

³ Körös-Maros National Park Directorate, Anna-liget 1, Szarvas 5540, Hungary

⁴ Kiskunság National Park Directorate, Liszt Ferenc u. 19, Kecskemet 6000, Hungary

⁵ Department of Zoology and Ecology, Hungarian University of Agriculture and Life Sciences, Páter Károly u. 1, Gödöllő 2100, Hungary

⁶ Dorcadion Kft., Kecskemet 6000, Hungary