LIVESTOCK TYPE IS MORE CRUCIAL THAN GRAZING INTENSITY: TRADITIONAL CATTLE AND SHEEP GRAZING IN SHORT-GRASS STEPPES

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ABSTRACT

In biodiversity conservation of agriculture-driven landscapes, grasslands have an outstanding importance; their conservation became a top priority both in research and practice. In many regions, sheep or cattle grazing are the best options for biodiversity conservation. In our study, we compared the effects of cattle and sheep grazing on short-grass steppe vegetation under various grazing intensities. We tested the following study hypotheses: (i) sheep grazing maintains a lower taxonomic and functional diversity, lower amount of forbs compared with cattle grazing; and (ii) the effects of grazing are highly intensity dependent: the differences detected between cattle and sheep grazing are more pronounced at low grazing intensities than at high ones, because the selectivity of grazing decreases at higher intensities. We found lower taxonomic and functional diversity, and lower cover of forbs in sheep-grazed steppes compared with cattle-grazed ones. Grazing intensity had a significant effect only on species richness, while on Shannon diversity and evenness, only livestock type had a significant effect. While most single trait indices were affected by the type of the grazer, significant effect of intensity was detected only in few cases. These findings indicated that the selection of the livestock type is the most crucial in conservation; however, for proper ecosystem functioning and high trait variability, the suitable grazing intensity should also be carefully adjusted. Copyright © 2016 John Wiley & Sons, Ltd.

KEY WORDS: plant trait; grassland; biodiversity conservation; restoration; functional diversity

INTRODUCTION

Traditionally managed landscapes in Europe and also elsewhere are facing a large-scale degradation nowadays, caused by increasing influence of agriculture and/or improper management, often in the form of overgrazing (Bakker & Berendse, 1999, Angassa, 2014, Hu et al., 2015). In conservation of biodiversity in such agriculture-driven landscapes, mesic and dry grasslands have an outstanding importance (WallisdeVries, et al. 1998, Dengler et al., 2014). However, in the last few decades, most of the grasslands were subjected to degradation. This resulted in the loss of important ecosystem functions and services, which had a detrimental effect on sustainable land-use causing degradation and a considerable loss of biodiversity at both local and landscape scales (Tscharntke et al., 2012, Papanastasis et al., 2015, Sutcliffe et al., 2015). Thus, the recovery of local grassland biodiversity became a top priority both in scientific research and practice (Habel et al., 2013). In many areas, biodiversity conservation and management of dry grasslands are feasible by using various forms of grazing management (Dostálek & Frantik, 2008). Selection of the proper grazing livestock and setting the proper intensity are the most crucial points of grassland conservation (Metera et al., 2010). The proper selection of both the type of grazing animal and grazing intensity is especially crucial under dry conditions, where grazing could be one of the driving forces of land degradation and desertification (Cerdà & Lavee, 1999, Palacio et al., 2014, Pulido et al., 2018). For designing management plans, it is very important to know the livestock-specific and intensity-specific effects of grazing on the respective grassland type. Most studies focus on species richness and compositional changes in the vegetation in relation to (i) a single livestock type under various intensity of grazing (mostly grazed and ungrazed; Díaz et al., 2001), (ii) comparing the effects of multiple livestock types by using the same grazing intensity (Dumont et al., 2011) or (iii) studying the effect of a single livestock type and grazing intensity on the composition and diversity of multiple grassland types (Török et al., 2014).

Beyond the analyses of species diversity and composition, functional trait-based approaches became increasingly involved in analysing and explaining the effects of grazing in grassland ecosystems (Teuber et al., 2013; Kechang et al., 2015; Komac et al., 2015). Trait-based functional approaches can help to reveal the underlying mechanisms and support to sustain diversity and related ecosystem functions (Villéger et al., 2008, Carmona et al., 2012). It was proven that grazing has very specific effects on plant traits, which are difficult to generalise for a global scale (Díaz et al., 2001). For example, functional responses are strongly linked to the type of the grazing animal (i.e. selectivity) and the affected habitat type (i.e. productivity and related abiotic

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factors) (Peco et al., 2012). These facts underline the necessity of fine-scale analyses of functional characteristics of grasslands in relation to grazing.

The response of plant communities can be highly variable regarding the grazing intensity; however, most studies provided only grazed and ungrazed sites for comparison (Díaz et al., 2007, Overbeck, 2014, Tarhouni et al., 2015). In general, in habitats with high productivity increased intensity of grazing supports species diversity by suppressing the dominant competitor species and providing gaps in the dense vegetation cover for the establishment of subordinated species (mostly short-lived and/or dicot species, Bullock et al., 2001). In habitats with low productivity, it was found that increased intensity of grazing can be detrimental to species richness by eliminating scattered populations of palatable species (Lezama et al., 2014). The responses at the species and trait levels cannot be easily generalised, and it was suggested that for evaluating the intensity dependent effects of grazing case studies operating with multiple grazing levels and livestock types should be implemented (Bullock et al., 2001, Overbeck, 2014).

In spite of the widespread use of cattle and sheep grazing in the maintenance and conservation of grasslands in Europe, there is a considerable lack of knowledge, especially concerning the effects of grazing on functional attributes of grassland vegetation (Ausden et al., 2005, Dumont et al., 2011). The differences between sheep and



Figure 1. Geographical location of the study sites. [Colour figure can be viewed at wileyonlinelibrary.com]

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intensities (Cornelissen & Vulink, 2015). MATERIAL AND METHODS Characteristics of the Study Area and Sites The study area is situated in the Hortobágy National Park (Hungary) near to villages Egyek, Kunmadaras, Pürpökladány Haidúszoboszló Balmazújváros and

cattle grazing and their effects on vegetation was

summarised by Rook et al. (2004), Metera et al. (2010)

and Jerrentrup et al. (2015). It was indicated that the effect

of cattle and sheep grazing could be different on the vegeta-

tion characteristics because of (i) the different body size, (ii)

grazing height, (iii) foraging strategy and selectivity of the

two livestock types. However, studies focusing on multiple

types of livestock and intensity in relation with the func-

tional plant attributes are still scarce (but see Klimešová

et al., 2008, de Bello et al., 2006, Jerrentrup et al., 2015).

This comparison would be especially crucial in grasslands

where multiple options for grazing livestock types and inten-

cattle and sheep grazing on the vegetation of short-grass

steppes under different grazing intensities. Based on former

assumptions, we set the following study hypotheses: (i)

sheep grazing maintains a lower taxonomic and functional

diversity, lower amount of forbs compared with cattle

grazing (Pykälä, 2005, Jerrentrup et al., 2015); and (ii) the

effects of grazing are highly intensity-dependent: the differ-

ences detected between cattle and sheep grazing are more

pronounced at low grazing intensities than at high ones,

because the selectivity of grazing decreases at higher

In the present study, we aimed to compare the effect of

sities are available for conservation and management.

Püspökladány, Hajdúszoboszló, Balmazújváros and Hortobágy within a radius of 35 km (Figure 1). The climate of the area is moderately continental; the mean annual temperature is 9.5 °C, and the mean annual precipitation is of 550 mm. The yearly maximum of precipitation is in June with a mean of 80 mm characterised by high year-to-year fluctuations (Lukács et al., 2015). The weather of the year before the study (2013) was characterised by generally higher precipitation and temperature than the climatic average, but very high fluctuations were typical for the whole year. The spring of 2014 was warm but humid compared with the average (Hungarian Meteorological Service, 2015), which circumstances enabled for most characteristic short-lived species to establish successfully. The research area is flat and characterised by small wet depressions and a small-scale microtopographic heterogeneity (Deák et al., 2014 and Deák et al., 2015).

Short-grass steppes are generally used as pastures, grazed by cattle or sheep, and are characterised by high cover of fescue (up to a cover of 70% *Festuca pseudovina*). The selected steppes are generally species poor, the species pool is limited. Short-grass steppes are frequently moist in springtime and become dry in early summer (Kelemen et al., 2013). The soil of short-grass steppes is clayey, characterised by low organic matter content and low to medium salinity in the upper soil layers (Valkó et al., 2014). In the vegetation, the characteristic species subordinated to *F. pseudovina* are *Artemisia santonicum*, *Achillea setacea*, *A. collina*, *Gypsophila muralis*, *Trifolium angulatum*, *T. striatum*, *T. retusum*, *Carex stenophylla*, *Podospermum canum*, *Plantago lanceolata*, *Inula britannica*, *Bupleurum tenuissimum*, *Limonium gmelinii* subsp. *hungarica*. In some heavily grazed stands *Bromus mollis*, *Matricaria inodora*, *Polygonum aviculare*, *Cynodon dactylon* or *Elymus repens* can be frequent (more details see Török et al., 2011 and Deák et al., 2014).

We studied the effect of low to medium, and high intensity sheep and cattle grazing on vegetation characteristics of short-grass steppes, in Hungary. We selected altogether 28 grazed short-grass steppe stands (i.e. management units) in the study region at the high vertical position in the steppe landscape grazed by both type of grazers (sheep or cattle). The levels of grazing intensity corresponded to the typical grazing regimes applied in the region (Török et al., 2016a). For low to medium, the level of grazing intensity was 0.5-1.5 animal unit/ha, and for the high level of 2.5-3.0animal unit/ha, respectively (the grazing intensity was similar to the last five consecutive years before the study). The steppes were grazed by sheep (13 steppes, 5 low to medium and 8 high grazing intensity) or Hungarian grey cattle (15 steppes, 10 low to medium and 5 high grazing intensity). The grazing histories of the sites were documented by the Hortobágy National Park authorities; they also helped us to minimise the effect of site history differences by selecting the most typical sites for comparison. We recorded the cover of vascular plant species in ten 2×2 -m-sized plots evenly distributed in a typical 1-ha-large area in each steppe, in late May 2014 (altogether 280 plots, near to the peak of biomass production in this type of grassland habitats; Kelemen et al., 2013). The site heterogeneity was not measured, but because of the limited species pool and regional sampling these types of steppes were quite similar to each other. The site selection was influenced only by the pattern of short-grass steppe patches. This type of vegetation can be easily identified in the field and can be also easily distinguished from other rather tall-growing vegetation types (i.e. loess grassland patches, alkali meadows or marsh vegetation) or from very open alkali grasslands dominated mostly by halophytes. We included only patches with short-grass steppe vegetation. Depressions with hygrophytes and patches with other vegetation types (including loess grasslands) were avoided in sampling.

Data Collection and Analyses

Data were obtained from the regional identification book (Király, 2009) for the simplified life form groups (shortlived and perennial forbs and graminoids), start of flowering (starting month) and total flowering period (in months), rosette forming (yes/no) and for specific plant heights. For the lateral clonal spreading ability, we used the CLO-PLA database (Klimešová & de Bello, 2009); species were classified into four ordinal categories based on potential distance of clonal spreading (m/year): first—no clonal spreading,

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second—<0.01 m/year, third—0.01-0.25 m/year, and fourth—>0.25 m/year (based on the classification used by Kelemen et al. 2015). Leaf traits: leaf dry matter content (LDMC), leaf dry weight (LDW), specific leaf area (SLA) and leaf area (LA) were obtained either from LEDA trait base (Kleyer et al., 2008) or we used own measurements obtained by using standardised measurement protocols (Cornelissen et al., 2003). We also classified the species as 'legume' and 'non legume' species groups for the analyses. For the seed weights, we used a local database (published in Török et al., 2013 and Török et al., 2016b).

To evaluate vegetation response to grazing, we calculated species richness, Shannon diversity and evenness scores for each plot. Multi-trait Rao's quadratic entropy, functional divergence and evenness were calculated using cover weighted quantitative traits (flowering period, flowering start, specific plant height, LDMC, LDW, SLA, LA and seed weight) (Pla et al., 2012). We also calculated community weighted means (CWM) for all studied traits, and functional divergence for each single trait. For the calculation of all of the indices, we used FDiversity programme package; in calculations, we used for weighting Euclidean distances calculated using cover scores (Casanoves et al., 2011). We compared the vegetation characteristics of steppes with different grazing intensity using two-way univariate Generalised Linear Models (GLMs) where grazing 'intensity' and identity of 'grazing livestock' were included as fixed factors. To control the habitat heterogeneity and species composition/dominance differences between the studied steppes, we included 'steppe' as a random weighting factor into the analyses to control the site dependent effects. GLM analyses were executed by using SPSS 17.0 program package (SPSS Inc. Released 2008. SPSS Statistics for Windows, Version 17.0. Chicago: SPSS Inc.).

RESULTS

Vegetation Composition

We found 107 species in the 280 plots with a typical number of 8-15 species per plot. Out of this, 8 species were short-lived graminoids, 53 short-lived forbs; 15 species were perennial graminoids, and 31 species perennial forbs. Species richness was lower in the sheep-grazed plots compared with cattle-grazed ones; however, the species richness decreased with increased grazing intensity regardless of the type of the grazer (Table I, Figure 2a). Shannon diversity and evenness scores were affected only by the type of grazer, not by the grazing intensity (Table I, Figure 2b and c); lower scores were typical in sheep-grazed plots. The cover of short-lived graminoids decreased with increased grazing intensity of cattle, and decreased in case of sheep. The cover of forbs (both perennial and short-lived) was lower in sheep-grazed plots than in cattle-grazed ones regardless to the grazing intensity (Table I, Figure 2e and g). A significantly lower cover of legume species was typical in sheep-grazed plots compared with cattle-grazed ones (Table I, Figure 2h).

	Intensity		Grazing livestock		Intensity × Grazing livestock	
Characteristic	р	F	р	F	р	F
Species richness	0.001	10.533	<0.001	16.167	0.647	0.211
Shannon diversity	0.48	0.500	<0.001	75.539	0.330	0.952
Evenness	0.237	1.406	<0.001	73.584	0.443	0.590
Cover of short-lived graminoids	0.031	4.701	0.559	0.342	0.019	5.548
Cover of short-lived forbs	0.141	2.181	<0.001	53.597	0.019	5.583
Cover of perennial graminoids	0.691	0.158	0.116	2.482	0.128	2.327
Cover of perennial forbs	<0.001	21.52	0.024	5.179	0.934	0.007
Cover of legume species	0.232	1.434	< 0.001	32.320	0.929	0.008

Table I. Effect of livestock type and grazing intensity on vegetation characteristics of short-grass steppes

Significant differences obtained by univariate GLM, all scores were calculated by cover weighting.

Functional Trait Indices

The multi-trait functional diversity expressed by Rao's quadratic entropy was significantly higher in cattle-grazed plots than in sheep-grazed ones and was not affected by the grazing intensity. In contrast, the functional evenness was affected only by the grazing intensity, and significantly

lower scores were typical at the lower grazing intensities (Tables II and III). The multi-trait functional divergence was also affected by grazing intensity; however, different trends were detected for sheep and cattle. For sheep, the functional divergence decreased, while for cattle increased with increasing grazing intensity (Tables II and III). In case of single trait indices, most of the CWM and single-trait



Figure 2. Vegetation characteristics of sheep and cattle-grazed short-grass steppes. [Colour figure can be viewed at wileyonlinelibrary.com]

	Intensity		Livestock		Intensity × Livestock	
Characteristic	р	F	р	F	р	F
Multitrait indices						
Rao's quadratic entropy	0.201	1.640	0.004	8.264	0.423	0.645
Functional evenness	0.009	6.965	0.889	0.020	0.130	2.309
Functional divergence	0.044	4.079	0.156	2.027	<0.001	22.340
Single trait indices						
Community weighted mean (CWM)						
Flowering period	0.926	0.009	<0.001	23.338	0.089	2.914
Flowering start	0.053	3.782	<0.001	13.419	0.003	8.853
Specific plant height	0.313	1.021	0.835	0.043	0.248	1.341
LDMC	0.488	0.482	<0.001	20.450	0.790	0.071
LDW	0.012	6.416	<0.001	30.068	0.121	2.413
SLA	0.353	0.864	<0.001	27.372	0.986	0.001
LA	0.399	0.714	<0.001	32.070	0.871	0.026
Seed Weight	0.013	6.241	<0.001	48.744	0.015	5.993
Clonal spreading	0.757	0.096	0.601	0.273	0.262	1.266
Rosette forming	0.468	0.528	<0.001	17.507	0.191	1.720
Functional divergence ^a						
Flowering period	0.459	0.550	<0.001	15.84	0.209	1.587
Flowering start	0.454	0.561	0.232	1.43	0.177	1.825
Specific plant height	<0.001	31.854	<0.001	75.73	0.004	8.447
LDMC	0.035	4.480	<0.001	13.94	0.018	5.633
LDW	0.104	2.667	<0.001	76.76	0.138	2.212
SLA	0.237	1.407	0.003	9.09	0.066	3.417
LA	0.559	0.343	<0.001	76.20	0.305	1.057
Seed Weight	<0.001	14.245	<0.001	81.47	0.238	1.400

Table II. Functional trait characteristics of short-grass steppes grazed with different livestock and intensity

^aValues are calculated using only quantitative traits (see these traits in single-trait functional divergence).

Significant differences obtained by univariate GLM.

functional divergence was affected by the type of the grazer (except for CWM of specific plant height, clonal spreading ability and functional divergence of flowering start), while significant effect of intensity was detected only in few cases. For sheep grazing lower CWM scores of flowering period, flowering start, seed weight, lower LDW, LA and SLA, and higher LDMC were typical compared with cattle grazing. While the CWM of specific plant height was not affected neither by the type of grazer nor by the intensity, the functional divergence of this trait was significantly higher in cattle-grazed plots. For five quantitative traits (flowering period, SLA, LDW, LA and seed weight), the functional divergence showed the same patterns as in case of CWMs (Table III). For sheep grazing, the CWM of LDMC was higher, while functional divergence of LDMC was lower than in cattle-grazed plots. Neither the grazing intensity nor the livestock type affected the clonal spreading ability, while the rosette forming was affected regardless of intensity by the livestock type and higher scores were typical in sheep-grazed steppes (Tables II and III).

DISCUSSION

Effect of Livestock Type on Diversity and Trait Composition Based on the former findings, we assumed that in the studied steppes, sheep grazing provides lower taxonomic and

lower specific plant heights in comparison with cattle grazing (Pykälä, 2005, Jerrentrup et al., 2015). Almost all of these assumptions were clearly confirmed by our findings. In accordance with some former studies (Rook et al., 2004, Sebastià et al., 2008 and Jerrentrup et al., 2015), we found lower taxonomic and functional diversity in sheep-grazed steppes compared with cattle-grazed ones. It was found by Dumont et al. (2011) and also by Sebastià et al. (2008) that sheep grazing has a higher level of selectivity for forbs (and also for legumes, Nolan et al., 2001). These findings were also supported by the present study. The cover of both short-lived and perennial forbs was significantly lower in sheep-grazed plots than in cattle-grazed ones, and the same trend was also valid for legume cover (Table I, Figure 2e and g). The gut capacity of sheep is much lower than that of cattle; thus, to provide the energy required, they select for plants with easier digestibility and/or higher nutrient contents (Rook et al., 2004). The lower selectivity of cattle for forbs can be explained by the findings of Török et al. (2014), where it was demonstrated that cattle is likely opt for patches with higher biomass than for certain species. In addition, the two livestock types have a different feeding strategy reviewed by Jerrentrup et al. (2015): sheep are biting single plants with their incisors close to the ground (Rook et al., 2004), but cattle wrap the plant biomass by their tongue. In latter case, the feeding is less selective for

functional richness and also lower amount of forbs and

Table III. Functional traits of short-grass steppes grazed with unrefent investock and intensity	Table III.	Functional traits of	of short-grass steppes	grazed with different	livestock and intensity.
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	Grazing intensity					
	Low to	moderate	High			
Characteristic	Sheep	Cattle	Sheep	Cattle		
Multitrait indices						
Rao's quadratic entropy	$426,836 \pm 2,450,160$	$2,030,700 \pm 10,148,900$	$218,472 \pm 1,130,120$	$1,122,000 \pm 4,779,110$		
Functional evenness	0.34 ± 0.25	0.31 ± 0.32	0.36 ± 0.34	0.39 ± 0.27		
Functional divergence	0.71 ± 0.23	0.60 ± 0.26	0.66 ± 0.30	0.72 ± 0.22		
Single trait indices						
Community weighted means						
Flowering period (months)	2.73 ± 0.84	2.90 ± 0.95	2.63 ± 0.78	2.99 ± 0.59		
Flowering start (month)	5.43 ± 0.66	5.46 ± 0.60	5.24 ± 0.52	5.50 ± 0.65		
Specific plant height (cm)	36.38 ± 4.57	35.47 ± 13.74	34.93 ± 5.84	35.56 ± 10.03		
LDMC (mg \times g ⁻¹)	273.96 ± 45.23	25.60 ± 58.50	277.42 ± 58.39	260.14 ± 43.74		
LDW (g)	10.73 ± 20.33	28.61 ± 57.67	8.24 ± 14.90	18.23 ± 24.97		
SLA $(mm^2 \times g^{-1})$	14.57 ± 4.72	16.06 ± 5.06	14.30 ± 3.60	15.80 ± 2.62		
$LA (mm^2)$	203.82 ± 420.47	43135 ± 849.54	162.15 ± 373.78	403.13 ± 538.54		
Seed Weight (mg)	0.40 ± 0.65	0.65 ± 0.86	0.41 ± 0.40	0.93 ± 1.31		
Clonal spreading (1 to 4)	2.27 ± 0.40	2.21 ± 0.66	2.22 ± 0.56	2.24 ± 0.53		
Rosette forming (0 or 1, %)	0.66 ± 0.33	0.58 ± 0.44	0.71 ± 0.37	0.57 ± 0.34		
Functional divergence*						
Flowering period	0.28 ± 0.22	0.32 ± 0.22	0.25 ± 0.22	0.33 ± 0.12		
Flowering start	0.06 ± 0.07	0.07 ± 0.09	0.06 ± 0.08	0.06 ± 0.05		
Specific plant height	0.20 ± 0.23	0.32 ± 0.35	0.26 ± 0.31	0.49 ± 0.25		
LDMC	0.19 ± 0.11	0.28 ± 0.32	0.19 ± 0.15	0.21 ± 0.11		
LDW	0.65 ± 0.47	0.88 ± 0.21	0.72 ± 0.43	0.88 ± 0.12		
SLA	0.22 ± 0.20	0.28 ± 0.20	0.23 ± 0.20	0.24 ± 0.15		
LA	0.69 ± 0.44	0.90 ± 0.18	0.72 ± 0.43	0.89 ± 0.16		
Seed Weight	0.74 ± 0.31	0.88 ± 0.14	0.81 ± 0.23	0.92 ± 0.09		

^aValues are calculated using only quantitative traits (see these traits in single-trait functional divergence).

All scores were calculated by cover weighting (mean \pm SD).

respective species or individuals and effective only in high vegetation (Pykälä, 2005). This distinctive grazing strategy is also supported by our results in terms of rosette forming: regardless to intensity the cover of rosette forming species was significantly higher in sheep-grazed plots than in cattle-grazed ones.

In our study, neither the livestock type nor the intensity had an effect on the cover of perennial graminoids. A possible explanation could be that dominant plants in stressed habitats are highly adapted to abiotic stress, resource competition and have the ability to form strong and deep root system and tussock-form canopy structure, which make them also highly resistant to grazing (Osem et al., 2002, Lezama et al., 2014, Kelemen et al., 2015). This phenomenon also could be partly explained by the habitat dependent strategy shift between maximising for forage quality and maximising intake strategy of sheep grazing stressed by Mladek et al. (2013). However, it also should be taken in account that several studies indicated that sheep grazing can be highly selective for forbs (see details for example in Jerrentrup et al., 2015). It means that the foraging strategy of sheep shifts between the two mentioned contrasting feeding strategies, which also affects their selectivity. The selectivity is also influenced by the species composition of the habitats (i.e. by different assemblages of traits), which could be remarkably different and can cause a high

selectivity towards forbs even in case of maximising intake strategy. In sheep-grazed steppes, we found a much lower multi-trait functional diversity expressed by Rao's quadratic entropy, regardless to intensity. This means that mostly forb species vanish from the vegetation because of the highly selective sheep grazing. Therefore, the species pool of sheepgrazed steppes contains species with more similar functional traits than the cattle-grazed ones. These findings in livestock type dependent selectivity were also stressed by de Bello et al. (2006).

For specific plant height, our results seemingly not confirmed the hypothesis, because the CWM of specific plant height was influenced neither by the grazing intensity nor by the livestock type. However, the functional divergence was lower in sheep-grazed plots than in cattle-grazed ones. This means, that higher variability of specific plant heights can be expected in case of cattle grazing than in sheep grazing, which is well in accordance with our expectation. The most likely explanation for the above-mentioned phenomenon could be differences in the selectivity of the two livestock types for fobs. Most of the variance in plant height in the studied steppes is due to the forb species. Because the sheep are highly selective for forbs and validated also by the current study and Jerrentrup et al. (2015), they decreased the cover of both the tall and short forbs, thus decreased the functional divergence but not the CWM.

The much higher selectivity of sheep compared with cattle was also validated by the single trait analyses. It was found that in sheep-grazed plots lower LDW, lower LA and SLA was detected, and the LDMC was higher than in cattle-grazed plots. The lower LA and SLA means that sheep was more selective for species with large, soft and thin leaves with lower amount of stiffening tissues (Vesk et al., 2004, Westoby, 1999) compared with cattle, which are normally more generalist in their diet selection (Rook et al., 2004). These results are also well in line with that the sheep were highly selective for forb species, especially for legume species. It was found by Mladek et al. (2013) that sheep grazing affected in higher magnitude the late flowering grasses than the early flowering ones. The late flowering species provide a higher forage quality for longer period (typically until the flowering) than the early flowering ones. In line with these findings, we found that in sheepgrazed plots, both the means of the flowering period and flowering start of species were lower compared with cattlegrazed ones. It means that sheep grazing was selective to

the late and/or longer flowering plants compared with cattle.

Intensity Dependent Effects of Grazing

Previous research have found that low-intensity extensive grazing had a positive effect, while high intensity grazing had a negative effect on grassland diversity (Fischer & Wipf, 2002, Metera et al., 2010). There were many, mostly single livestock-type studies, where intensity dependent effects of grazing was found for life forms (proportion/cover of annual species increases, while perennials decreases with increasing intensity, Klimešová et al., 2008, Díaz et al., 2001), plant height (lower with the increasing grazing intensity, Díaz et al., 2001, Klimešová et al., 2008), leaf size (LA or LDW, lower with increasing intensity; Díaz et al., 2001, Cruz et al., 2010), SLA (depends both on intensity and diet selectivity, in some cases increasing with increasing intensity; Vesk et al., 2004, Westoby, 1999, in other decreasing; Cruz et al., 2010), LDMC (decreasing with intensity, as a consequence of decreasing selectivity of grazing; Cruz et al., 2010), flowering period (longer with increasing intensity; de Bello et al., 2005), rosette forming (higher with the increasing intensity; de Bello et al., 2006, Klimešová et al., 2008), or for seed weights (Vesk et al., 2004). Grazing intensity had a significant effect only on species richness, while on diversity measures (Shannon diversity and evenness) exclusively the livestock type had a significant effect. Most single-trait indices were affected by the type of the grazer, while significant effect of intensity was detected only in few cases. Quite similar findings for leaf traits (LDMC and LA; Golodets et al., 2009) and belowground bud bank (Qian et al., 2014) were reported, where no significant correlations were detected between grazing intensity and abovementioned traits. In our study, the most likely reason for this contradiction could be that the effect of livestock type overrides the effects of intensity in the studied short-grass steppes. Small differences between the means was mostly occurred for the effect of intensity (Table II), and in these cases, the effect of intensity was not significant. In case of the livestock type, the detected differences were between the means ranged typically (in case of significant differences) from at least 10% to more than 100%.

In most cases, one year would not be enough to evaluate changes in vegetation caused by grazing. But there were several circumstances in our study, which all increased the predictive value of the results: (i) the grazing was not started in the year of monitoring, we selected such sites where the grazing management was similar to at least five consecutive years (with quite similar intensity and the same livestock type); and (ii) the warm and humid spring of 2014 enabled most of the short-lived species (generally with low and fluctuating success in establishment because of harsh conditions) to establish successfully in the sites. Thus, differences between their scores in sites were influenced rather by grazing animal or intensity than by abiotic establishment limitations. (iii) The vegetation sampling was done near to the peak of biomass production (Kelemen et al. 2013).

With increasing grazing intensity, we found an increasing functional evenness in steppes regardless of livestock type. The most likely explanation of this phenomenon is that with increasing grazing intensity some subordinate species vanished, which phenomenon resulted in a lower variability in the cover of constituting species. We found that the functional divergence was affected by the grazing intensity but showed an opposite trend in sheep and cattle-grazed steppes (Tables II and III). The high functional divergence in a stable community means a higher rate of utilisation of available niche space and thus, enables high ecosystem stability and stable ecosystem functioning (Mason et al., 2005). The reason for the intensity-dependent decrease of functional divergence in case of sheep can be explained by the highly selective grazing of sheep compared with cattle, which is much more marked at higher intensity (at least in the case of functional divergence)-somewhat in contrast with our second study hypothesis. The likely explanation of intensity dependent increase of functional divergence in case of cattle grazing could be the higher cattle mediated endozoochorous seed dispersal, which enabled together with the fact that cattle avoids grazing near to its dung pats (Jerrentrup et al., 2015) the establishment of several shortlived weedy forbs (see also Table I). This also broadened the plant trait spectrum of steppes causing an increased species richness and functional divergence.

CONCLUSIONS

Our results suggest that cattle grazing creates a more speciesrich and trait-rich vegetation with higher cover of forbs compared with sheep grazing. However, sheep grazing would be a much better choice to suppress forbs, including weedy ones, than cattle grazing. Our findings clearly indicate that most of the studied characteristics were significantly affected by the type of grazer (i.e. cattle or sheep grazing), while fewer intensity-dependent effects were confirmed. These findings suggest that the selection of the livestock type is more crucial in biodiversity conservation and management than the adjustment of grazing intensity, but for the optimal ecosystem functioning and for highest variability of traits, the proper grazing intensity should be also carefully set and fine tuned in respect of the habitat type and grazing animal.

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REFERENCES

- Angassa A. 2014. Effects of grazing intensity and bush encroachment on herbaceous species and rangeland condition in Southern Ethiopia. *Land Degradation & Development* **25**: 438–451. DOI:10.1002/ldr.2160.
- Ausden M, Hall M, Pearson P, Strudwick T. 2005. The effects of cattle grazing on tall-herb fen vegetation and molluscs. *Biological Conservation* 122: 317–326.
- Bakker JP, Berendse F. 1999. Constraints in the restoration of ecological diversity in grassland and heathland communities. *Trends in Ecology* and Evolution 14: 63–68.
- Bullock JM, Franklin J, Stevenson MJ, Silvertown J, Coulson SJ, Gregory SJ, Tofts R. 2001. A plant trait analysis of responses to grazing in a longterm experiment. *Journal of Applied Ecology* 38: 253–267.
- Carmona CP, Azcárate FM, de Bello F, Ollero HS, Lepš J, Peco B. 2012. Taxonomical and functional diversity turnover in Mediterranean grasslands: interactions between grazing, habitat type and rainfall. *Journal of Applied Ecology* **49**: 1084–1093.
- Casanoves F, Pla L, Di Rienzo JA, Díaz S. 2011. FDiversity: a software package for the integrated analysis of functional diversity. *Methods in Ecology and Evolution* **2**: 233–237.
- Cerdà A, Lavee H. 1999. The effect of grazing on soil and water losses under arid and mediterranean climates. *Implications for desertification*. *Pirineos* 153-154: 159–174.
- Cornelissen JHC, Lavoral S, Garnier E, Diaz S, Buchmann N, Gurvich DE, Reich PB, ter Steege H, Morgan HD, van der Heijden MGA, Pausas JG, Poorter H. 2003. A handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany* **51**: 335–380.
- Cornelissen P, Vulink JT. 2015. Density-dependent diet selection and body condition of cattle and horses in heterogeneous landscapes. *Applied Animal Behaviour Science* **163**: 28–38.
- Cruz P, De Quadros FLF, Theau JP, Frizzo A, Jouany C, Duru M, Carvalho PCF. 2010. Leaf traits as functional descriptors of the intensity of continuous grazing in native grasslands in the south of Brazil. *Rangeland Ecology and Management* 63: 350–358.
- de Bello F, Lepš J, Sebastià M-T. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology* **42**: 824–833.

- de Bello F, Lepš J, Sebastià M-T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. *Ecography* 29: 801–810.
- Deák B, Valkó O, Alexander C, Mücke W, Kania A, Tamás J, Heilmeier H. 2014. Fine-scale vertical position as an indicator of vegetation in alkali grasslands—case study based on remotely sensed data. *Flora* 209: 693–697.
- Deák B, Valkó O, Török P, Kelemen A, Miglécz T, Sz S, Szabó G, Tóthmérész B. 2015. Micro-topographic heterogeneity supports plant diversity: fine-scale patterns and age effect. *Basic and Applied Ecology* 16: 291–299.
- Dengler J, Janisová M, Török P, Wellstein C. 2014. Biodiversity of Palaearctic grasslands: a synthesis. Agriculture, Ecosystems & Environment 182: 1–14.
- Díaz S, Noy-Meir I, Cabido M. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38: 497–508.
- Dostálek J, Frantík T. 2008. Dry grassland plant diversity conservation using low-intensity sheep and goat grazing management: case study in Prague (Czech Republic). *Biodiversity and Conservation* 17: 1439–1454.
- Dumont B, Carrère P, Ginane C, Faruggia A, Lanore L, Tardif A, Decuq F, Darsonville O, Louault F. 2011. Plant-herbivore interactions affect the initial direction of community changes in an ecosystem manipulation experiment. *Basic and Applied Ecology* **12**: 187–194.
- Fischer M, Wipf S. 2002. Effect of low-intensity grazing on the species-rich vegetation of traditionally mown subalpine meadows. *Biological Conservation* **104**: 1–11.
- Golodets C, Sternberg M, Kiegel J. 2009. A community-level test of the leaf-height-seed ecology strategy scheme in relation to grazing conditions. *Journal of Vegetation Science* **20**: 392–402.
- Habel JC, Dengler J, Janišová M, Török P, Wellstein C, Wiezik M. 2013. European grassland ecosystems: threatened hotspots of biodiversity. *Biodiversity & Conservation* 22: 2131–2138.
- Hu G, Liu H, Yin Y, Song Z. 2015. The roles of legumes in plant community succession of degraded grasslands in Northern China. Land Degradation and Development. DOI:10.1002/ldr.2382.
- Hungarian Meteorological Service. 2015. The weather of last few years (2001-2014) (in Hungarian). Webpage link:http://met.hu/eghajlat/magyarorszag_eghajlata/eghajlati_visszatekinto/elmult_evek_idojarasa/
- Jerrentrup JS, Seither M, Petersen U, Isselstein J. 2015. Little grazer species effect on the vegetation in a rotational grazing system. Agriculture, Ecosystems & Environment 202: 243–250.
- Király G (ed). 2009. New Hungarian Herbal. The Vascular Plants of Hungary. Identification keys. Aggtelek National Park Directorate: Jósvafő.
- Kleyer M, Bekker RM, Knevel IC, Bakker JP, Thompson K, Sonnenschein M, Poschlod P, Van Groenendael JM, Klimeš L, Klimešová J, Klotz S, Rusch GM, Hermy M, Adriaens D, Boedeltje G, Bossuyt B, Dannemann A, Endels P, Götzenberger L, Hodgson JG, Jackel A-K, Kühn I, Kunzmann D, Ozinga WA, Römermann C, Stadler M, Schlegelmilch J, Steendam HJ, Tackenberg O, Wilmann B, Cornelissen JHC, Eriksson O, Garnier E, Peco B. 2008. The LEDA traitbase: a database of life-history traits of Northwest European flora. *Journal of Ecology* **96**: 1266–1274.
- Klimešová J, Latzel V, de Bello F, Groenendael JM. 2008. Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits. *Preslia* **80**: 245–253.
- Klimešová J, de Bello F. 2009. CLO-PLA: the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science* **20**: 511–516.
- Kechang N, He J-H, Zhang S, Lechowicz MJ. 2015. Grazing increases functional richness but not functional divergence in Tibetan alpine meadow plant communities. *Biodiversity & Conservation*. DOI:10.1007/s10531-015-0960-2.
- Kelemen A, Török P, Valkó O, Miglécz T, Tóthmérész B. 2013. Mechanisms shaping plant biomass and species richness: plant strategies and litter effect in alkali and loess grasslands. *Journal of Vegetation Science* 24: 1195–1203.
- Kelemen A, Török P, Valkó O, Deák B, Tóth K, Tóthmérész B. 2015. Both facilitation and limiting similarity shape the species coexistence in dry alkali grasslands. *Ecological Complexity* 21: 34–38.
- Komac B, Pladevall C, Domènech M, Fanlo R. 2015. Functional diversity and grazing intensity in sub-alpine and alpine grasslands in Andorra. *Applied Vegetation Science* 18: 75–85.

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- Lezama F, Baeza S, Altesor A, Cesa A, Chaneton EJ, Paruelo JM. 2014. Variation of grazing-induced vegetation changes across a large-scale productivity gradient. *Journal of Vegetation Science* 25: 8–21.
- Lukács BA, Török P, Kelemen A, Várbíró G, Radócz S, Takács S, Miglécz T, Tóthmérész B, Valkó O. 2015. Rainfall fluctuations and vegetation patterns in alkali grasslands – Self-organizing maps in vegetation analysis. *Tuexenia* 35: 381–397.
- Mason NWH, Muillot D, Lee WG, Wilson JB. 2005. Functional richness, functional evenness and functional divergence: the primary components of functional diversity. *Oikos* 111: 112–118.
- Metera E, Sakowski T, Słoniewski K, Romanowicz B. 2010. Grazing as a tool to maintain biodiversity of grassland a review. *Animal Science Papers and Reports* **28**: 315–334.
- Mladek J, Mládková P, Hejcmanová P, Dvorský M, Pavlu V, de Bello F, Duchoslav M, Hejcman M, Pakeman R. 2013. Plant trait assembly affects superiority of Grazer's foraging strategies in species-rich grasslands. *PLoS One* 8: e69800.
- Nolan T, Conolly J, Wachendorf M. 2001. Mixed grazing and climatic determinants of white clover (*Trifolium repens* L.) content in a permanent pasture. *Annals of Botany* 88: 713–724.
- Osem Y, Perevolotsky A, Kigel J. 2002. Grazing effects on diversity of annual plant communities in a semi-arid rangeland: interactions with small-scale spatial and temporal variation in primary productivity. *Journal of Ecology* **90**: 936–946.
- Overbeck GE. 2014. The effects of grazing depend on productivity, and what else? *Journal of Vegetation Science* 24: 6–7.
- Palacio RG, Bisigato AJ, Bouza PJ. 2014. Soil erosion in three grazed plant communities in Northeastern Patagonia. *Land Degradation and Development* 25: 594–603. DOI:10.1002/ldr.2289.
- Papanastasis VP, Bautista S, Chouvardas D, Mantzanas K, Papadimitriou M, Mayor AG, Koukioumi P, Papaioannou A, Vallejo RV. 2015. Comparative assessment of goods and services provided by grazing regulation and reforestation in degraded Mediterranean rangelands. *Land Degradation and Development DOI*. DOI:10.1002/ldr.2368.
- Peco B, Carmona CP, de Pablos I, Azcárate FM. 2012. Effects of grazing abandonment on functional and taxonomic diversity of Mediterranean grasslands. Agriculture, Ecosystems and Environment 152: 27–32.
- Pla L, Casanoves F, Di Rienzo J. 2012. Quantifying Functional Biodiversity. Springer: Berlin.
- Pulido M, Schnabel S, Lavado Contador JF, Lozano-Parra J, González F. 2018. The impact of heavy grazing on soil quality and pasture production in rangelands of SW Spain. *Land Degradation and Development* 29: 219–230. https://doi.org/10.1002/ldr.2501.
- Pykäla J. 2005. Plant species responses to cattle grazing in mesic semi-natural grassland. Agriculture, Ecosystems and Environment 108: 109–117.
- Qian J, Wang Z, Liu Z, Busso CA. 2014. Belowground bud bank responses to grazing intensity in the inner-mongolia steppe. *China. Land Degradation and Development*. DOI:10.1002/ldr.2300.
- Rook AJ, Dumont B, Isselstein J, Osoro K, WallisdeVries MF, Parente G, Mills J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. *Biological Conservation* 119: 137–150.
- Sebastià M-T, de Bello F, Puig L, Taull M. 2008. Grazing as a factor structuring grasslands in the Pyrenees. *Applied Vegetation Science* **11**: 215–222.
- Sutcliffe LME, Batáry P, Kormann U, Báldi A, Dicks LV, Herzon I, Kleijn D, Tryjanowski P, Apostolova I, Arlettaz R, Aunins A, Aviron A,

Baležentiene L, Čierna-Plassmann M, Fischer C, Gabrielová J, Halada L, Hartel T, Helm A, Hristov I, Jelaska SD, Kaligarič M, Kamp J, Klimek S, Koorberg P, Kovács-Hostyánszki A, Kuemmerle T, Leuschner C, Lindborg R, Loos J, Maccherini S, Marja R, Máthé O, Proença V, Rey-Benayas J, Sans FX, Seifert C, Stalenga J, Timaeus J, Török P, van Swaay C, Viik E, Tscharntke T. 2015. Harnessing the biodiversity value of Central and Eastern European farmland. *Diversity & Distributions* **21**: 722–730.

- Tarhouni M, Ben Hmida W, Neffati M. 2015. Long-term changes in plant life forms as a consequence of grazing exclusion under arid climatic conditions. *Land Degradation & Development*. DOI:10.1002/ldr.2407.
- Tscharntke T, Tylianakis JM, Rand TA, Didham RK, Fahrig L, Batáry P, Bengtsson J, Clough Y, Crist TO, Dormann CF, Ewers RM, Fründ J, Holt RD, Holzschuh A, Klein AM, Kleijn D, Kremen C, Landis DA, Laurance W, Lindenmayer D, Scherber C, Sodhi N, Steffan-Dewenter I, Thies C, van der Putten WH, Westphal C. 2012. Landscape moderation of biodiversity patterns and processes —eight hypotheses. *Biological Reviews* 87: 661–685.
- Teuber LM, Hölzel N, Fraser LH. 2013. Livestock grazing in intermountain depressional wetlands-Effects onplant strategies, soil characteristics and biomass. Agriculture, Ecosystems & Environment 175: 21–28.
- Török P, Kapocsi I, Deák B. 2011. Conservation and management of alkali grassland biodiversity in Central-Europe. In Grasslands: Types, Biodiversity and Impacts, Zhang WJ (ed). Nova Science Publishers Inc: New York; 109–118.
- Török P, Miglécz T, Valkó O, Tóth K, Kelemen A, Albert Á, Matus G, Molnár VA, Ruprecht E, Papp L, Deák B, Horváth O, Takács A, Hüse B, Tóthmérész B. 2013. Seed weights support Social Behaviour Types - Analysis and new thousand seed weight records of the Pannonian flora. Acta Botanica Hungarica 55: 429–472.
- Török P, Valkó O, Deák B, Kelemen A, Tóthmérész B. 2014. Traditional cattle grazing in a mosaic alkali landscape: effects on grassland biodiversity along a moisture gradient. *PlosONE* 9: e97095.
- Török P, Valkó O, Deák B, Kelemen A, Tóth E, Tóthmérész B. 2016a. Managing for species composition or diversity? Pastoral and free grazing systems of alkali grasslands. *Agriculture, Ecosystems & Environment*. DOI:10.1016/j.agee.2016.01.010.
- Török P, Tóth E, Tóth K, Valkó O, Deák B, Kelbert B, Bálint P, Radócz Sz, Kelemen A, Sonkoly J, Miglécz T, Matus G, Takács A, Molnár VA, Süveges K, Papp L, Papp L jr., Tóth Z, Baktay B, Málnási Csizmadia G, Oláh I, Peti E, Schellenberger J, Szalkovszki O, Kiss R, Tóthmérész B. 2016b. New measurements of thousand-seed weights of species in the Pannonian Flora. Acta Botanica Hungarica 58: 187–198.
- Vesk PA, Leishman MR, Westoby M. 2004. Simple traits do not predict grazing response in Australian dry shrublands and woodlands. *Journal of Applied Ecology* **41**: 22–31.
- Villéger S, Mason NW, Mouillot D. 2008. New multidimensional functional diversity indices for a multifaceted framework in functional ecology. *Ecology* 89: 2290–2301.
- WallisDeVries MF, Bakker JP, van Wieren SE (eds). 1998. Grazing and Conservation Management. Kluwer Academic Publishers: Dordrecht.
- Westoby M. 1999. The LHS strategy scheme in relation to grazing and fire. In VIth International Rangeland Congress, Vol. 2xx, Eldrige D, Freudenberger D (eds); 893–896.