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Scale-dependent effects of grazing on the species richness of alkaline and sand grasslands

Auswirkungen der Beweidung auf den Artenreichtum von Salz- und Sandtrockenrasen

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Abstract

Extensively managed pastures harbour rare and endangered species and have a decisive role in maintaining grassland biodiversity. Traditional herding of local robust cattle breeds is considered as a feasible tool for preserving these habitats. We studied the scale-dependent effects of grazing on the species richness and composition of three dry grassland types in the Great Hungarian Plain: *Achilleo setaceae-Festucetum pseudovinae* and *Artemisio santonici-Festucetum pseudovinae* alkaline grasslands, and *Potentillo arenariae-Festucetum pseudovinae* sand grassland. We asked the following questions: (1) Does extensive grazing have a scale-dependent effect on plant species richness of alkaline and sand grasslands? (2) How does grazing affect the proportion of specialists, generalists and weeds in the three grassland types? We sampled ten sites of each grassland type, including five extensively grazed and five non-grazed sites (altogether we had 30 sites). We used a series of nested plots each consisting of 10 plots from the size of 0.01 m² to 16 m². We revealed that grazing has contrasting effects in the three grassland types, and had a considerable effect on their species richness even at small scales. In both alkaline grassland types, total species richness was overall higher in grazed plots but it increased in a similar manner for both ungrazed and grazed habitats across plot sizes. Small-scale heterogeneity likely due to the uneven distribution of grazing, trampling and defecation together with mitigated rate of competition allowed more species to co-exist even at small scales in grazed alkaline grasslands. Grazing increased the richness of specialists, but likely due to the salt stress, establishment of weeds was hampered. Open gaps formed by trampling likely supported the establishment of several specialist species such as *Plantago tenuiflora* and *Puccinellia limosa* which are typical to open alkali grasslands. Contrary, in sand grasslands, we did not detect any effect of grazing on total species richness, likely due to the adverse effect of grazing on the species richness of specialists and weeds. In contrast with the former findings we detected significantly higher species richness in 0.01 m² and 0.0625 m² plots in the grazed sand grasslands, but found no differences at larger scales. Whilst species richness of specialists was significantly decreased, richness of weeds was increased by grazing. Decrease in the specialist species richness was likely due to the lack of their evolutionary adaptation to grazing. Degradation caused by grazing and trampling together with the propagule pressure from the neighbouring anthropogenic habitats resulted in an increased richness of weeds in the grazed sites.

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Erweiterte deutsche Zusammenfassung am Ende des Artikels

1. Introduction

Dry grasslands of Europe harbour several rare and endangered species and are thus an important target for nature conservation. Several specialist plant and animal taxa are confined to dry grasslands, and endemic species are also well represented in these habitats (DENGLER et al. 2014). Despite their vital importance, dry grasslands have suffered a remarkable habitat loss during the last centuries, mainly due to their conversion into arable land and urbanisation (RÖSCH et al. 2013, LINDBORG et al. 2014, DEÁK et al. 2016a, b). For instance, MOLNÁR et al. (2008) reported that less than 7% of the previously existing loess and sand grasslands remained for the 21th century in Hungary. As a consequence of habitat loss, formerly connected habitats became fragmented and isolated by an unsuitable matrix, which resulted in a loss of grassland specialist species and an increase in generalists in the long term (TSCHARNTKE et al. 2012, DEÁK et al. 2016a). Besides land transformation processes, changes in land use practices also pose a significant threat to the biodiversity of remaining grasslands (POSCHLOD & WALLIS DE VRIES 2002, VALKÓ et al. 2012). For preserving species composition and biodiversity of remaining dry grasslands it is essential to reintroduce the traditional management practices which mimic the natural disturbance factors (TÖRÖK et al. 2014, GILHAUS & HÖLZEL 2015, RUPPRECHT et al. 2016, VALKÓ et al. 2016a).

Wild grazing ungulates had a major effect in the development and maintenance of grasslands by selective biomass removal and trampling (POSCHLOD & WALLIS DE VRIES 2002). During the last millennia, their role was replaced by domestic animals (PÄRTEL et al. 2005, TÖRÖK et al. 2014, GILHAUS et al. 2017). Extensively managed pastures, i.e. pastures managed in a traditional and low-intensity manner, have a decisive role in maintaining biodiversity both in a local and a landscape scale (TÖLGYESI et al. 2015, TÖRÖK et al. 2016a). In case of short-grass dry grasslands, such as alkaline and sand grasslands, traditional management typically applies grazing by robust cattle breeds and/or sheep (HÁZI et al. 2012, TÓTH et al. 2016). Even though grazing was typical in these habitats till the end of the 20th century, due to the recent socio-economical changes the overall number of grazing animals was drastically decreased in many regions; grazing was even ceased or replaced by mowing (ISSELSTEIN et al. 2005, TÖRÖK et al. 2014). When compared to mowing, grazing was reported to have a more positive effect on the biodiversity of semi-natural grasslands, although the effects vary across dry and wet grasslands and management intensity (TÄLLE et al. 2016, TÓTH et al. 2016).

To sustain the biodiversity of pastures, nature conservation managers are seeking for cost-effective and proper management measures, which are feasible both from an economic sustainability view and from the view of biodiversity conservation (TÖRÖK et al. 2014). Traditional herding of local robust cattle breeds is considered as a feasible tool to achieve conservation goals in many habitats of Europe (MANN & TISCHEW 2010, GILHAUS et al. 2013, TÖRÖK et al. 2014). As a considerable part of grasslands have been traditionally managed by extensive cattle grazing in the past, application of grazing as an active conservation tool can be an ideal solution. However, even being a promising tool for nature conservation projects it is crucial to have comprehensive evidence-based knowledge on the effects of grazing on these grasslands regarding the changes in species richness and the scale-dependence of the management.

Grazing can influence species richness through the dynamic interaction of several mechanisms especially driving survival and colonisation dynamics of plant species (OLFF & RITCHIE 1998). Some studies showed that moderate grazing enhances plant species diversity by suppressing dominant species with a good competitive ability, thus promotes the co-existence of a wide set of less competitive species (DE BELLO et al. 2007, METERA et al. 2010). The paper of OLFF & RITCHIE (1998) suggests that grazing increases plant diversity at small spatial scales by enhancing species co-existence. Grazing can enhance species richness by increasing structural habitat heterogeneity, by supporting colonisation due to facilitated and directed seed dispersal and by providing proper microsites for establishment (POSCHLOD & WALLIS DE VRIES 2002, de BELLO et al. 2007, FREUND et al. 2015). Colonisation processes can be influenced by the landscape context (species pool at larger spatial scales) via the composition of the available seed sources in general, and especially via the availability of grassland specialist species and weeds (OLFF & RITCHIE 1998).

In the Pannonian basin, the extended alkaline and sand grasslands have been typically managed by grazing, which maintained their biodiversity. Given their uniqueness 'Pannonic Salt Steppes and Salt Marshes' and 'Pannonic Sand Steppes' of the region are listed as priority habitats in Annex I of the Habitats Directive (EUROPEAN COMMISSION 2007). The aim of our study was to estimate the scale-dependent effects of grazing in three dry grassland types: *Artemisio santonici-Festucetum pseudovinae* Soó in Máthé 1933 corr. Borhidi 1996, *Achilleo setaceae-Festucetum pseudovinae* Soó (1933) 1947 corr. Borhidi 1996 alkaline grasslands and *Potentillo arenariae-Festucetum pseudovinae* Soó (1938) 1940 sand grassland, called hereafter *Achilleo-Festucetum*, *Artemisio-Festucetum* and *Potentillo-Festucetum*.

Alkali vegetation of the Pannonian Ecoregion involves several halophytic and sub-halophytic phytosociological classes such as *Festuco-Puccinellietea*, *Phragmito-Magnocaricetea*, *Festuco-Puccinellietea*, *Thero-Salicornietea*, *Crypsietea* and *Juncetea maritimi* (ELIÁŠ et al. 2013). They harbour several endemic species such as *Cirsium brachycephalum*, *Plantago schwarzenbergiana, Puccinellia peisonis* and *Suaeda pannonica*. The most widespread, relatively dry, short-grass alkaline grassland types such as *Achilleo-Festucetum* and *Artemisio-Festucetum* are typically managed by grazing (BORHIDI et al. 2012). The dominant grass species of both grasslands are *Festuca pseudovina* and *Poa angustifolia*; however, *Cynodon dactylon* can gain dominance in *Achilleo-Festucetum* grasslands due to overgrazing.

Artemisio-Festucetum grasslands occur on moderately alkaline solonetz soils characterised by a salt accumulation layer and a reduced amount of humus in the topsoil layer. Given these abiotic constrains *Artemisio-Festucetum* grasslands harbour many halophytic species (including *Artemisia santonicum*, *Aster tripolium* subsp. *pannonicum*, *Limonium gmelinii* subsp. *hungaricum*) and are generally species-poor compared to *Achilleo-Festucetum* grasslands (DEÁK et al. 2014a). *Achilleo-Festucetum* grasslands show some transition to loess grasslands regarding their species composition (*Dianthus pontederae*, *Filipendula vulgaris*, *Koeleria cristata*, *Salvia austriaca, Silene viscosa* and several *Trifolium* species such as *T. angulatum*, *T. fragiferum*, *T. retusum*, *T. striatum*, *T. strictum*) due to their less alkaline and more humus-rich soil (BORHIDI et al. 2012, TÓTH & HÜSE 2014). In alkaline grasslands, open micro-sites formed by grazing can enhance either grassland specialists or disturbance-tolerant species (such as *Camphorosma annua*, *Erophila verna*, *Matricaria recutita* and

Myosurus minimus) but also generalists and weeds such as *Carduus nutans*, *Cynodon dactylon*, *Eryngium campestre*, *Gypsophila muralis*, *Hordeum hystrix* and *Polygonum aviculare* (TÖRÖK et al. 2016b).

The most typical and widespread grassland of 'Pannonic Sand Steppes' of the study region is the *Potentillo-Festucetum* (BORHIDI et al. 2012). These sand grasslands have lost huge areas in the past centuries because of improper management, e.g., overgrazing, land transformation, ploughing and afforestation (HALADA et al. 2011). This grassland is usually formed on higher elevations (top of dunes and slopes), with moderately loose and humus-rich soils. It is characterized by the dominance of *Festuca pseudovina* which is a perennial tuft-forming grass and *Potentilla arenaria* which can form dense patches. Other typical species are *Poa bulbosa, Carex supina* and *Koeleria glauca*. It harbours several rare and protected species such as *Adonis vernalis*, *Orchis morio*, *Pulsatilla grandis* and in some cases the endemic *Pulsatilla pratensis* subsp. *hungarica*. The typical disturbance-tolerant species are *Melandrium album*, *M. viscosum, Scleranthus annuus*, *Minuartia viscosa* and *Trifolium repens*. As a response to overgrazing, weeds and prickly plants may become abundant and the vegetation can be shifted towards the *Cynodonti-Poëtum angustifoliae* Rapaics ex Soó 1957 association, characterised by a high cover of *Cynodon dactylon*, which is a grazing and trampling tolerant species of dry grasslands (BORHIDI et al. 2012).

In our study, we asked the following questions: (1) Does extensive grazing have a scale-dependent effect on plant species richness of alkaline and sand grasslands? (2) How does extensive grazing affect the proportion of specialists, generalists and weeds in the studied grassland types?

2. Material and Methods

2.1 Study sites and vegetation sampling

Our study areas are located in the Hungarian Great Plain (Hortobágy: N 47°34', E 21° 9' and Nyírség: regions N 47° 55', E 21° 41'), in East-Hungary. Hortobágy is characterised by a mosaic of vast semi-natural habitats such as alkaline and loess grasslands, wetlands, alkaline marshes and a relatively low proportion of agricultural lands (DEÁK et al. 2015). Nyírség is a highly transformed landscape harbouring small acidic sand grasslands, wet meadows and sand oak forests in the matrix of arable lands, urban areas and tree plantations. Both regions have a continental climate. In the Hortobágy, the elevation ranges between 88–102 m a.s.l., the average annual precipitation is 550 mm, and the mean annual temperature is 9.5 ºC with high inter-annual fluctuations (LUKÁCS et al. 2015). In the Nyírség, elevation ranges between 115–150 m a.s.l., the mean annual temperature is 10°C, and the mean annual precipitation is 600 mm (TÖRÖK et al. 2009, NOVÁK et al. 2014).

We examined the effect of grazing by studying vegetation of grazed and non-grazed sites. Grazed sites were managed by moderate grazing with robust cattle breeds from mid-April till the end of September; the grazing pressure was moderate (0.5 animal unit/ha). Sites were grazed at least for five years before the field survey. The non-grazed sites were located in the close vicinity (less than 500 metres) of the grazed sites and were not grazed at least for five years before the study. No other management was present on the study sites. We designated in total 30 sample sites; one grazed and one non-grazed site in five study locations per each grassland type (Fig. 1). Sampling took place in June 2008. In order to study the scale-dependent effect of grazing and assessing the effects of within-site heterogeneity we used a nested plot design at the sample sites, which means that from one corner of the 16-m²-sized plot, nested series of 10 square- or rectangle-shaped subplots of the sizes 0.01 m², 0.0625 m², 0.125 m², 0.25 m², 0.5 m², 1 m², 2 m², 4 m², and 8 m² were placed and sampled (Supplement E1). Starting from the smallest plot size, we recorded the presence of all vascular plant species in each plot. Nomenclature followed KIRÁLY et al. (2009).

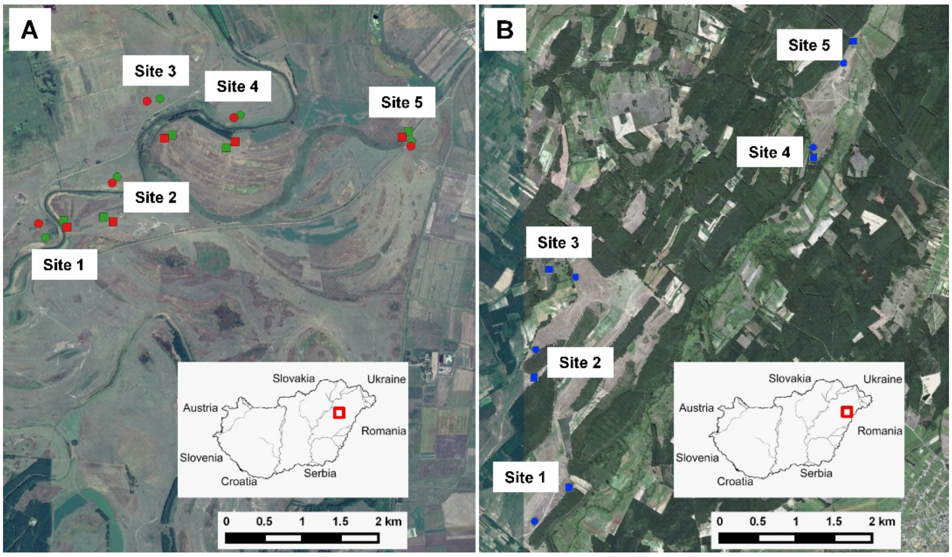

Fig. 1. Map of the study sites. A – Hortobágy region; B – Nyírség region. Notifications: red symbols – *Artemisio-Festucetum*; green symbols – *Achilleo-Festucetum*; blue symbols – *Potentillo-Festucetum*; circle – grazed; square – non-grazed (Source of the map: Google Earth Open Layers Plugin).

Abb. 1. Karte der Untersuchungsfläche. A – Region Hortobágy; B – Region Nyírség. Erläuterungen: rote Symbole – *Artemisio-Festucetum*; grüne Symbole – *Achilleo-Festucetum*; blaue Symbole – *Potentillo-Festucetum*; Kreis – beweidet; Quadrat – nicht beweidet (Quelle der Karte: Google Earth Open Layers Plugin).

2.2 Data analysis

Herbaceous species of the *Festuco-Brometea, Koelerio-Corynephoretea* and *Puccinellio-Salicornietea* phytosociological classes were considered as specialist species (HORVÁTH et al. 1995). Generalist and weed species were classified using the Social Behaviour Type categories of BORHIDI (1995) which is based on the model of GRIME (1979) and was adapted for the Hungarian conditions: generalists (G) were considered as 'generalists', while adventives competitors (AC), ruderal competitors (RC) and weeds (W) were considered as 'weeds'. We analysed the effect of management and plot size and their interaction (predictors) on the dependent variables (total species richness, the richness of specialists, generalists and weed species, respectively). Dependent variables were log-transformed to approximate them to normal distribution. To reveal the effects of predictors on dependent variables, two models, a linear regression and a quadratic regression model were built in R (R CORE TEAM 2016). Then, we compared these two models using ANOVA and we retained the quadratic model if the unexplained variation of dependent variable (residual sum of squares, RSS) in this model was significantly lower than in the linear model. To test the differences in total species richness and richness of specialist, generalist and weed species of different plot sizes under different management regimes we used Wilcoxon signed-rank test (ZAR 1999), calculated using SPSS 20 program. To calculate the number of species shared between the plots of same size but with different management (similarity in species richness) we used the Jaccard similarity index. We calculated the means of the Jaccard similarity indices between grazed and ungrazed plots for each plot size category. To show the compositional (presence/absence) differences in the vegetation we calculated DCA (detrended correspondence analysis) ordination using the CANOCO 4.5 program (LEPŠ & ŠMILAUER 2003). For the ordination we used the presence-absence values of the species in the 16 m^2 plots.

3. Results

In total, we found 24 species in *Artemisio-Festucetum*, 41 in *Achilleo-Festucetum* and 60 in *Potentillo-Festucetum* grasslands, respectively. There were 22, 39 and 36 species in the grazed and 9, 23 and 44 in the non-grazed *Artemisio-Festucetum*, *Achilleo-Festucetum* and *Potentillo-Festucetum* grasslands, respectively (Supplements E2–4). We found that in case of plot sizes quadratic models explained significantly higher proportion of the variance than linear models (except in case of generalist species of *Artemisio-Festucetum*), thus we decided to focus on the results derived from the quadratic models. Using quadratic models we found that in *Artemisio-Festucetum* grasslands both grazing and increasing plot sizes increased total species richness, species richness of specialists and weeds (Figs. 2–3). Species richness of generalists was similar in grazed and non-grazed plots regardless to the plot size (Fig. 3, Table 1). Jaccard similarity of the vegetation of grazed and non-grazed plots was not affected by plot size (Fig. 4). In *Achilleo-Festucetum* grasslands grazing and increasing plot size increased total species richness and species richness of specialists, generalists and weeds (Figs. 2–3, Supplement E3). Jaccard similarity of the vegetation of grazed plots to non-grazed plots increased with increasing plot size (Fig. 4). In *Potentillo-Festucetum* grasslands, grazing increased the richness of generalists and weeds, whilst it decreased the richness of specialists. Total species richness was not affected by management (Fig. 2, Table 1). Species richness of all groups increased with increasing plot size. Jaccard similarity of the vegetation of grazed plots to non-grazed plots increased with increasing plot size (Fig. 4). We found significant interactions between grazing and plot size in case of the species richness of weeds in all habitat types (Table 1).

The vegetation composition of the three studied grassland types was well separated by the DCA ordination. The three studied grassland types were sorted according to their edaphic attributes along the 1st axis. *Artemisio-Festucetum* grasslands (characterised by alkaline soil) and *Potentillo-Festucetum* grasslands (characterised by sandy soils) were located at the two extremes of the gradient. Plots of *Achilleo-Festucetum* grasslands (characterised by a moderately salty and humus-rich soil) were situated in an intermediate position (Fig. 5). Vegetation of grazed and non-grazed plots was also well separated in each studied grassland. Vegetation of grazed *Artemisio-Festucetum* grasslands harboured *Atriplex littoralis*, *Plantago schwarzenbergiana*, *P. tenuiflora*, *Puccinellia limosa* and *Trifolium* spp. with a high frequency (for detailed information please refer to Supplement E2). Non-grazed *Artemisio-Festucetum* grasslands harboured *Artemisia santonicum*, *Aster tripolium*, *Elymus repens* and *Limonium gmelinii* subsp. *hungaricum.* Vegetation of grazed and non-grazed *Achilleo-Festucetum* was more similar to each other than that of the other grasslands. A high frequency of *Ornithogalum kochii*, *Plantago lanceolata*, and *Trifolium* spp. was typical in the grazed plots, whilst *Achillea collina* and *Podospermum canum* were represented in non-grazed plots. In the grazed plots of the *Potentillo-Festucetum Apera spica-venti*, *Carex stenophylla*, *Conyza canadensis*, *Cynodon dactylon*, *Eryngium campestre* and *Scleranthus annuus* had a high frequency. Non-grazed plots were characterised by *Agrostis stolonifera*, *Carex supina*, *Chondrilla juncea*, *Potentilla arenaria* and *Thymus glabrescens* subsp. *degenianus*.

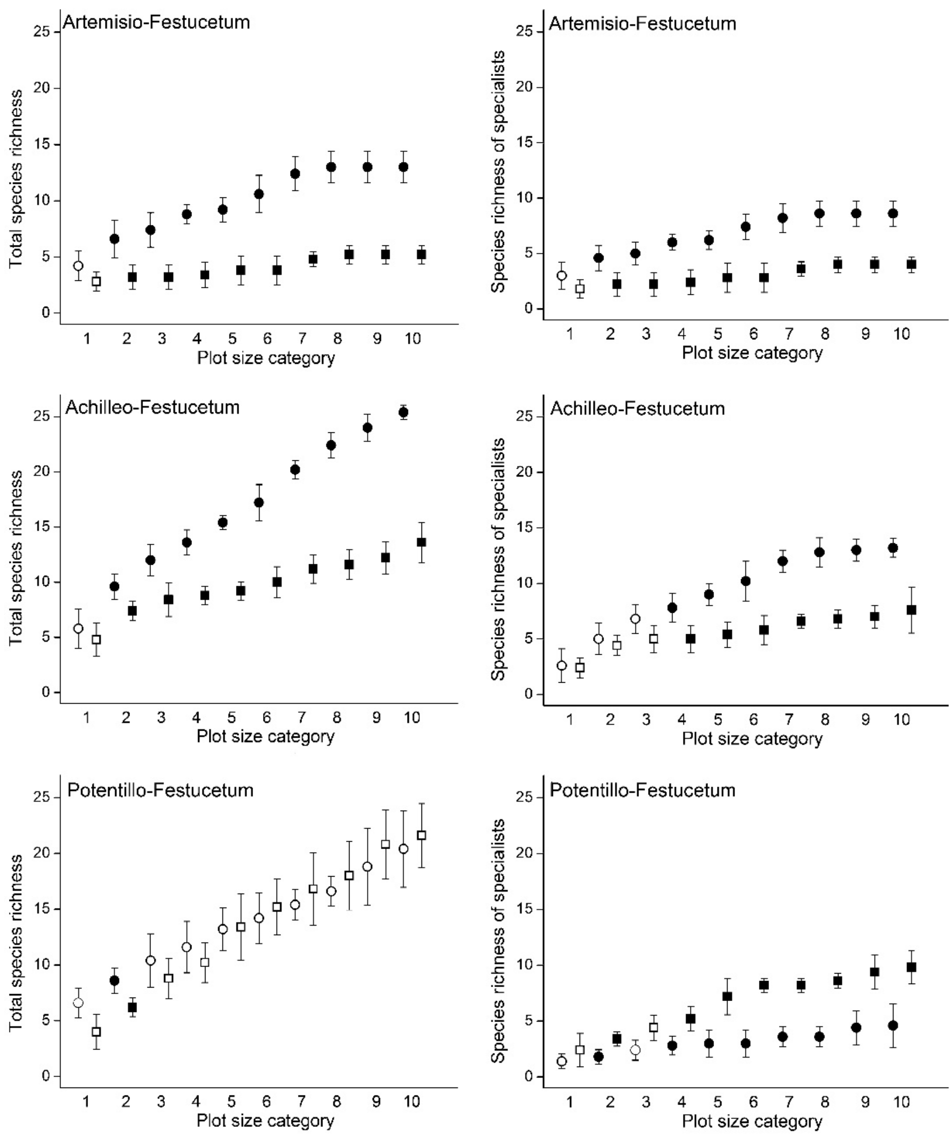

Fig. 2. Effect of grazing and plot size on the total species richness and richness of specialists in the three studied grassland types. Notifications: circle – grazed, square – non-grazed. Significant differences between the grazed and non-grazed plots of the same size are marked with full symbols (Wilcoxon signed-rank test; $p < 0.05$). The error bars represent the standard error.

Abb. 2. Effekt von Beweidung und Flächengröße auf die absolute Artenzahl und die Zahl der Spezialisten in den drei untersuchten Graslandtypen. Erläuterung: Kreis – beweidet, Quadrat – nicht beweidet. Signifikante Unterschiede zwischen den beweideten und nicht beweideten Probeflächen der gleichen Größe sind mit ausgefüllten Symbolen markiert (Wilcoxon Vorzeichen-Rank-Test; $p < 0,05$). Die Fehlerbalken zeigen den Standardfehler an.

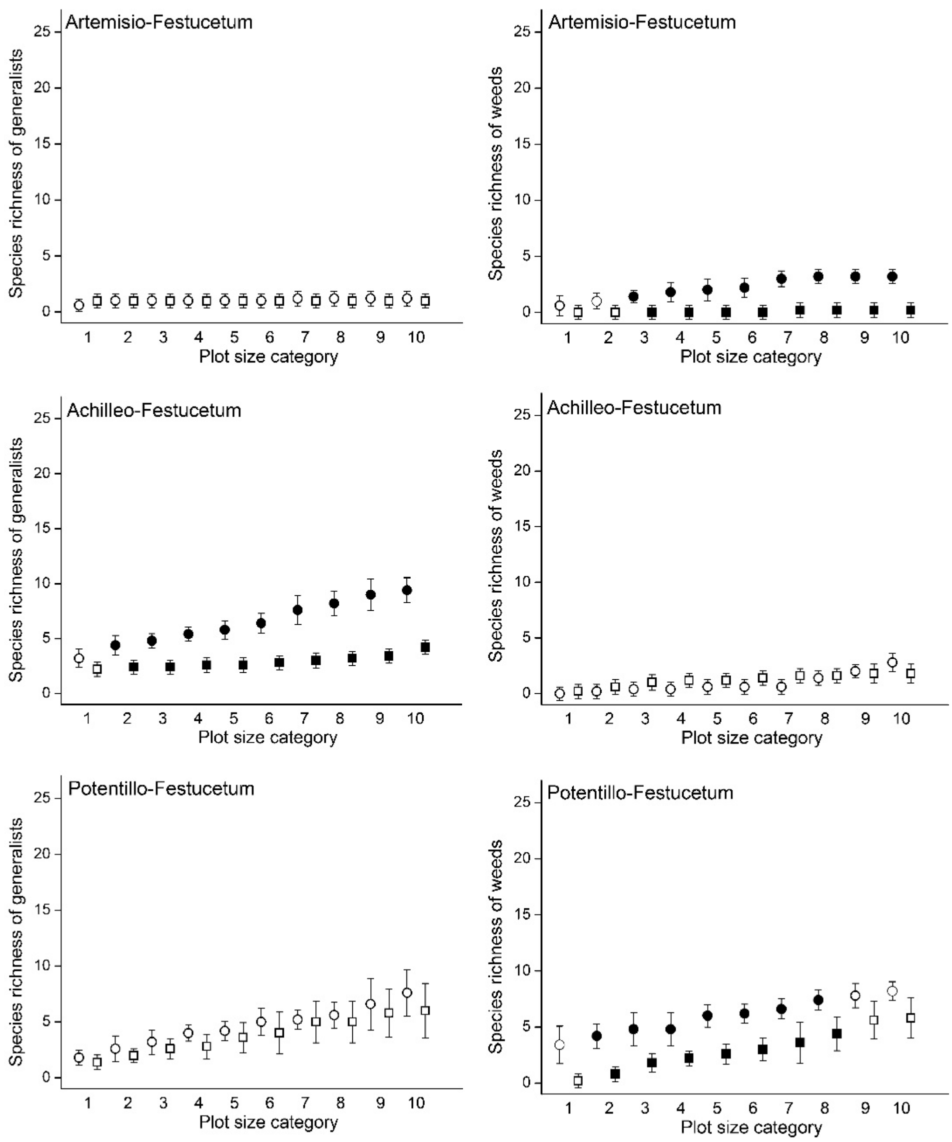

Fig. 3. Effect of grazing and plot size on the species richness of generalists and weeds in the three studied grassland types. Notifications: circle – grazed, square – non-grazed. Significant differences between the grazed and non-grazed plots of the same size are marked with full symbols (Wilcoxon signed-rank test; $p < 0.05$). The error bars represent the standard error.

Abb. 3. Effekt von Beweidung und Flächengröße auf die die Zahl der Spezialisten und Unkräuter in den drei untersuchten Graslandtypen. Erläuterung: Kreis – beweidet, Quadrat – nicht beweidet. Signifikante Unterschiede zwischen den beweideten und nicht beweideten Probeflächen der gleichen Größe sind mit ausgefüllten Symbolen markiert (Wilcoxon Vorzeichen-Rank-Test; $p < 0,05$). Die Fehlerbalken zeigen den Standardfehler an.

Table 1. Effect of grazing and plot size on total species richness and species richness of specialists, generalists and weeds in the three studied grasslands (quadratic regression model). To reveal the effects of predictors on dependent variables, two models, a linear regression and a quadratic regression model were built (Plot, $Plot^2$). Notations: SR – species richness, n.s. non significant; *** $p < 0.001$; ** $p < 0.01$; * $p < 0.05$.

Tabelle 1. Effekt der Beweidung und Flächengröße auf die Gesamtartenzahl und die Artenzahl von Spezialisten, Generalisten und Unkräutern in den drei untersuchten Grasländern (quadratisches Regressionsmodell). Um die Effekte von Prädiktoren auf abhängige Variablen zu verdeutlichen, wurden zwei Modelle, eine lineare Regression und ein quadratisches Regressionsmodell erstellt (Plot, $Plot^2$). Anmerkungen: SR – Artenreichtum, n.s. nicht signifikant; *** $p < 0,001$; ** $p < 0,01$; * $p < 0,05$.

		Plot size			Plot size ^{2}			Grazing			Grazing × plot size^2		
		Estimate	t-value	Sig.	Estimate	t-value	Sig.	Estimate	t-value	Sig.	Estimate	t-value	Sig.
Artemisio-Festucetum	Total SR	0.055	7.164	***	0.003	5.129	***	0.315	13.903	***	0.001	0.727	n.s.
	SR of specialists	0.001	6.511	***	0.001	4.828	***	0.001	11.273	***	0.001	0.015	n.s.
	SR of generalists	0.008	2.021	*	0.001	1.158	n.s.	-0.004	-0.382	n.s.	0.001	1.356	n.s.
	SR of weeds	0.046	4.917	***	0.002	3.084	**	0.416	15.207	***	0.001	2.153	*
Achilleo-Festucetum	Total SR	0.065	7.953	***	0.003	5.188	***	0.183	7.644	***	0.001	1.380	n.s.
	SR of specialists	0.066	6.603	***	0.003	4.570	***	0.158	5.358	***	0.001	1.003	n.s.
	SR of generalists	0.041	7.185	***	0.001	4.222	***	0.261	15.784	***	0.001	1.267	n.s.
	SR of weeds	0.096	4.083	***	0.002	2.993	**	-0.139	-4.702	***	0.001	3.420	***
Potentillo-Festucetum	Total SR	0.079	8.201	***	0.004	6.013	***	0.039	1.377	n.s.	-0.001	-0.977	n.s.
	SR of specialists	0.064	6.301	***	0.003	4.642	***	-0.257	-8.578	***	-0.001	-0.584	n.s.
	SR of generalists	0.066	6.624	***	0.003	4.460	***	0.068	2.339	*	0.001	0.303	n.s.
	SR of weeds	0.079	7.073	***	0.004	5.512	***	0.315	9.647	***	-0.001	-2.127	*

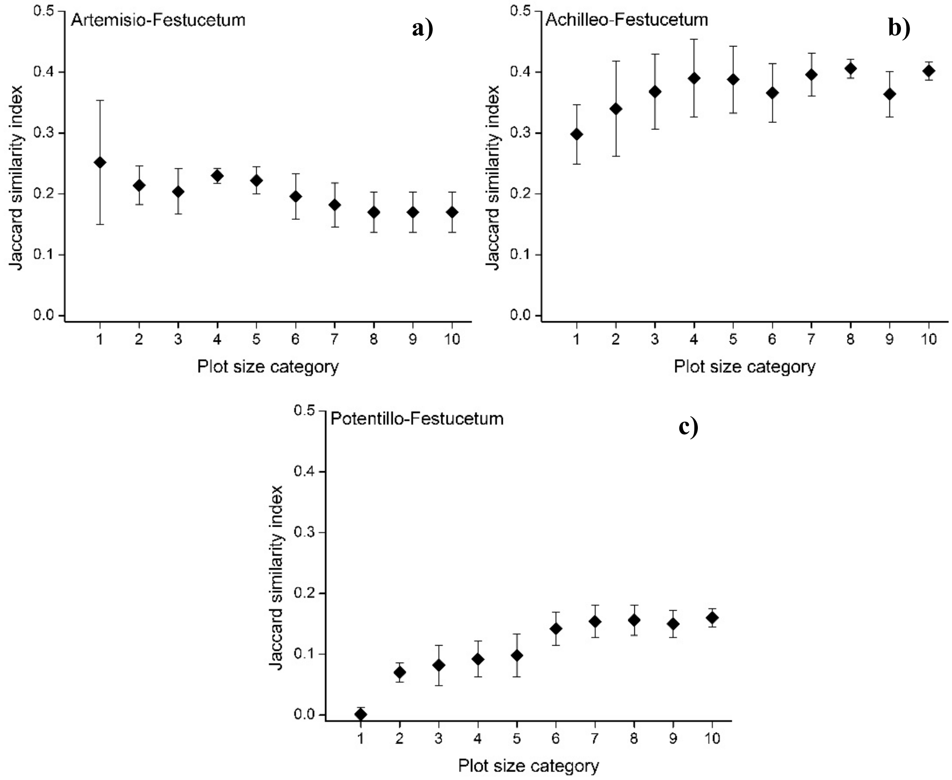

Fig. 4. Jaccard similarity between grazed and non-grazed plots of the same size in the three studied grassland types: **a)** *Artemiso-Festucetum*; **b)** *Achilleo-Festucetum*; **c)** *Potentillo-Festucetum*. The error bars represent the standard error.

Abb. 4. Jaccard-Ähnlichkeit zwischen beweideten und nicht beweideten Probeflächen der gleichen Größe in den drei untersuchten Graslandtypen: **a)** *Artemiso-Festucetum*; **b)** *Achilleo-Festucetum*; **c)** *Potentillo-Festucetum*. Die Fehlerbalken zeigen den Standardfehler an.

4. Discussion

We revealed that both grazing and spatial scale have considerable effects on the species richness and composition of alkaline and sand grasslands. Effects of grazing were similar in the two alkaline communities (*Achilleo-Festucetum* and *Artemisio-Festucetum*), while we found different effects of grazing in the *Potentillo-Festucetum* sand grasslands. The most probable reasons for the differences were the habitat characteristics (e.g., soil salt content, moisture) and landscape context.

4.1 Alkaline grasslands

OLFF & RITCHIE (1998) hypothesised that at small spatial scales species richness is higher in grazed areas compared to non-grazed ones. They also assumed that this might not be valid in salt-affected communities, as high level of stress can mask the effects of grazing, and thus in salt-affected habitats grazing does not change total species richness, or can even decrease it. Our results did not confirm the latter assumption, in spite of the differences in

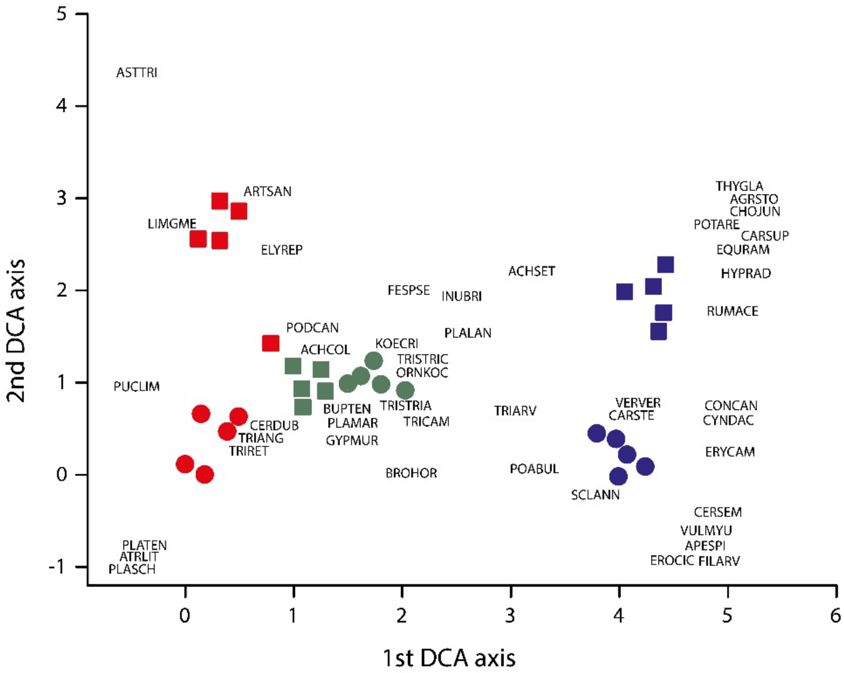

Fig. 5. The effects of grazing on the species composition in the three studied grassland types displayed by a DCA calculated on presence-absence datasets. Species with a frequency of 4 and 5 are plotted (for species names and frequency scores please refer to Supplements E2-4). Eigenvalues were 0.734 and 0.322 for the first and second axis respectively. Cumulative percentage variance of species data for the first and the second axis were 22.4% and 32.3% respectively. Notifications: circle – grazed; square – non-grazed; red symbols – *Artemisio-Festucetum*; green symbols – *Achilleo-Festucetum*; blue symbols – *Potentillo-Festucetum*.

Abb. 5. Die Effekte der Beweidung auf die Artenzusammensetzung in den drei untersuchten Graslandtypen, dargestellt als DCA auf der Grundlage von Präsenz-Absenz-Datensätzen. Arten mit einer Frequenz von 4 und 5 sind aufgetragen (Artnamen und Frequenzwerte s. Anhänge E2-4). Die Eigenwerte betrugen 0,734 bzw. 0,322 für die erste bzw. zweite Achse. Die kumulative prozentuale Varianz der Artdaten für die erste und zweite Achse betrug 22,4 % und 32,3 %. Erläuterungen: Kreis – beweidet; Quadrat – nicht beweidet; rote Symbole – *Artemisio-Festucetum*; grüne Symbole – *Achilleo-Festucetum*; blaue Symbole – *Potentillo-Festucetum*.

total species richness (23 species in *Artemisio-Festucetum*, 41 species in *Achilleo-Festucetum*) we detected a significant increase in total species richness in the grazed grasslands above the 0.0625 m² plot size in case of both alkaline grasslands. Differences between the species richness of grazed and non-grazed plots at the studied small spatial scales were likely to be influenced by altered competition and microsite availability. Small-scale heterogeneity of grazed sites through increased availability of the various microsites formed by the uneven distribution of grazing, trampling and defecation allowed more species to co-exist at small scales (0.0625 m²) (see also METERA et al. 2010, DENGLER et al. 2014). Furthermore enhanced zoochorous dispersal of propagules might also contribute to the increased species richness in grazed sites, as animals could transport the propagules of the species into the neighbouring areas by their fur, hoove and by their dung (POSCHLOD & WALLIS DE VRIES 2002).

The differences in the composition of specialist species refers to the differences in the soil properties, as specialist species of *Artemisio-Festucetum* sites involved several salt-tolerant species of alkaline grasslands, while *Achilleo-Festucetum* grasslands harboured both specialist species of alkaline and non-alkaline loess grasslands (DEÁK et al. 2014a, b). As it was found by VALKÓ et al. (2016a) increase in open gaps can facilitate salt accumulation in alkaline grasslands, as open soil surfaces enhance the transportation of salts to the upper soil layers via enhanced evaporation. Besides lowering competition, increased salt content of the soil can support several specialist species typical to alkaline grasslands. The effect of this process was more obvious in *Artemisio-Festucetum* grasslands, which harbour mostly halophyte or at least salt-tolerant species (such as *Aster tripolium*, *Atriplex littoralis*, *Camphorosma annua*, *Limonium gmelinii* subsp. *hungaricum*, *Matricaria recutita* and *Plantago schwarzenbergiana*; Supplement E2). In the open gaps formed by trampling, several short-growing grassland specialist species typical to open alkaline grasslands could establish such as *Plantago tenuiflora* and *Puccinellia limosa*. While open gaps were proper sites for specialists, due to the salt stress, the establishment of weedy species was hampered there (VALKÓ et al. 2016b).

We found that the richness of generalists and weeds in *Artemisio-Festucetum* and *Achilleo-Festucetum* alkaline grasslands were lower compared to the *Potentillo-Festucetum* sand grasslands. This can be explained by the semi-natural landscape context of the surveyed grasslands, and the fact that these grasslands are formed on alkaline soils. Alkaline grasslands harbour a reduced number of generalist and weed species, due to the filtering effect of stress caused by the salt accumulation in the upper soil layers (DEÁK et al. 2014a). This especially stands for the *Artemisio-Festucetum* grasslands, where both the generalists (*Alopecurus pratensis* and *Festuca pseudovina*) and ruderals (*Bromus hordeaceus*, *Lepidium ruderale* and *Polygonum aviculare*) were represented by low species richness regardless to the management, however species richness of weeds was moderately higher in grazed sites. The humus-rich upper soil layer and moderate salt accumulation in the deeper soil layers in *Achilleo-Festucetum* allowed the presence of higher number of generalist species compared to *Artemisio-Festucetum*. Accordingly we detected an increase in the species richness of generalists (such as *Achillea collina*, *Inula britannica*, *Lotus corniculatus*, *Plantago lanceolata* and *Trifolium campestre*) in the grazed sites even at small scales. We detected a low number of weeds in the grazed sites (represented by *Bromus hordeaceus*, *B. sterilis*, *Capsella bursa-pastoris*, *Crepis tectorum*, *Polygonum aviculare* and *Scleranthus annuus*). Even though moderate grazing induced weed encroachment, richness of weeds was extremely low at all spatial scales.

Whilst Jaccard similarity between grazed and non-grazed plots increased with plot size in the *Achilleo-Festucetum*, it was the same for both grazed and non-grazed plots at all spatial scales in case of *Artemisio-Festucetum*. In case of *Achilleo-Festucetum* grasslands higher dissimilarity in the vegetation at small scales can be explained by the potential of grazing for increasing habitat heterogeneity at small scales (OLFF & RITCHIE 1998, TÓTH et al. 2016). Mosaic of gaps and patches with different amount of biomass caused by grazing and random dung deposition highly influences species sorts at the small spatial scales in the grazed sites. With increasing plot size, this small-scale variability becomes balanced and the similarity in vegetation richness of grazed and non-grazed plots increases. The likely reason for the constant scores in the *Artemisio-Festucetum* is the small total species pool, which is due to the high level of stress. High level of stress on the one hand filters out most of the generalist and weed species present in the landscape. On the other hand it decreases the level of competition independently from grazing, thus allowing coexistence of species even in a small spatial scale.

4.2 Sand grasslands

In contrast to alkaline grasslands, we did not detect any effect of grazing on total species richness in *Potentillo-Festucetum* sand grasslands. This was due to the adverse effect of grazing on the species richness of specialists and weeds. While species richness of specialists was significantly decreased by grazing, richness of generalists and weeds significantly increased. It suggests that contrary to alkaline grasslands, sand grasslands cannot cope with the same intensity grazing. This might be due to the lack of evolutionary adaptation to grazing and the nutrient-poor and arid environment (see also DE BELLO et al. 2007). Studies on the effects of grazing in dry grasslands suggest that under dry conditions grazing can decrease species richness at small scales and can be a significant driver of land degradation (DE BELLO et al. 2007, TÓTH et al. 2016). In contrast with these findings we found no differences in the species richness at larger scales, but we detected significantly higher species richness in the 0.01 m² and 0.0625 m² plots. In case of weeds grazing had a scale dependent effect, which is shown by the significant interaction of plot size and grazing, with decreasing differences by increasing plot size. Trampling and grazing can lead to a decrease in the water availability in the upper soil layers of dry habitats, and thus can increase the proportion of bare soil (PECO et al. 2006, TÖRÖK et al. 2016). In our case, unfavourable environmental conditions likely formed by grazing might have result in a significant decrease in the richness of specialists in the grazed sand grasslands compared to ungrazed ones. Sand grassland specialists (*Carex stenophylla*, *C. supina*, *Equisetum ramosissimum*, *Potentilla arenaria* and *Thymus glabrescens* subsp. *degenianus*) were more typical for the non-grazed sites than for the grazed sites.

Degradation caused by grazing and trampling together with the propagule pressure from the neighbouring unsuitable matrix characterised by arable lands, fallows, urban areas and tree plantations resulted in an increased richness of weeds in the grazed sites. In the grazed plots, we observed both weed species typical to the neighbouring arable lands and fallows (*Apera spica-venti*, *Crepis* spp., *Conyza canadensis* and *Setaria viridis*) and weeds directly favoured by grazing (*Bromus hordeaceus*, *B. tectorum*, *Cynodon dactylon*, *Rumex acetosa* and *Verbascum phlomoides*). A high proportion of weeds, especially those present at the grazed sites, are able to disperse by zoochory (such as *Apera spica-venti*, *Conyza canadensis*, *Erodium cicutarium*, *Eryngium campestre*, *Poa bulbosa* and *Scleranthus annuus*). However, it should be noted that zoochorous weed species were also present in the non-grazed plots, although with a lower proportion. This can be explained by the fact that although these species predominantly disperse by animals, they can spread by other ways as well, such as anemochory e.g., in case of *Conyza canadensis*.

4.3 Conservation remarks

Based on our findings traditional herding of local robust cattle breeds with a moderate grazing pressure can be considered as a feasible tool for preserving and enhancing biodiversity of alkaline habitats. In sand grasslands, we recommend to apply a lower grazing pressure or grazing in shorter periods in order to avoid the degradation of the habitat.

Erweiterte deutsche Zusammenfassung

Einleitung – Extensiv bewirtschaftete Trockenrasen beherbergen seltene und gefährdete Arten und spielen eine entscheidende Rolle für die Bewahrung der Artenvielfalt im Offenland (DENGLER et al. 2014). Trotz dieser enormen naturschutzfachlichen Bedeutung hat sich ihre Fläche im Lauf des vergangenen Jahrhunderts dramatisch verringert, hauptsächlich durch Umwandlung in Ackerland und Ausweitung von Siedlungen (DEÁK et al. 2016a, b). Die floristische Zusammensetzung und Diversität der verbliebenen Trockenrasen wird nur durch Wiedereinführung der traditionelle Bewirtschaftung zu erhalten sein, welche die ursprünglichen natürlichen Störungsfaktoren ersetzen. Beweidung durch lokale, robuste Rinderrassen gilt hierzu als praktikables Instrument (TÖRÖK et al. 2014).

Im Rahmen der vorliegenden Studie wurde die Wirkung von Beweidung in drei verschiedenen Typen von pannonischen Trockenrasen und auf unterschiedlichen Flächenskalen untersucht. Unsere Fragestellung lautete: (1) Hat extensive Beweidung einen Einfluss auf die Gefäßpflanzenvielfalt von Salz- und Sandtrockenrasen, und wenn ja, ist dieser Einfluss je nach betrachteter Flächengröße unterschiedlich? (2) Wie wirkt sich Beweidung auf den Anteil der Spezialisten, Generalisten und gesellschaftsfremden Arten („Unkräuter“) in den drei Rasentypen aus?

Methoden – Unsere Untersuchungsgebiete liegen in der Großen Ungarischen Tiefebene im östlichen Ungarn. Wir untersuchten die folgenden drei Gesellschaften: *Artemisio santonici-Festucetum pseudovinae*, *Achilleo setaceae-Festucetum pseudovinae* (beides Salztrockenrasen) und *Potentillo arenariae-Festucetum pseudovinae* (Sandtrockenrasen). Es wurden sowohl beweidete als auch nicht-beweidete Flächen untersucht. Die beweideten Flächen wurden seit mindestens fünf Jahren jeweils von Mitte April bis Ende September mit robusten Rindern bestoßen. Insgesamt wurden im Juni 2008 30 Flächen aufgenommen, und zwar jeweils eine beweidete und eine unbeweidete, an fünf Lokalitäten pro Gesellschaft (Abb. 1). Um die Wirkung der Beweidung auf verschiedenen räumlichen Skalenebenen zu untersuchen, verwendeten wir ein „nested plot design“: In einer Ecke der 16 m² großen quadratischen Aufnahmeflächen wurden zusätzlich jeweils 10 quadratische bzw. rechteckige Teilflächen von 0.01 m², 0.0625 m², 0.125 m², 0.25 m², 0.5 m², 1 m², 2 m², 4 m² und 8 m² Größe erhoben (Anhang E1). Beginnend mit der kleinsten Teilfläche wurden alle Gefäßpflanzen notiert. Um den Effekt von Beweidung und Flächengröße sowie deren Interaktion zu analysieren, erstellten wir lineare und quadratische Regressionsmodelle und verglichen diese mit ANOVA. Unterschiede zwischen beweideten und nicht-beweideten Flächen wurden mit Wilcoxon signed-rank test, Jaccard similarity index und DCA untersucht.

Ergebnisse – Wir fanden insgesamt 24 Arten im *Artemisio-Festucetum*, 41 im *Achilleo-Festucetum* und 60 im *Potentillo-Festucetum*. In den beweideten Flächen betrug die Gesamtartenzahl 22, 39 und 36 und in den nicht-beweideten Flächen 9, 23 und 44 (Anhänge E2-4). Im *Artemisio-Festucetum* nahm sowohl die Gesamtartenzahl als auch die Zahl der Spezialisten und Unkräuter mit der Beweidung zu, nicht aber die Zahl der Generalisten. Im *Achilleo-Festucetum* nahm die Artenzahl in allen Kategorien zu. Im *Potentillo-Festucetum* führte die Beweidung zwar zu einer Zunahme der Generalisten und Unkräuter, die Zahl der Spezialisten nahm jedoch ab, während die Gesamtartenzahl gleich blieb (Abb. 2–3, Tab. 1). Die floristische Ähnlichkeit zwischen beweideten und nicht-beweideten Flächen nahm im *Achilleo-Festucetum* und *Potentillo-Festucetum* mit der Flächengröße zu, im *Artemisio-Festucetum* änderte sie sich mit der Flächengröße nicht (Abb. 4). In der Ordination wurden sowohl die drei Gesellschaften als auch die beweideten und nicht-beweideten Flächen deutlich voneinander getrennt. Die 1. Achse entspricht dabei dem Bodengradienten mit von links nach rechts abnehmendem Salzeinfluss. (Abb. 5).

Diskussion – Wir konnten zeigen, dass Beweidung einen deutlichen Einfluss auf die Artenzahl und floristische Zusammensetzung der drei untersuchten Rasentypen hat. In den Salztrockenrasen (*Achilleo-Festucetum* and *Artemisio-Festucetum*) wurde die Diversität durch Beweidung gefördert. Wir fanden – in teilweisem Widerspruch zu der Hypothese von OLFF & RITCHIE (1998) – eine signifikante Zunahme der Artenzahl oberhalb von 0.0625 m², was mit veränderten Konkurrenzbedingungen und einem höheren Angebot an Mikrostandorten erklärt werden kann (METERA et al. 2010, DENGLER et al. 2014).

Auffallend ist, dass sich speziell im *Artemisio-Festucetum* kaum ruderale Arten etablieren konnten. Dies hängt wohl mit der hohen Salzkonzentration im Boden zusammen (DEÁK et al. 2014a, VALKÓ et al. 2016a, b). Im Gegensatz dazu fanden wir in den Sandtrockenrasen (*Potentillo-Festucetum*) keine Zunahme der Artenzahl. Die Zahl der Spezialisten nahm durch Beweidung sogar ab, während die Unkräuter zunahmen. Der Grund hierfür ist wohl in der fehlenden Anpassung der Arten an Beweidung und den sehr trockenen Standortsbedingungen (DE BELLO et al. 2007), aber auch im Landschaftskontext zu suchen. Die trittbedingte Degradation der Standorte in Kombination mit Diasporendruck aus den umliegenden Ackerflächen und Brachen führt zu einer Ruderalisierung der Bestände.

Schlussfolgerungen für den Naturschutz – Traditionelle, mäßig intensive Beweidung durch lokale, robuste Rinderrassen kann als brauchbares Instrument zur Erhaltung und Förderung der Biodiversität in Salztrockenrasen angesehen werden. In Sandtrockenrasen sollte die Beweidung dagegen nur in sehr geringer Intensität und nur für kurze Zeit stattfinden, um eine Degradation der Standorte zu verhindern.

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Supplements

Additional supporting information may be found in the online version of this article.

Zusätzliche unterstützende Information ist in der Online-Version dieses Artikels zu finden.

Supplement E1. Sample design showing the nested series of subplots.

Anhang E1. Stichprobenplan, der die genestete Serie von Teilfächen zeigt.

Supplement E2. Species list, species groups and frequency of species in grazed and non-grazed *Artemisio-Festucetum* grasslands.

Anhang E2. Artenliste, Artengruppen und Frequenz der Arten in beweideten und nicht beweideten *Artemisio-Festucetum*-Grasländern.

Supplement E3. Species list, species groups and frequency of species in grazed and non-grazed *Achilleo-Festucetum* grasslands.

Anhang E3. Artenliste, Artengruppen und Frequenz der Arten in beweideten und nicht beweideten *Achilleo-Festucetum*-Grasländern.

Supplement E4. Species list, species groups and frequency of species in grazed and non-grazed *Potentillo-Festucetum* grasslands.

Anhang E4. Artenliste, Artengruppen und Frequenz der Arten in beweideten und nicht beweideten *Potentillo-Festucetum*-Grasländern.

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