High species richness of sheep-grazed sand pastures is driven by disturbance tolerant and weedy short-lived species

Gergely Kovacsics-Vári[1], Judit Sonkoly[1], Katalin Tóth[1], Andrea McIntosh-Buday[2], Patricia Díaz Cando[1], Viktória Törő-Szijgyártó[1], Nóra Balogh[1], Luis Guallichico Suntaxi[1], Francis Espinoza Ami[1], Gábor Matus[1], Béla Tóthmérész[3], and Peter Torok[1]

[1]University of Debrecen
[2]HUN-REN-UD Functional and Restoration Ecology RG
[3]Debrecen University

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Abstract

We selected 15 sheep-grazed sand pastures along increasing grazing intensity to study fine scale biomass patterns of main fractions (green biomass, litter) and that of plant species and functional groups (life forms and social behaviour types). We classified them into five grazing intensity levels based on stocking rate, proximity to drinking and resting places, and the number of droppings and other tracks of grazing animals. We formulated three study questions: i) How does increasing intensity of sheep grazing affect the amount of green biomass, species richness and their relationship in sand pastures? ii) How does increasing intensity of sheep grazing affect the biomass of perennial and short-lived graminoids and forbs? iii) How does disturbance value (expressed in the biomass ratio of disturbance tolerant and ruderal species) change along the gradient of grazing intensity? A unimodal relationship between green biomass and species richness was detected. Along the grazing intensity gradient, we found an increasing trend for species richness; significant differences for green biomass (decreasing trend) and litter (decreasing trend), moreover for graminoids (decreasing trend), and short-lived forbs (increasing trend). We found an increasing amount of disturbance tolerant and ruderal species with increasing grazing intensity. We concluded that stocking rate and proximity to drinking and resting places jointly affected vegetation and created an uneven pattern for composition and amount of biomass in all grazing intensity levels. Our findings might be instructive for pastures in densely populated regions which are prone to the encroachment of disturbance-tolerant and ruderal species.

Introduction

It is a truism in ecology that grazing has a crucial role in maintaining grassland biodiversity (Briske, 1996; Metera et al., 2010); although it is a disturbance that affects both morphological characteristics and functional trait composition of plant communities (WallisDeVries et al., 2002; Díaz et al., 2007). Effects of grazing on species composition, vertical and horizontal structure, regeneration capacity, and functional composition are necessary to study to avoid overgrazing (Dong et al., 2012; Hao & He, 2019), which is one of the most serious problems in sustainable management of pastures in many regions of the world (Gao & Li, 2016; Li et al., 2018a; Török & Dengler, 2018). Former research found that plant community responses along a gradient of grazing intensity showed marked changes, which leaded to altered stability and ecosystem functioning (Li et al., 2018b). When studying the effect of grazing, grazing intensity, livestock and habitat types can be regarded as sort of main approaches, and various combinations of these approaches can be found in the scientific literature.

Sheep grazing has some specific characteristics, for example i) there is a higher selectivity for forbs compared to cattle grazing; in addition, ii) sheep can consume plant parts closer to the ground, iii) and sheep rather prefers vegetative plant parts (Metera et al., 2010; Jerrentrup et al., 2015; Tóth et al., 2018). Sheep grazing likely supports seedling establishment on bare soil surfaces: (i) seeds lying on the soil surface can be buried to an optimal depth for germination by sheep trampling (Eichberg et al., 2005); (ii) flocks usually consist of up to a few hundred head of sheep, and are frequently herded by shepherds for relatively long distances; consequently, they can contribute to high dispersal distance for certain seeds (Rosenthal et al., 2012), (iii) moreover, sheep trampling opens dense vegetation cover, and it can create safe sites for seedling emergence and establishment (Faust et al., 2011; Freund et al., 2014).

Species richness often shows a humped-back curve along a gradient of increasing disturbance or along an increasing amount of biomass; these patterns can be explained by the intermediate disturbance hypothesis (Connell, 1978; Gao & Carmel, 2020). These findings are also supported by studies dealing with sheep grazing (del Pozo et al., 2006; Süss et al., 2007; Lázaro et al., 2016). However, the spatial (Süss et al., 2007) and temporal scale of the study (del Pozo et al., 2006) can influence the detection of a humped-back relationship and monotonously decreasing species richness can be also detected, which was the case for example in sheep-grazed desert steppes (Zhang et al., 2018).

Beside of the nature and patterns of biodiversity, a further important question arises is how changes in species richness are reflected in the abundance of plant life- and growth forms. In their meta-analysis, Díaz et al. (2007) analysed plant trait responses to grazing. They found that increasing grazing intensity favoured stoloniferous plants, rosette formation likeliness, short height, and increased the abundance of short-lived and fast-growing species when climatic conditions and grazing history were both taken into consideration. Some findings of the above meta-analysis were partly confirmed for sheep-grazed pastures by Pettit et al. (1995), Yang et al. (2022) and Farmilo et al. (2023). However, none of the above papers studied the biomass of life- and growth form groups along a gradient of grazing intensity in sheep grazed pastures.

Studying sheep-grazed pastures can lead to a better understanding of the functioning of low productivity ecosystems (Süss et al., 2007) like the less-studied sand grasslands classified in the EU Habitat Directive as Pannonian and Pontic sandy steppes (E 1.1a). Sandy steppes are situated in Central and Southeast Europe and are critically endangered according to EC Directorate-General for Environment et al. (2017). With the study of sand pastures maintained by an increasing intensity of sheep grazing we aimed to address the following study questions: i) How does increasing intensity of sheep grazing affect the amount of green biomass, species richness and their relationship in sand pastures? ii) How does increasing intensity of sheep grazing affect the biomass of perennial and short-lived graminoids and forbs? iii) How does disturbance value (expressed in the biomass ratio of disturbance tolerant and ruderal species) change along the gradient of grazing intensity?

Materials and Methods

Study area

We selected altogether 15 sand pastures (Table 1) for study in the Nyírség region, East Hungary where there is a high proportion of man-made habitats such as croplands and tree plantations (Botta-Dukát, 2008). The Nyírség region is characterised by an annual rainfall ranging between 530–680 mm, while the average temperature is between 9.4–9.8°C (Dövényi, 2010). In some years, annual rainfall is even less than 400 mm and some serious drought events occur (Négyesi, 2018). The physical soil type of the selected sites is typically coarse sand. The pH of the studied sites ranged from 4.45–5.71, except for site 12 which is characterised by a pH of 7.26 (site codes are found reported in Table 1). Soils of the studied pastures are rather poor in humus (0.6–2.6 m/m %). Some further characteristics of the soil of the study sites are summarised in Table 2.

Sampling

We sampled the biomass of 15 pastures from late May to early June 2021 (Table 1). The pastures were managed by seasonal pastoral sheep grazing (Merino breed, typically from early April to the end of October). Two sites had been fenced for 13 years (since the summer of 2008) to exclude livestock grazing (Aszalósné Balogh et al., 2023). With the selected pastures, our aim was to cover a broad range of grazing intensity.

For the pasture and site selection beside livestock unit/hectare (LU/ha), the proximities of drinking and/or resting places of livestock, the number of droppings and other tracks of livestock grazing were considered (see further details for intensity classification in Table 1 and Table 3). Information on current and past livestock type and intensity levels were provided by National Park rangers, and current grazing intensities have also been refined during the field sampling by inspecting herders and livestock herds. National Park rangers also helped in site selection and supported our assumption that stocking rate (LU/ha) in itself is not sufficient for evaluating grazing intensity levels, which was also stressed by some former studies (e.g., Tonn et al., 2019). Considering this information, we classified our sampling sites into five grazing intensity categories explained more in detail in Table 3.

In each pasture, we designated a 10 m × 10 m sampling site to ensure uniform biomass sample heterogeneity. Before the biomass sampling, we recorded the complete list of vascular plant species in the sites to ease the biomass sorting in the laboratory. In each sampling site, we harvested the total aboveground biomass in ten, 20 cm × 20 cm plots (altogether 150 samples) using secateurs. Standing litter and the litter layer were also included in the samples. The samples were dried using a laboratory oven (65°C for 48 hours). After drying, biomass was sorted to main fractions such as moss, lichen, litter (including both the litter layer and standing litter) and green biomass. Green biomass was further sorted to vascular plant species while moss and lichen fractions were not sorted further. The sorted biomass fractions were measured by a tare balance (accuracy: 0.01 g).

We also collected pooled soil samples during the biomass sampling (at least 500 g air-dried soil in total for each sampling site, pooled soil samples collected from the ten biomass sampling plots) from the upper 5 cm soil layers in each site where biomass was harvested to characterise the average site properties,. Soil samples were analysed in an accredited laboratory; the physical soil type, pH, humus content, NO_2^- and NO_3^- contents, K_2O, $P_4 O_{10}$, $CaCO_3$, and water-soluble salt contents were assessed (Table 2).

Data processing and analyses

Supporting the functional analysis of the sorted biomass of vascular plant species, we obtained regional plant trait data from the Pannonian Database of Plant Traits (PADAPT, Sonkoly et al., 2023). We also classified the species into simplified morpho-functional groups of short-lived forbs, short-lived graminoids, perennial forbs, and perennial graminoids using PADAPT and Király (2009). We classified the detected species to Social Behaviour Types (SBT, a refined CSR classification adapted to the Hungarian flora by Borhidi, 1995). Using the SBT classification system, we grouped the species into three categories along an increasing disturbance tolerance of the species: 1) sand grassland species including the categories competitors (C), specialists (S), generalists (G) and natural pioneers (NP) of sand grasslands, 2) natural disturbance tolerant species (DT), and 3) ruderal weedy species including the categories ruderal competitors (RC), adventive competitors (AC), and weeds (W). For each plot, we calculated community-weighted means (CWMs) of this ordinal variable (groups 1, 2, and 3, respectively) weighted by biomass values and used it as an ecological indicator value of disturbance (= disturbance value) in the analyses. We used generalized linear mixed-effect models (GLMMs) to assess the impact of sheep grazing (intensity level included as a fixed factor, site identity as a random factor) on dependent variables (see listed variables in Table 4, SPSS 26.0 program package; IBM Corp., 2019). We plotted the species richness along increasing green biomass and analysed their relationship by fitting second order polynomial fit. The biomass composition of sites and grazing intensities were explored by Canonical correspondence analysis (CCA) calculated by CANOCO 5.0 program package (Šmilauer & Lepš, 2014). We included seven variables (soil phosphorous content, pH, soil compactness, soil nitrogen content, soil potassium content, disturbance value, soil humus content) to secondary explanatory matrix of the CCA and selected significant predictors by a Monte-Carlo permutation test. Only significant explanatory variables are shown in the figure (499 permutations,p <0.008).

Results

We detected 84 species in the samples consisting of 24 graminoids (8 short-lived and 16 perennial), and 60 forbs (36 short-lived and 24 perennial). Grazing intensity had a significant effect on green biomass + litter, green biomass, litter, the biomass of perennial forbs, perennial graminoids, short-lived forbs as well as on the species richness and disturbance (Table 4). The species richness at the fourth and fifth level of intensity was significantly higher than that of the second level, and we detected the highest richness at the fourth level of grazing intensity (Figure 1A). For disturbance values, the fifth level was significantly higher compared to all other levels (Figure 1B). We detected a humped-back relationship between the amount of green biomass and the species richness (Figure 2).

We also detected significant differences for green biomass + litter, litter (highest scores at the first level of intensity). For litter, we detected higher scores at the first and second level of intensity compared to the other levels (Figure 3A, B, C); moss + lichen biomass did not show a significant difference along the intensity levels (Table 2; Figure 3D). Perennial forb biomass showed the highest scores at the fourth level of intensity (Figure 4A). The perennial graminoids' biomass was significantly higher at the second level of intensity than at the fourth and fifth levels (Figure 4B). We found no significant difference in the biomass of short-lived forbs between the first and fourth level of intensity while that of at the fifth level was significantly higher compared to the other levels (Figure 4C). The biomass of short-lived graminoids did not show significant differences (Table 4; Figure 4D).

The CCA identified only two significant predictors for the species compositional patterns : soil humus content and disturbance tolerance, but these two predictors were weakly correlated with each other (Figure 5). We found no clear separation of pastures grazed with different levels of intensity based on the biomass composition and sites with increasing levels of grazing intensity were also not separated along the predictors. The samples of the different sites did not show clear separation along either the axis of green biomass quantity or the species richness also in Figure 2.

Discussion

Species richness and green biomass

We found a humped-back relationship between species richness and green biomass that supports the intermediate disturbance hypothesis (Connell, 1978; Gao & Carmel, 2020). Moderate levels of disturbance provide favourable conditions for a wider range of species (Metera et al., 2010). The highest species richness were detected at the fourth and fifth grazing intensity levels. In accordance with our results, several studies detected that species richness is higher under moderate grazing pressure than, for example, in ungrazed pastures (Sasaki et al., 2009; Fensham et al., 2011; Deng et al., 2013). According to the results of Deng et al. (2013), the density, the height, and the cover of vegetation were the highest in the ungrazed parcel. Furthermore, the density of dominant, good competitor species had the highest scores in the ungrazed parcel. When grazing intensity is low, better competitor plants can reach greater height as they acquire more resource, and can overcome resource limitation more effectively in dense, ungrazed vegetation and grow efficiently (Westoby et al., 1999; He et al., 2021). Livestock grazing decreases green biomass and litter (Magnano et al., 2019) which is obviously more pronounced under more intensive grazing. These findings can explain the higher proportion of biomass samples belonging to the first and second level of intensity at higher biomass values (Figure 2). Although we detected a humped-back relationship between species richness and green biomass in the studied pastures, the possibility of a decreasing trend should not be excluded in unusually arid years (Milchunas et al., 1988; Gao & Carmel, 2020).

One would expect that the samples originating from the same grazing intensity levels would cluster in the ordination, but this was not validated by the results (see Figure 5). The likely reason for this is that there might be a fine-scale heterogeneity of vegetation. Fine-scale heterogeneity may have several reasons we wish to detail on below. Godó et al. (2017), studying the vegetation composition of alkaline and sand pastures at multiple-scales, observed that there is a significant relationship between the plot size and grazing effects: with increasing plot size they found decreasing levels of differences in species composition, i.e. the small-sized plots showed higher beta diversity than larger ones. This is likely the reason why our fine-scale samples (harvested in 20 cm $\times$ 20 cm plots) were not clearly separated along the gradient of green biomass and species richness. Beside of the selective defoliation effects of grazing, fine-scale heterogeneity of vegetation is also supported by multiple fine-scale side effects provided by grazing: uneven patterns of trampling, defecation, and seed input with dung or fur (Ruifrok et al., 2014). Grazing also supports the formation of bare soil patches (Eichberg & Donath, 2018) and provides higher availability of light (Ruifrok et al., 2014). But the bare soil surfaces can also act as safe sites for weedy species to colonize. In pastures intensively grazed by sheep, we can expect higher amounts of bare soil surfaces than under lower grazing intensity based on the results of former research (Watt & Gibson, 1988; Süss & Schwabe, 2007; Teuber et al., 2013). However, the seeds of several species cannot successfully germinate if they fall on bare soil surface, unless they get buried to an optimal depth subsequently, which might be ensured by the trampling of sheep (Eichberg et al., 2005).

Plant species with variable characteristics are also able to diversify the fine-scale species richness and biomass: in grazed pastures, coexistence between plant species occurs more frequently if the grazing intensity is suitably low (Vázquez-Ribera & Martorell, 2022), which contributes to a vegetation consisted of more variable plants. Briske (1996) explains in detail how the different plant characteristics contribute to a better grazing resistance, for example herbivore accessibility is limited if plant height is lower. Based on this argument, it is reasonable that plant height is more varied at moderate levels of grazing where short and tall plants are alike occurred. This idea, the distribution of our samples, and the humped-back relationship are confirmed also by Oksanen (1996) who argued and visualized that humped-back relationship can even be artificially produced if following the rules that the number of plant individuals increases below a "crowding point" (where grazing resistant species are more frequent), but above it (where better competitor species are more frequent), plant size is what rather increases, therefore (in the sense of intermediate disturbance) the highest species richness is at intermediate biomass, if using small, fixed plot size. Beyond these assumptions, it should be added that the spatiotemporal patterns of grazed and ungrazed fine-scale patches is another important variable that reasonably becomes less marked with the extremely increased or decreased grazing intensity.

Main biomass fractions and the biomass of life forms

We found significant differences along the grazing intensity gradient for main biomass fractions and biomass of life forms as well. Both the green biomass + litter fraction and the litter fraction were significantly lower at higher grazing intensities. Consumption of plants by livestock contributes to a decreased green biomass and litter (Magnano et al., 2019). According to Kemp et al. (2000), perennial graminoids are the most sensitive to grazing, and with increasing grazing disturbance, subordinated species are enabled to spread (Grime & Mackey, 2002) which might explain why we detected significantly lower amounts of perennial graminoids at higher grazing intensities. Green biomass showed significant differences and though the biomass of short-lived forbs was significantly higher at the highest grazing intensity, total green biomass fraction decreased with increasing grazing intensity. Three explanations may be behind this pattern. First, grazing may be less selective at higher intensities (Golodets et al., 2009; Tóth et al., 2018), which causes a net loss of total green biomass, but at the same time it favours short-lived forbs, due to their fast regrowth rate and colonization ability in gaps (Westoby et al., 1999; Hofmann & Isselstein, 2004). Second, the mean height of species is typically lower at higher grazing intensities (Deng et al., 2013; Török et al., 2016), therefore, they may be represented by less biomass. Third, specific leaf area (SLA, mm^2/mg) is higher, and leaf dry matter content (LDMC, mg/g) is lower in case of annuals, thus, their dry weight is lower than those with higher LDMC and lower SLA (E-Vojtkó et al., 2020). In the meta-analysis of plant responses to grazing, Díaz et al. (2007) found that the abundance of perennial plant species decreased with increasing grazing intensity. This was also confirmed by our results to an extent, but a striking leap can be observed at the fourth level of intensity for perennial forbs. Among the detected perennial forbs, *Thymus glabrescens* had remarkably high values at this intensity level. Without this species, there would be a continuous decline of perennial forb biomass along the gradient of grazing intensity. Their extensive woody stems increase the biomass of perennial forbs, moreover, their large amount of biomass also shapes the differences of the total green biomass scores. Phytochemicals (monoterpenes) produced by *Thymus vulgaris* means protection against grazers (Cappuccino & Carpenter, 2005), therefore it is reasonable to think that *Thymus glabrescens* in our studied pastures is similarly not favoured by grazers. The meta-analysis mentioned above (Díaz et al., 2007) details the response of annuals to grazing; it was found that they increased together with the grazing intensity which is confirmed by our results in case of forbs. Another explanation for successfully spreading short-lived plants is their generally higher SLA values compared to perennials. High SLA is linked to fast re-growth ability (Helm et al., 2019) and higher SLA scores at higher grazing intensities were confirmed by a former study addressing livestock grazing in sand grasslands (Kovacsics-Vári et al., 2023). We found no significant differences for short-lived graminoids which is presumably due to their low species number and the even distribution of the species along the gradient of grazing intensity. For example,*Apera spica-venti* was represented by higher amounts at lower intensity levels, meanwhile *Bromus hordeaceus* had higher biomass at higher intensities.

Impact of grazing disturbance on species composition

Significantly higher biomass scores of disturbance tolerant and ruderal species were detected at the highest grazing intensity level. A process leading to overgrazing is written in a simply summarized form by Schulze et al. (2019): First, the vegetation composition changes; second, vegetation cover decreases, third, bare soil surfaces are formed, and fourth, soil erosion becomes more severe. Our results might support this description, but we presume that these stages are not reached step by step but occur in parallel. For example, when bare soil surfaces are formed, further changes can be expected also in vegetation cover as gap strategists take the advantage of disturbance and they establish quickly. When grazing tolerant species with a good colonising and/or fast-regrowth ability (Westoby et al., 1999) cannot keep up with the severity and frequency of grazing the fourth step may take effect. This fourth step might be in accordance with the slightly lower species richness at the fifth level of grazing intensity compared to the fourth level. In our study, the disturbance value did not differ strikingly between the first and the fourth intensity level, however, at the fifth level, scores were significantly higher compared that of other levels. Therefore, we can conclude that the proportions of disturbance tolerant and ruderal species were considerable at the highest grazing intensity, and this is well in accordance with the proportion of short-lived forb biomass as they typically represent these groups. The high disturbance values and proportions within the simplified morpho-functional groups indicated a stronger disturbance and a process leading to overgrazing. Midolo et al. (2021) valued plant species by disturbance categories, and they detected that annuals are favoured by disturbance as their ability to grow fits to circumstances which do not provide stable biotic and abiotic features that otherwise would be favoured by better competitors using resources efficiently on the long-run (Salguero-Gómez, 2017; Schulze et al., 2019). In contrast, Pettit et al. (1995) and Farmilo et al. (2023) found no significant differences between ungrazed and grazed samples for native annual forbs.

At the highest level of grazing intensity, the highest disturbance value confirms also the observation of Botta-Dukát (2008) according to whom open sand grasslands are among the most exposed habitats to disturbance in Hungary. The Nyírség region has been densely populated for centuries, and despite the low productivity of sand grasslands, large areas were cultivated with high cover of disturbance tolerant and ruderal weedy species. Thus, the vegetation composition of pastures with opening surfaces can be likely colonised by these species having typically a good dispersal ability (Schulze et al., 2019).

The fourth and fifth level of grazing intensity included sampling sites with relatively high stocking rates (1.1 to 4 LU/ha), and the highest scores of species richness were observed at these levels which is due to the higher number of short-lived species. Increasing species richness in more intensively grazed sites was also confirmed by Kiss et al. (2006). In their assessment of grazing intensity, they considered the proximity of study sites to stables, and similarly to us, they detected a higher proportion of disturbance tolerant and weedy species contributing to the higher species richness. We detected significantly higher species richness at the fifth and fourth level of intensity compared to the second level. At the fourth level, presence of grassland species is still substantial, in addition disturbance tolerant and weedy species appeared more frequently. One can find significantly different scores if second and fourth intensity levels are compared to the third and fifth intensity levels which implies the possibility that flocks of sheep graze and trample the sites representing the third and fifth level more frequently. These significant differences suggest that stocking rate (LU/ha) and proximity jointly drive changes in vegetation. A higher grazing frequency and intensity are presumed with the higher proximity to resting and watering points. The joint impact of proximity and stocking rate on plant characteristics can be similarly explored in the study by Kovacsics-Vári et al. (2023) for flowering period and life forms. In addition, the findings by Kiss et al. (2006) and Tonn et al. (2019) suggest that the effect of livestock should be studied on finer scales than the scale of a pasture, since LU/ha, as an important metric in grazing regimes, is determined for the entire pasture area.

Conclusions

We detected a humped-back relationship between green biomass and species richness in the studied sand pastures, but the plots characterised by different grazing intensities were not separated along the biomass gradient from each other. This clearly indicated that i) grazing intensity levels assessed by the stocking rate on the pasture level is too robust to assess effects of grazing intensity on the vegetation, and ii) even sheep grazing created a highly patchy vegetation at the scale of the biomass sampling both for species richness and biomass. These results also suggests that in case we would like to reveal the intensity-dependent distribution of biomass samples we need to use multiple scales for sampling, and a fine-scale assessment of grazing intensity. With this paper, we might take a step in revealing that the stocking rate and the grazing frequency can jointly drive the vegetation. In terms of grazing frequency, we formulated assumptions based on the impact of proximity but to find clearer effects, a broader knowledge about each pasture is needed e.g., with studying rotational grazing or elaborating other ideas.

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Tables

Table 1. Main characteristics of the studied sites. Notations: site codes are used for CCA (Figure 5). Grazing intensities are explained in Table 3.

Site codes	Settlement name	GPS coordinates	GPS coordinates	Elevation (m)	Area of pasture (ha)
1	Létavértes	47.41797	21.89950	116	200
2	Létavértes	47.42269	21.91110	117	200
3	Létavértes	47.44133	21.92817	120	130
4	Hajdúbagos	47.41580	21.68023	107	140
5	Hajdúbagos	47.41183	21.68336	109	140
6	Létavértes	47.42478	21.86181	116	200
7	Létavértes	47.42928	21.86382	114	200
8	Martinka	47.57292	21.77960	129	126
9	Martinka	47.57391	21.78137	130	126
10	Martinka	47.57486	21.79247	130	76
11	Monostorpályi	47.40945	21.77691	112	45

Site codes	**Settlement name**	**GPS coordinates**	**GPS coordinates**	**Elevation (m)**	**Area of pasture (ha)**
12	Monostorpályi	47.41554	21.78521	112	45
13	Martinka	47.58068	21.77093	132	57
14	Martinka	47.57541	21.79281	131	Grazing exclusion
15	Vámospércs	47.53241	21.95022	132	Grazing exclusion

Table 2. Soil properties of the studied sites. Notations: site codes are used for CCA (Figure 5). Total, water soluble salt content and $CaCO_3$ content were low and the same in the sample sites, therefore they are not shown in the table (total salt: <0.02 m/m%; $CaCO_3$ <0.1 m/m %). K_2O and P_4O_{10} are $C_3H_9O_3N$ soluble; NO_2^- and NO_3^- are KCl soluble. Ranges of physical soil type (KA): 25> (coarse sand); 25-30 (sand); 30-37 (sandy loam); 37-42 (loam); 42-50 (clay loam); 50-60 (clay); 60< (heavy clay).

Site codes	**pH (KCl 1:2.5)**	**pH (KCl 1:2.5)**	**Physical soil type [KA]**	**Humus [m/m%]**	**NO_2^- and NO_3^- [mg/kg]**	**K_2O [mg/kg]**	**P_4O_{10} [mg/kg]**
1	5.39	25	25	1.5	2	85	40
2	4.74	25	25	1.8	2	87	58
3	4.45	25	25	1.6	3	65	59
4	5.18	27	27	1.4	1	107	42
5	5.24	25	25	1.3	1	105	34
6	5.24	25	25	1.2	1	101	61
7	5.39	25	25	1.7	2	121	85
8	5.71	28	28	2.1	2	191	2.35
9	5.61	25	25	1.4	2	111	41
10	5.49	25	25	0.8	1	83	82
11	5.03	25	25	0.9	3	53	42
12	7.26	32	32	2.6	3	184	137
13	4.66	25	25	0.7	<1	58	39
14	5.01	25	25	0.6	1	58	38
15	5.22	25	25	0.8	1	75	40

Table 3. Important information of grazing intensities. One head of sheep is equivalent to 0.2 livestock unit per hectare (LU/ha).

Intensity levels	Stocking rate (LU/ha)	Proximity to resting and drinking places (m)	Number of droppings
1	Grazing exclusion	Grazing exclusion	Grazing exclusion
2	0.5 to 0.8	>150	0 to 20
3	0.5 to 0.8	<150	>20
4	1.1 to 4	>150	0 to 20
5	1.1 to 4	<150	>20

Table 4. Effects of sheep grazing on species richness, disturbance and biomass fractions. Significant values (p <0.05) are denoted with **bold face** .

Variables	**Grazing intensity**	**Grazing intensity**
	$F_{4,145}$	p

Variables	Grazing intensity	Grazing intensity
Species richness	5.66	<0.001
Disturbance	**6.24**	**<0.001**
Main biomass fractions		
Green biomass + litter	**11.04**	**<0.001**
Green biomass	**2.49**	**0.046**
Litter	**10.97**	**<0.001**
Moss + lichen	0.953	0.435
Specific biomass fractions		
Perennial forb	**25.88**	**<0.001**
Perennial graminoid	**3.21**	**0.015**
Short-lived forb	**11.20**	**<0.001**
Short-lived graminoid	0.27	0.897

Figure 1. Species richness (A) and disturbance values (B) along a grazing intensity gradient. The letters in the plots denote significant differences [generalised linear mixed-effect model GLMM), estimated mean ± SE and least significant differences]. The detailed explanation of grazing intensity levels 1 to 5, see Table 3.

Figure 2. The link between the green biomass and species richness (estimated mean +- SE). Circles denote the samples collected on site. '+' signs denote the centroids of the samples originating from the same sample site and intensity. Colours and symbols denote the intensity levels of grazing as follows: Intensity 1: green circles, 2: blue triangles, 3: orange diamonds, 4: red rectangles, and 5: lilac stars, second order polynomial fit with 95% confidence interval is displayed ($p<0.001$, $R^2 = 0.143$).

Figure 3. Green biomass + litter (A), green biomass (B), litter (C), and moss + lichen (D) (g, 20x20 cm sample) along the gradient of grazing intensity. The letters in the plots denote significant differences [generalised linear mixed-effect model (GLMM), estimated mean +- SE and least significant differences].

Figure 4. Biomass of perennial forbs (A), perennial graminoids (B), short-lived forbs (C), and short-lived graminoids (D) (g, 20x20 cm sample) along the gradient of grazing intensity. The letters in the plots denote significant differences [generalised linear mixed-effect model (GLMM), estimated mean +- SE and least significant differences]

Figure 5. Relationship between species composition, humus contents, and level of disturbance (CWM of SBT categories). For Canonical Correspondence Analysis, the biomass weights by species were used. Eigenvalues were 0.617 and 0.504 for the first and second axis, respectively. Cumulative percentage variance of species-environment relation was 82.2 for the first four axes. Numbers denote the sites (see Table 1) and their colours denote the intensity levels of grazing (1: green, 2: blue, 3: orange, 4: red, and 5: lilac). Eight-letter codes are consisted of the first four letters of genus name and the first four letters of species name. Full name of species with the codes are the followings: ACHICOLL (*Achillea collina*); AGROSTOL (*Agrostis stolonifera*); ANTHODOR (*Anthoxanthum odoratum*); ASPECYNA (*Asperula cynanchica*); CAREHIRT (*Carex hirta*); CAREPRAE (*Carex praecox*); CARESTEN (*Carex stenophylla*); CARESUPI (*Carex supina*); CENTAREN (*Centaurea arenaria*); CERAVULG (*Cerastium vulgare*); CHONJUNC (*Chondrilla juncea*); CORYCANE (*Corynephorus canescens*); ERYNCAMP (*Eryngium campestre*); EUPHCYPA (*Euphorbia cyparissias*); GALIVERU (*Galium verum*); HIERPILO (*Hieracium pilosella*); HYPEPERF (*Hypericum perforatum*); HYPORADI (*Hypochoeris radicata*); MEDIFALC (*Medicago falcata*); PLANLANC (*Plantago lanceolata*); POTEAREN (*Potentilla arenaria*); POTEARGE (*Potentilla argentea*); RUMEACES (*Rumex acetosella*); RUMEACET (*Rumex acetosa*); SILEOTIT (*Silene otites*); TARAERYT (*Taraxacum sect. Erythrosperma*); TARARUDE (*Taraxacum sect. Ruderalia*); THYMGLAB (*Thymus glabrescens*); TRIFREPE (*Trifolium repens*); VEROPROS (*Veronica prostrata*).

Data Accessibility Statement

In case of acceptance the authors will provide underlying data in an open access repository.

Competing Interests Statement

None declared.

Author Contributions section

Gergely Kovacsics-Vari : conceptualization (supporting); data curation (equal); investigation (equal), methodology (supporting), project administration (supporting); validation (supporting); visualization (supporting); writing - original draft preparation; writing - review & editing (supporting). **Judit Sonkoly** : conceptualization (supporting), data curation (supporting); investigation (supporting); validation (supporting); writing - review & editing (supporting). **Katalin Toth** : validation (lead); review & editing (supporting). **Andrea McIntosh-Buday** : data curation (supporting); investigation (supporting); validation (supporting); review & editing (supporting). **Patricia Elizabeth Diaz Cando** : investigation (supporting); review & editing (supporting).**Viktoria Torő-Szijgyártó** : data curation (supporting), investigation (supporting), review & editing (supporting). **Nóra Balogh** : investigation (supporting); review & editing (supporting).**Luis Roberto Guallichico Suntaxi** : investigation (supporting); review & editing (supporting). **Francis David Espinoza Ami** : investigation (supporting); review & editing (supporting).**Gábor Matus** : resources; review & editing (supporting).**Béla Tóthmérész** : conceptualization (supporting); writing - review & editing (supporting). **Péter Török** : conceptualization (lead), data curation (equal); formal analysis; funding acquisition; investigation (equal); methodology (lead); project administration (lead); validation (supporting); visualization (lead); writing - review & editing (lead).

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ORCID

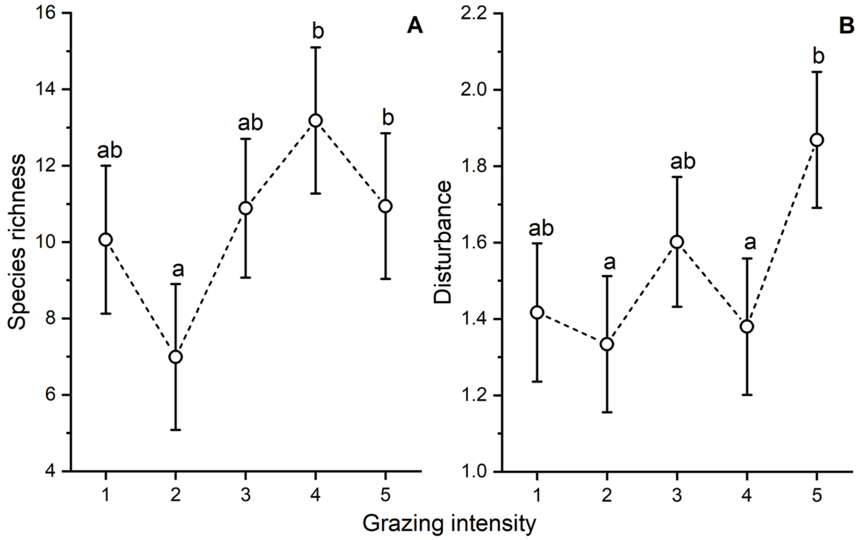
Gergely Kovacsics-Vári: https://orcid.org/0000-0002-9995-5733

Judit Sonkoly: https://orcid.org/0000-0002-4301-5240

Nóra Balogh: https://orcid.org/0000-0002-6156-0752

Béla Tóthmérész: https://orcid.org/0000-0002-4766-7668

Péter Török: https://orcid.org/0000-0002-4428-3327


A
B
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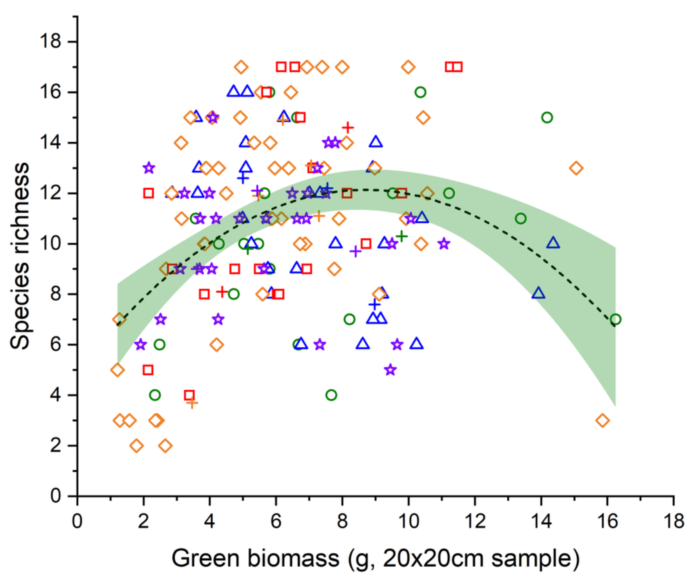
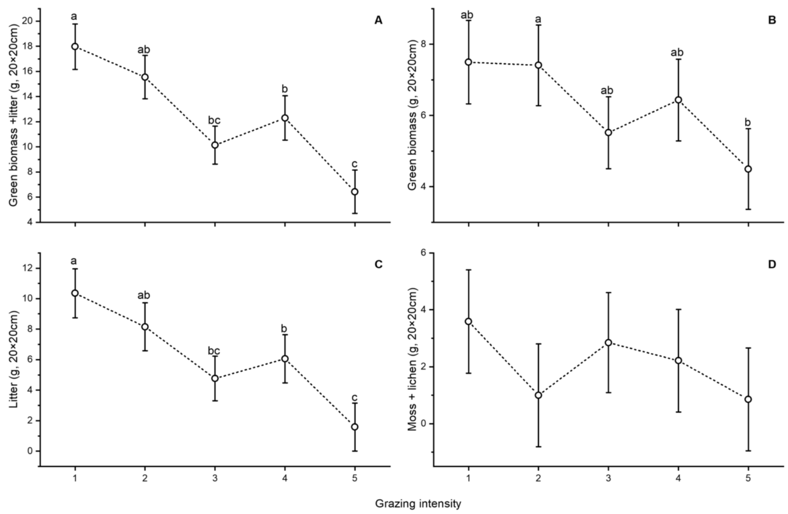
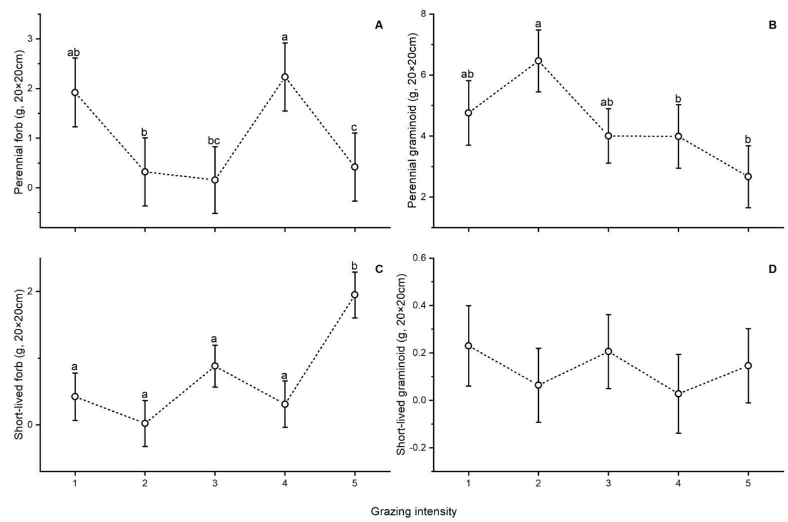
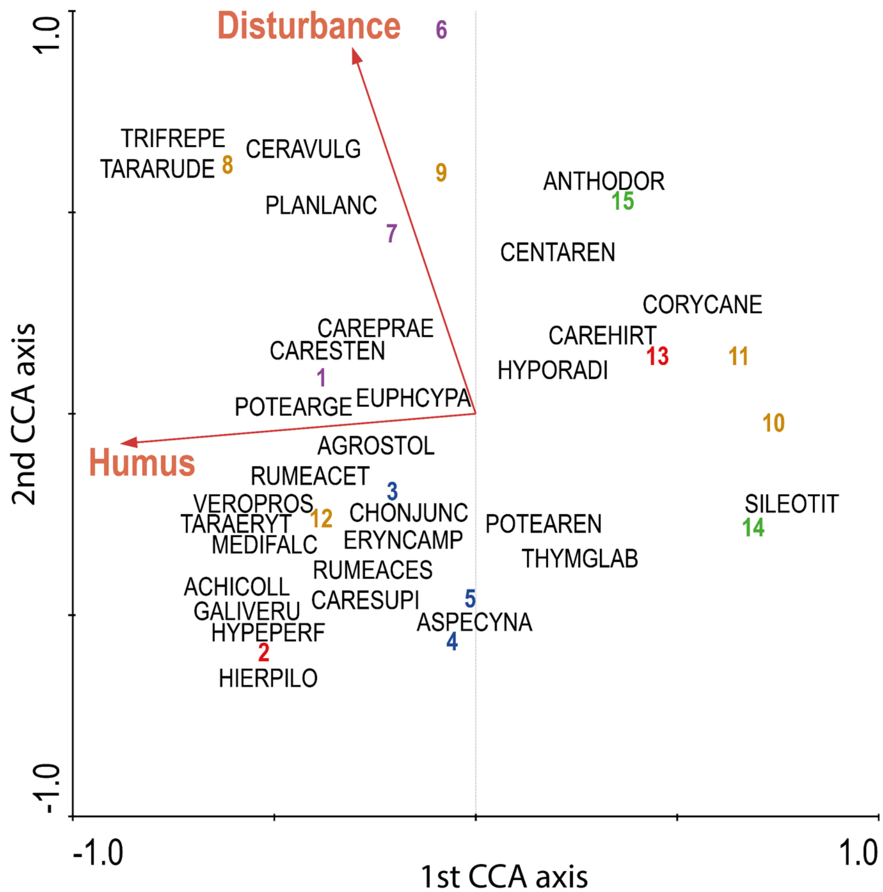
b
Species richness
Disturbance
Grazing intensity


Species richness
Green biomass (g, 20x20cm sample)


A
B
C
D
Green biomass +litter (g, 20×20cm)
Green biomass (g, 20×20cm)
Litter (g, 20×20cm)
Moss + lichen (g, 20×20cm)
Grazing intensity


A
B
C
D
Perennial forb (g, 20×20cm)
Perennial graminoid (g, 20×20cm)
Short-lived forb (g, 20×20cm)
Short-lived graminoid (g, 20×20cm)
Grazing intensity



Disturbance
Humus
1.0
-1.0
2nd CCA axis
1st CCA axis
TRIFREPE
TARARUDE
CERAVULG
PLANLANC
ANTHODOR
CENTAREN
CORYCANE
CAREPRAE
CARESTEN
CAREHIRT
HYPORADI
POTEARGE
EUPHCYPA
AGROSTOL
RUMEACET
VEROPROS
TARAERYT
MEDIFALC
CHONJUNC
ERYNCAMP
POTEAREN
SILEOTIT
THYMGLAB
RUMEACES
ACHICOLL
GALIVERU
HYPEPERF
CARESUPI
ASPECYNA
HIERPILO
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