






Intensity-dependent effects of cattle and sheep grazing in sand grasslands – Does livestock type really matter?

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Abstract

Aims: By analysing cattle- and sheep-grazed sand grasslands, we tested the following hypotheses: (i) livestock type has a stronger effect on the vegetation characteristics than grazing intensity; (ii) sheep grazing results in lower biomass and species and functional diversity than cattle grazing, regardless of intensity; and (iii) increased grazing intensity causes a shift of the trait composition in grasslands.

Location: Sand grasslands in the Nyírség region, East Hungary.

Methods: We selected 26 sand grassland sites grazed by cattle or sheep and classified them into four intensity levels. Vegetation composition was surveyed in 2 m × 2 m plots. We harvested the above-ground biomass from 20 cm × 20 cm plots; then dried and sorted it to live biomass, litter, moss, and lichen. We compared Rao dissimilarity index, species richness, Shannon diversity, evenness, and the community-weighted means of nine vegetative and generative traits along a grazing intensity gradient. We calculated functional richness, evenness, and divergence for comparison.

Results: We found that some diversity metrics and community-weighted means of most studied traits were significantly affected by grazing intensity. Several characteristics were also affected by the interaction of grazing intensity and livestock type, but none of the studied characteristics was affected by livestock type in itself. Increasing Rao dissimilarity index peaking at the fourth grazing intensity level was detected, but for other multitrait indices, no such changes were proven, except for functional divergence, which was the lowest at the first intensity level. Graminoid, forb, and litter biomass were significantly affected by intensity, but none of the biomass fractions was affected by livestock type.

Conclusions: We suggest that for the management of sand grasslands, grazing intensity should be carefully adjusted, considering not only livestock units per hectare. For practical recommendations, well-defined, long-term experiments studying different livestock and habitat types along an intensity gradient would be essential.

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KEYWORDS

cattle grazing, biomass, grazing, grazing intensity, pasture, plant traits, sand grassland, sheep grazing, steppe

1 | INTRODUCTION

Grassland habitats play a crucial role in maintaining landscape-scale biodiversity in agriculture-driven landscapes (Habel et al., 2013; Dengler et al., 2014). The area of grasslands in Europe is around 770,000 km² (not considering the European part of the Mediterranean Basin, and the European part of the Russian Federation; Dengler & Tischew, 2018; Török & Dengler, 2018; Török et al., 2018a). In Europe, management intensity changes in the form of either underuse or agricultural intensification can be considered as the most important drivers of the biodiversity decline of grasslands (Török & Dengler, 2018). Intensive management leads to diversity loss, particularly where humidity is higher (Rahmanian et al., 2020). It also causes decreased biomass (Eldridge et al., 2015), altered decomposition rate through photodegradation (Giese et al., 2009), increased soil compaction reducing water infiltration and microsite humidity, and consequently reduced microbial activity and decomposition rate (Vaieretti et al., 2010).

For sustaining grassland biodiversity, it is crucial to maintain the 'openness' of grasslands by preventing biomass/litter accumulation and shrub encroachment. Historically, open habitats have been maintained by free-ranging wild ungulates and other robust herbivores (Poschlod & WallisDeVries, 2002; Hejman et al., 2013), but in many regions of the World these have been replaced by domestic livestock (Pärtel et al., 2005; Gilhaus et al., 2017; Squires et al., 2018) which also resulted in a decreased diversity of grazers. It has already been stressed that the selectivity of grazers differs for instance between sheep and cattle (Tóth et al., 2018), partly due to their different grazing behaviour (Jerrentrup et al., 2015).

Grazing effects on vegetation include (i) selective biomass removal including live biomass and litter; (ii) alteration of reproductive success of species and modification of the competition-facilitation relationship and symmetry; (iii) alteration of vegetation patterns by influencing microclimate and patch dynamics; (iv) propagule transfer by zoochory; (v) nutrient support by dung and/or urine deposition; and (vi) modification of the physical environment by trampling (Dostálek & Frantík, 2008; Chillo & Ojeda, 2014; Eldridge et al., 2015; Rahmanian et al., 2020; Balogh et al., 2021; Price et al., 2022). These effects can be highly herbivore-specific; they also interact with each other, and they may vary both in space and time (i.e., the timing and duration of grazing should also be considered – Price et al., 2022).

Former studies have indicated that (i) the same levels of grazing intensity (expressed as the number of livestock units per hectare) can have different effects in the same grassland type when different livestock types were used for grazing (van Klink et al., 2016; Tóth et al., 2018), or (ii) the same livestock-type grazing with the same intensity can have different effects in different grassland types (Mládek et al., 2013; Török et al., 2018b). Despite these results,

subsidy systems, including various forms of agri-environmental schemes consider mostly just grazing intensity, but they are less sensitive to the differences between the effects of different livestock types like sheep, cattle, and horse, or to the possible differences between grassland types (Primdahl et al., 2003). It is therefore crucial to analyse grazing effects of different livestock types along an intensity gradient in various grasslands, and report valuable case studies for nature conservation practice and ecological theory, and to analyse the effects not only on the species diversity, but on the functional diversity and composition of the subjected grasslands as well.

Sand grasslands are widely distributed in Europe, harbouring large areas covered with acidic or calcareous sandy substrates. Sand grasslands are used in many regions as sand pastures, and their conservation in the absence of robust wild grazers is highly dependent on livestock grazing. Sand grasslands, especially in the Pannonian region (Pannonian and Pontic sandy steppes according to the EC Directorate-General for Environment et al., 2017), are highly threatened by plant invasions and changes in management intensity (Botta-Dukát, 2008); therefore, their conservation management and the restoration of degraded areas is crucial. Only a few studies dealt with the effect of grazing on sand grasslands (but see Ónodi et al., 2006, 2008). An analysis of grazing effects including multiple levels of grazing intensity and more than a single type of livestock is still lacking.

In our study, the focus is on the effects of increasing intensities of cattle and sheep grazing on the species and trait composition of sand grassland vegetation. We tested the following hypotheses: (i) 'dominance of grazer' hypothesis: livestock type has a higher impact on the studied vegetation than the intensity of grazing; (ii) 'grazer-dependent selectivity' hypothesis: regardless of grazing intensity, sites grazed by sheep have a lower biomass and lower species and functional diversity than sites grazed by cattle; and (iii) 'intensity-induced trait shift' hypothesis: increased grazing intensity causes a shift in the trait composition of the grasslands.

2 | MATERIALS AND METHODS

2.1 | Study area

The studied sand grasslands are in the Nyírség region, East Hungary, in the vicinity of eight settlements (Bagamér, Hajdúbagos, Létavértes, Martinka, Monostorpályi, Nyírbrány, Penészlek and Vámospércs; Figure 1, Appendix S1). The climate of the region is moderately continental, with a mean annual temperature of 9.8°C and a mean annual precipitation of 550–600 mm (Kövendi-Jakó et al., 2019). The physical soil type of the sampling sites is mostly sand, in some sites

sandy-loam or loam with an acidic to neutral soil pH (4.45–7.26). The soil of the sites is characterised by low CaCO_3 and salt contents, and by variable amounts of soil nutrients and humus content (see details in Appendix S2). Compared to other regions of the Great Hungarian Plain, the Nyírség is characterised by high topographic heterogeneity by alternation of sand dunes and depressions and with variable groundwater levels which contribute to the development of different habitats such as marshlands and fen meadows in the depressions and grasslands and oak woods on the dunes (Papp & Dudás, 1988). Anthropogenic activities fragmented and/or eliminated most of these natural habitat mosaics in the 19th and 20th centuries. Nowadays, the Nyírség is covered by a high proportion of native or non-native tree plantations and arable lands (Botta-Dukát, 2008).

2.2 | Sampling setup

The studied sand grasslands are typically managed by various intensities of seasonal and mostly pastoral sheep or cattle grazing, typically between late April and the end of October, with the exception of the pastures of Vámospércs where grazing starts in late July. We selected 26 sand grassland sites with different levels of grazing intensity (Appendix S1). All the selected sites are in the Hortobágy

National Park Directorate. National Park rangers provided information on the grazing intensity levels (expressed as livestock unit per hectare, LU/ha) and livestock types and helped in site selection. Based on the information provided by the national park rangers, the intensity of grazing in the 2017–2021 period was relatively constant with a single exception that a site in Bagamér was not grazed in 2018 (site code: 15 – see Appendix S1). It was stressed by national park rangers and by former studies (e.g., Tonn et al., 2019) that stocking rate expressed in livestock units alone is not sufficient to evaluate the effects of intensity. Thus, when designating the surveyed areas, we considered first the grazing intensity expressed as LU/ha, then the proximity of watering/resting places and number of droppings and other tracks of grazing. Based on the collected information we classified the grazed sites into four grazing intensity levels: First intensity level [intensity was lower than 1 LU/ha, ranging from 0.5 to 0.8, far from watering/resting places (>150m) and low number of droppings detected (typically 0–10 but no more than 20 droppings in 100-m² area)], second [intensity was lower than 1 LU/ha, ranging from 0.5 to 0.8 and close to a watering/resting place (<150m) and high number of droppings detected (more than 20 droppings per 100 m²)], third [>1 LU/ha ranging from 1.1 to 4, far from watering/resting places (>150 m) and low number of droppings detected (typically 0–10 but no more than 20 droppings per 100 m²)], and fourth

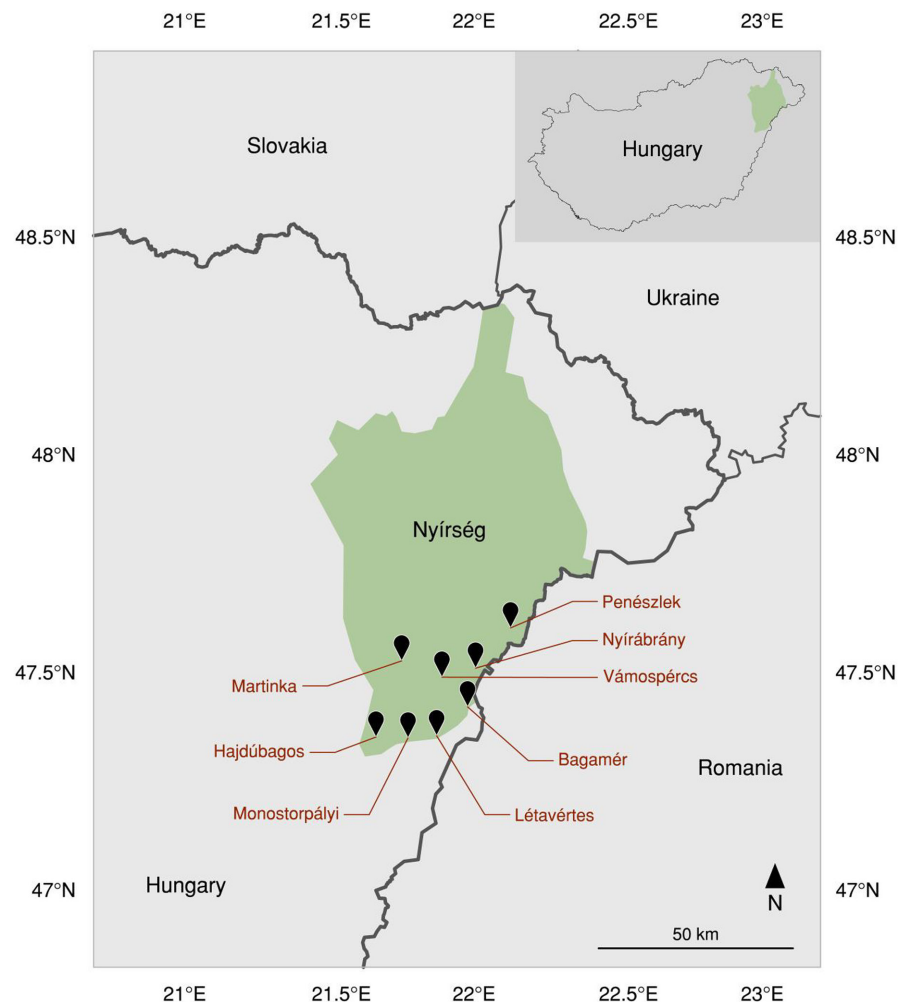


FIGURE 1 The distribution of the study sites in the Nyírség region, East Hungary.

intensity level [>1 LU/ha ranging from 1.1 to 4, located close to a watering/resting place (<150 m) and high number of droppings detected (more than 20 droppings per 100 m^2)]. Satellite imaging was used to assess proximity to watering and resting places and droppings and other tracks of grazing were visually assessed in the field.

To unify sampling variability, in each site, we have designated a $10 \text{ m} \times 10 \text{ m}$ area to survey the vegetation and collect biomass samples. We recorded the percentage cover of vascular plant species, mosses, lichens and litter in $2 \text{ m} \times 2 \text{ m}$ plots (from mid-May to early June 2021, five plots placed evenly in the $10 \text{ m} \times 10 \text{ m}$ area, altogether 130 plots). The total above-ground biomass (including live biomass, standing litter and the litter layer) was harvested in $20 \text{ cm} \times 20 \text{ cm}$ plots. Biomass was cut by secateurs down to the ground level. There were altogether 260 biomass samples collected (10 samples per designated area and close to the vegetation plots) for sorting. The harvested biomass was dried at 65°C (48 h) and then sorted to vascular plant species, mosses, lichen and litter (including both standing litter and the litter layer) fractions. Finally, dry weights were measured with an accuracy of 0.01 g .

2.3 | Plant traits

For functional analyses we used the plant trait data stored in the regional database PADAPT (Sonkoly et al., 2022). We used trait data on average taxon height (plant height hereafter), duration of flowering, thousand-seed weight (TSW), simplified life-form groups, rosette formation, leaf area (LA), leaf dry weight (LDW), specific leaf area (SLA) and leaf dry matter content (LDMC). In case of rosette formation, we used CLO-PLA (Klímešová & de Bello, 2009; Klímešová et al., 2017) and drawings of the New Hungarian Herbal (Király, 2009) for the species classification. For collecting seed and leaf trait data we used also E-Vojtkó et al. (2020), Gyalus et al. (2022), McIntosh-Buday et al. (2022), Lhotsky et al. (2016), and Török et al. (2013) and Török et al. (2016a). Used traits and data sources are summarised in more detail in Appendix S3.

2.4 | Statistical analyses

We calculated species richness, Shannon diversity and evenness. We also calculated community-weighted means (CWMs) of traits, and three components of functional diversity (F_{Rich} , richness; F_{Eve} , evenness; F_{Div} , divergence; Laliberté & Legendre, 2010) based on Mason et al. (2005). To measure the functional similarity among the characteristic species of the assemblages we calculated functional dispersion (F_{Dis}), where high dispersion scores reflect high levels of niche differentiation and likely decreasing levels of competition (Mason et al., 2005; Villéger et al., 2008). Functional diversity was calculated by the *FDiversity* program package using Gower distance (Casanoves et al., 2011). We also calculated Rao dissimilarity index, which is based on trait distances between species and the relative abundance of those species (Botta-Dukát, 2005).

A generalised linear mixed-effect model (GLMM) was calculated to assess the effect of grazing intensity and livestock type (as fixed factors) on the dependent variables (for the list of variables see Table 1). We included sampling site as a random factor into the analyses and we used Bonferroni–Holm corrections in the analyses for the paired comparisons; we used SPSS 26.0 for the statistical analyses (IBM, 2019). We made a canonical correspondence analysis (CCA) using species abundances by CANOCO 4.5 (Lepš & Šmilauer, 2003). To select the significant explanatory trait CWMs, we applied a forward selection. To test the effect of the CWMs (plant height, duration of flowering, lifeform, TSW, rosette formation, LA, LDW, SLA, and LDMC, Appendix S3) on the species abundance matrix we applied the Monte-Carlo permutation test on a full model with 499 unrestricted permutations (the highest level of significance for this setup is 0.002). Only significant CWMs were added to the final CCA.

3 | RESULTS

We found that Rao dissimilarity index, functional divergence, and most CWMs of traits (except that of TSW, LDW and LA) were significantly affected by grazing intensity (GLMM, Table 1). Several characteristics were also affected by the interaction of grazing intensity and livestock type, but none of the studied diversity characteristics were affected by livestock type in itself. Higher mean scores were, however, typical in cattle-grazed sites. An increasing trend was found for Rao dissimilarity index (Figure 2d), but in case of other species diversity metrics (species richness, Shannon diversity and evenness) (Figure 2a–c) and multitrait indices the intensity-dependent changes were significant only for functional divergence, which was the lowest at the first level of intensity (Figure 2e–h).

The CWMs of traits showed various responses along the intensity gradient (Figures 3 and 4). While a rather decreasing trend was detected for plant height (Figure 3a), the flowering period (Figure 3c) and rosette formation (Figure 3e) showed an opposite trend, while the lifeform showed a ‘zig-zag’ change along the intensity gradient. Out of the studied four leaf traits, the change of the CWMs of SLA and LDMC were significant; they displayed an increasing trend for SLA (Figure 4c), and a decreasing trend for LDMC; for the latter, we found that the scores for the first two levels of intensity were significantly higher compared to the third and fourth level of intensity (Figure 4d).

Graminoid biomass, litter biomass and moss biomass were significantly affected by grazing intensity (Table 1 and Figure 5). None of the studied biomass fractions were affected by livestock type; however, for most biomass fractions higher mean values were detected in cattle-grazed sites. While for graminoid biomass (Figure 5a) and litter (Figure 5c) we found a decreasing trend with increasing grazing intensity, for the moss biomass we found no clear trends in the scores (Figure 5d).

Five out of the nine trait CWMs, (lifeform, rosette formation, and three leaf traits) were proven to be significant in the forward selection for the CCA (Figure 6). The four axes of the CCA explained 41.8% of the cumulative variance for species data and 73.1% of that

TABLE 1 Effect of grazing intensity, livestock type and their interaction on species and trait diversity, and the biomass of subjected sand grasslands.

Characteristic	Grazing intensity		Livestock type		Grazing intensity × livestock type	
	<i>F</i> _{3,122}	<i>p</i>	<i>F</i> _{1,132}	<i>p</i>	<i>F</i> _{3,132}	<i>p</i>
Species diversity						
Species richness	1.70	0.170	0.66	0.418	4.89	0.003
Shannon diversity	1.83	0.145	0.82	0.368	2.56	0.058
Evenness	2.14	0.099	0.51	0.478	3.81	0.012
Multitrait indices						
Rao dissimilarity index	30.34	<0.001	0.54	0.464	7.00	<0.001
Functional richness	1.46	0.229	0.06	0.810	1.97	0.122
Functional evenness	1.92	0.130	0.11	0.743	2.20	0.092
Functional divergence	4.53	0.005	0.03	0.863	5.44	0.002
Functional dispersion	0.27	0.844	0.33	0.565	3.55	0.017
CWMs of single traits						
Plant height	6.48	<0.001	0.50	0.483	2.18	0.093
Lifeform	13.01	<0.001	0.01	0.932	2.39	0.072
Flowering period	15.96	<0.001	0.11	0.746	11.18	<0.001
Thousand-seed weight (TSW)	2.02	0.114	0.28	0.595	2.15	0.097
Rosette formation	7.59	<0.001	0.24	0.623	4.35	0.006
Leaf dry weight (LDW)	0.85	0.471	0.37	0.54	2.45	0.067
Leaf area (LA)	0.25	0.862	0.60	0.441	3.84	0.011
Specific leaf area (SLA)	16.67	<0.001	0.01	0.979	2.96	0.035
Leaf dry matter content (LDMC)	13.74	<0.001	0.01	0.999	1.76	0.158
Biomass						
	<i>F</i> _{3,252}	<i>p</i>	<i>F</i> _{1,252}	<i>p</i>	<i>F</i> _{3,252}	<i>p</i>
Graminoid	9.14	<0.001	2.18	0.14	5.70	0.001
Forb	0.16	0.926	0.42	0.517	0.13	0.941
Litter	12.82	<0.001	0.75	0.387	2.12	0.098
Moss	3.02	0.031	0.44	0.506	1.05	0.371
Lichen	2.15	0.094	0.06	0.809	3.77	0.011

Note: Significant effects are denoted in bold face ($p < 0.05$), marginally significant effects ($p < 0.1$) in italics (GLMM).

of the species-environment relation. While some sample areas were highly separated from others (like area 22 and 11), others formed a rather homogeneous point cloud with some separation displayed for areas with different grazing intensity. Based on the CCA we found that the CWM of lifeform is negatively correlated with the LDW, rosette formation and SLA, while it was not correlated with the LDMC.

4 | DISCUSSION

4.1 | 'Dominance of grazer' hypothesis

In line with the findings of Tóth et al. (2018) in alkaline grasslands, we hypothesised that livestock type has a greater effect on the studied characteristics of sand grasslands than the grazing intensity as they found that there is a difference in selectivity between sheep and cattle grazing. Surprisingly, this hypothesis was not supported by

our results. We found that none of the studied characteristics were significantly affected by the type of grazing livestock. In contrast, strong intensity-dependent effects were found for several characteristics including Rao dissimilarity index, functional divergence and most traits' CWMs.

A likely explanation of the absence of livestock-dependent effects could be the increased likeliness of weed infestation with increased intensity of grazing (found also by Godó et al., 2017). In alkaline grasslands, weed infestation is more limited because of strong species filtering caused by astatic water regime within the year, and salt stress (Egan & Ungar, 2000). Sand grasslands are prone to infestation by both natural weeds and invasive species, which contribute to changing vegetation composition and structure. In Hungary, the anthropogenic conversion of most natural sand steppes to agricultural areas resulted in a landscape in which there are croplands and old-fields in the close vicinity of sand steppes, and these areas can act as sources of invasive plants, which characterise these secondary

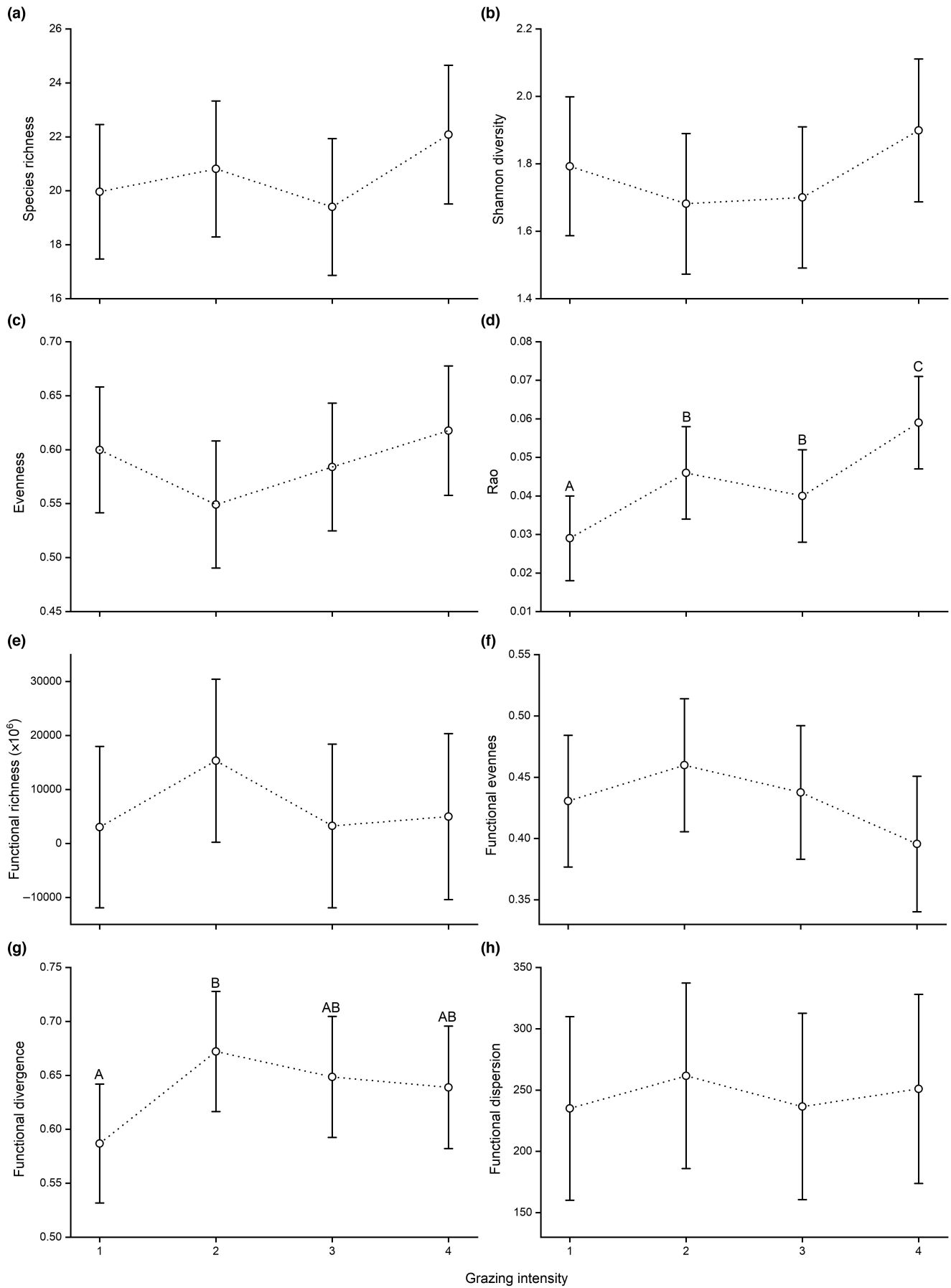


FIGURE 2 Change of species diversity and multitrait functional diversity indices along the grazing-intensity gradient. Significant differences are denoted by different letters [estimated mean \pm SE, generalised linear mixed-effect model (GLMM) and least significant differences]. Intensity levels denoted by numbers: first (1) [intensity was lower than 1 livestock unit (LU)/ha, ranging from 0.5 to 0.8, far from watering/resting places (>150m) and low number of droppings detected (typically 0–10 but no more than 20 droppings in 100-m² area)]; second (2) [intensity was lower than one LU/ha, ranging from 0.5 to 0.8 and close to a watering/resting place (<150m) and high number of droppings detected (more than 20 droppings per 100 m² area)]; third (3) [>1 LU/ha ranging from 1.1 to 4, far from watering/resting places (>150m) and low number of droppings detected (typically 0–10 but no more than 20 droppings per 100 m²)]; and fourth (4) [>1 LU/ha ranging from 1.1 to 4, located close to a watering/resting place (<150m) and high number of droppings detected (more than 20 droppings per 100m² area)].

habitats with high abundance (Botta-Dukát, 2008). The probability of bare soil formation is higher in drier habitats because trampling and grazing reduce water availability in the upper soil layer (Godó et al., 2017), which is likely due to increased compaction and evaporation resulting in less available water in more intensively disturbed sites. These conditions favour gap colonisers because otherwise bare soil promotes seedling emergence up to a point (Hofmann & Isselstein, 2004).

4.2 | 'Grazer-dependent selectivity' hypothesis

We hypothesised that regardless of grazing intensity, sites grazed by sheep have lower biomass and species and functional diversity than sites grazed by cattle. This hypothesis was not supported by our findings. While for example the graminoid and litter biomass were significantly affected by grazing intensity, none of the biomass fractions were affected by the livestock type. However, it is worth mentioning that although livestock type did not have a statistically significant effect on any of the diversity metrics and any of the biomass fractions, diversity and biomass were consistently higher in cattle-grazed sites. Consistent with former studies, the higher biomass scores were likely due to the less selective defoliation by cattle (Sebastià et al., 2008; Jerrentrup et al., 2015; Tóth et al., 2018). By a lower grazing selectivity, biomass fractions are more evenly spared from consumption, and therefore the fractions represent higher quantities on average. The graminoid biomass showed a decreasing trend with increasing grazing intensity, which is in accordance with the trend of litter biomass (Figure 5a,c). Graminoid species were the most characteristic element of the vegetation in the studied sites. Thus, they produced the most litter, but in heavily grazed sites, both litter and graminoids were reduced due to more intensive defoliation (Magnano et al., 2019). There was no significant trend found for forbs, and forb biomass did not decrease at higher intensities (Figure 5b). As grazing causes a decrease in litter and graminoid biomass, the number of vegetation gaps suitable for colonisation increases (Hofmann & Isselstein, 2004) and in our study, gap strategists were mainly weedy forbs which are able to quickly colonise the available gaps, which might compensate the consumption of perennial forb biomass.

Based on former studies (Török et al., 2018b), it is reasonable to think that plants colonising gaps could have an acquisitive strategy, that is, those plants may have higher SLA. We found an increasing

CWM of SLA peaking at the fourth level of grazing intensity in our study (Figure 4c). The increase in SLA may seem controversial if we consider the findings of Westoby (1998) that SLA is intensity-dependent and plants with high SLA are favoured and more likely to be consumed by grazers. Thus, the abundance of plants with high SLA consequently should decrease with increasing grazing intensity, but their rapid regrowth could be achieved before they are consumed again. The likely explanation could be that grazers became less selective in intensively grazed sites and more likely to consume plants with a low SLA (Vesk et al., 2004). These observations were confirmed also by Golodets et al. (2009) and Török et al. (2016b). The CWM of SLA was significantly affected by grazing intensity, while forb biomass was not. This has several possible reasons: (i) plants with higher SLA have generally lower dry weight (see e.g., E-Vojtkó et al., 2020); (ii) small-statured plants were typical at higher intensities (see Figure 3a), and consequently, they could have lower weight, especially when SLA is higher; furthermore (iii) some graminoids could obviously have higher SLA than some forbs, and intra-specific trait variability may be more pronounced in graminoids than in forbs (Streit et al., 2022).

Slightly variable length and timing of the grazing period can occur in the studied pastures, which might have also affected the amount of the harvested biomass but litter accumulation over years can mask differences between variable management durations of the different pastures.

4.3 | 'Intensity-induced trait shift' hypothesis

We assumed that increased grazing intensity causes a shift in the trait composition of the grasslands. This hypothesis was supported by the results. Rao dissimilarity index, F_{Div} , and most of the single-trait indices (except TSW, LDW and LA) were affected significantly by grazing intensity, regardless of the livestock type. As mentioned before, more intensive grazing causes a decline in graminoid and litter biomass, but not in forb biomass because trampling and the consumption of graminoid biomass (Hofmann & Isselstein, 2004; Godó et al., 2017) can enhance the colonisation and establishment of gap colonisers, which are mainly forbs in the studied sites. Grazing can also suppress competition between plants, making co-existence more frequent (Vázquez-Ribera & Martorell, 2022).

Rao dissimilarity index and F_{Div} were affected significantly by the grazing intensity while the effects on F_{Eve} , F_{Rich} and F_{Dis} were

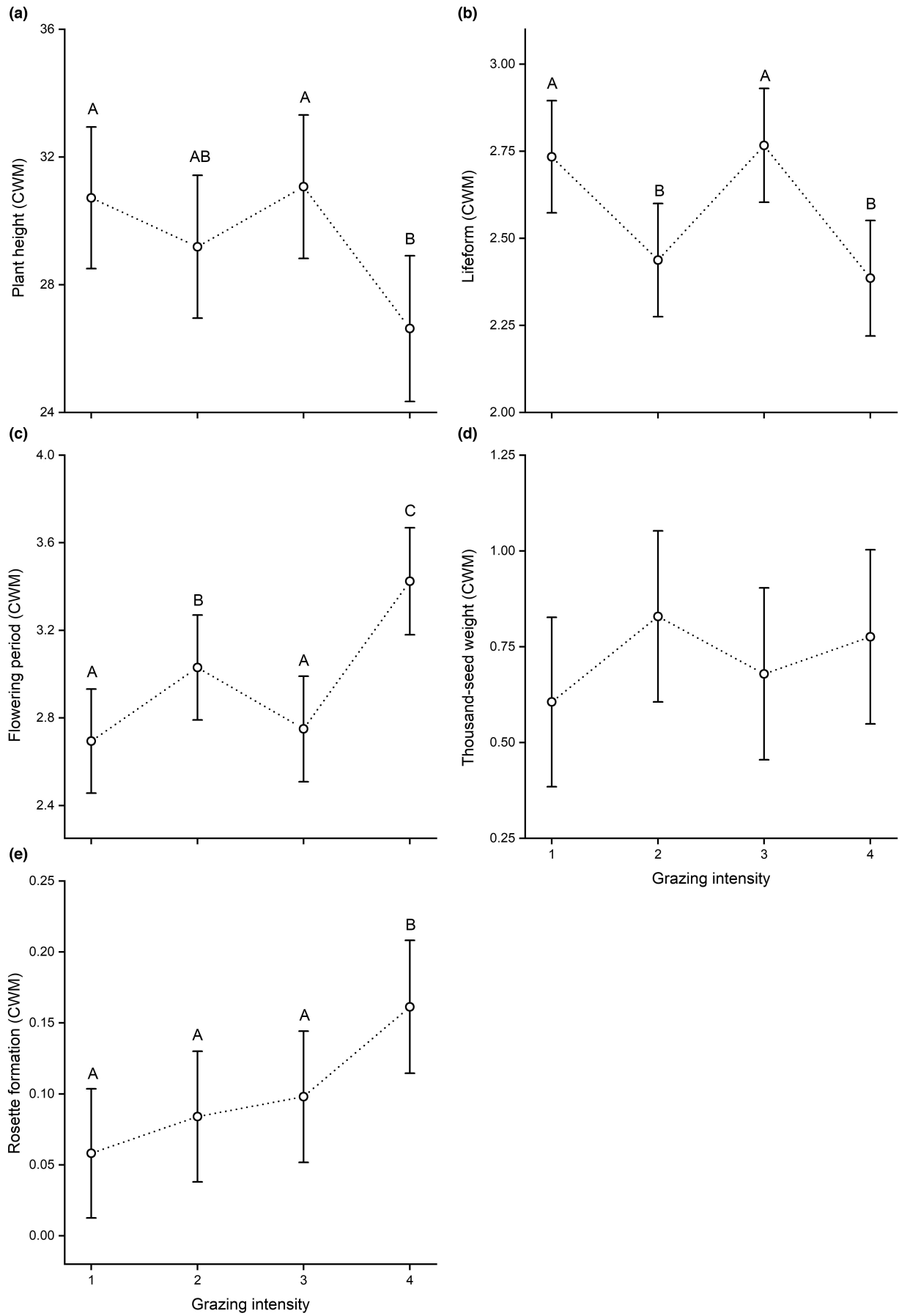


FIGURE 3 Change of community-weighted means (CWM) of plant height (a), lifeform (b), flowering period (c), thousand-seed weight (d), and rosette formation (e) along the grazing intensity gradient. Significant differences are denoted by different letters [estimated mean \pm SE, generalised linear mixed-effect model (GLMM) and least significant differences].

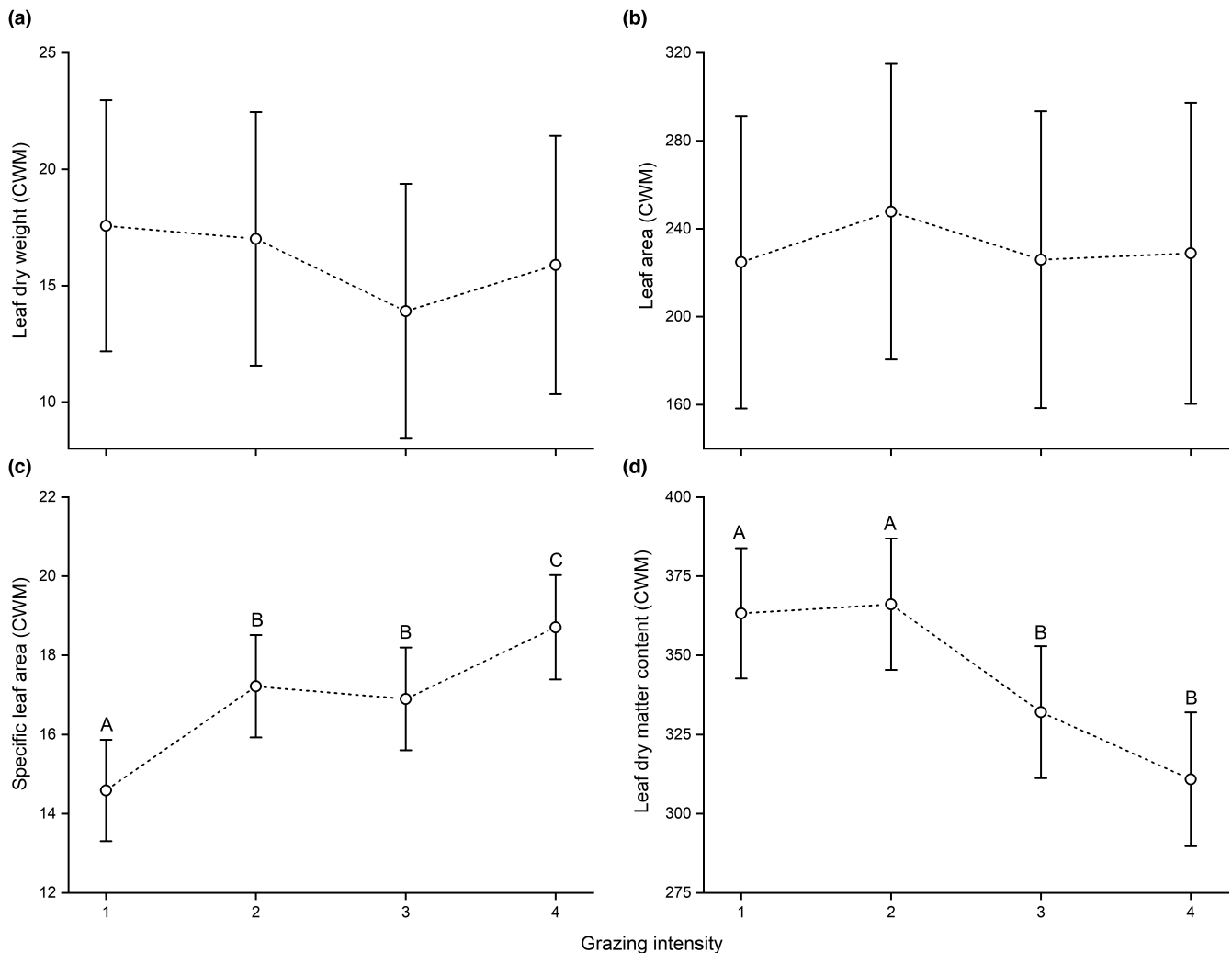


FIGURE 4 Change of community-weighted means (CWM) of leaf traits along the grazing intensity gradient. Significant differences are denoted by different letters [estimated mean \pm SE, generalised linear mixed-effect model (GLMM) and least significant differences].

not significant (Figure 2d-h). Rao dissimilarity index showed a rather increasing trend. We can conclude that functionally dissimilar species mean a higher probability of functional loss in more intensively grazed sites. The probability of functional loss is higher as overrepresented traits are resistant to grazing and the loss of function is not random (disturbance-sensitive functions are obviously more exposed). F_{Div} scores peaked at the second level of intensity (Figure 2g). This is somewhat in contrast with the results of Török et al. (2016b) who studied alkali steppes and observed the highest F_{Div} scores at 'high' (2.5 LU/ha) grazing intensity and the lowest scores at 'medium' (1.5 LU/ha) intensity. These discrepancies support the results of Török et al. (2018b) that F_{Div} is highly habitat-dependent and indicates higher co-existence between plants along with higher niche differentiation. Grazing supports co-existence; however, stronger disturbance favours grazing-tolerant species (Vázquez-Ribera &

Martorell, 2022) and it likely implies a decline in F_{Div} . Moreover, F_{Div} is also significantly affected by the interaction of grazing intensity and livestock type because co-existence between plants is promoted presumably more by cattle grazing.

Most single-trait CWMs were significantly affected by increasing grazing intensity, with the exception of TSW, LDW and LA (Figure 4). Rosette formation and SLA were positively affected by increasing grazing intensity (Figure 6) both peaking at the fourth intensity level (Figures 3e and 4c). The increase of SLA was discussed formerly. The more frequent rosette forming at higher intensity levels is not surprising as leaves developing close to the ground make plants more resistant to grazing (Jerrentrup et al., 2015; Török et al., 2016b). LDW was negatively correlated with the lifeform, rosette formation and SLA (Figure 6). A possible explanation could be that graminoids mainly represent the

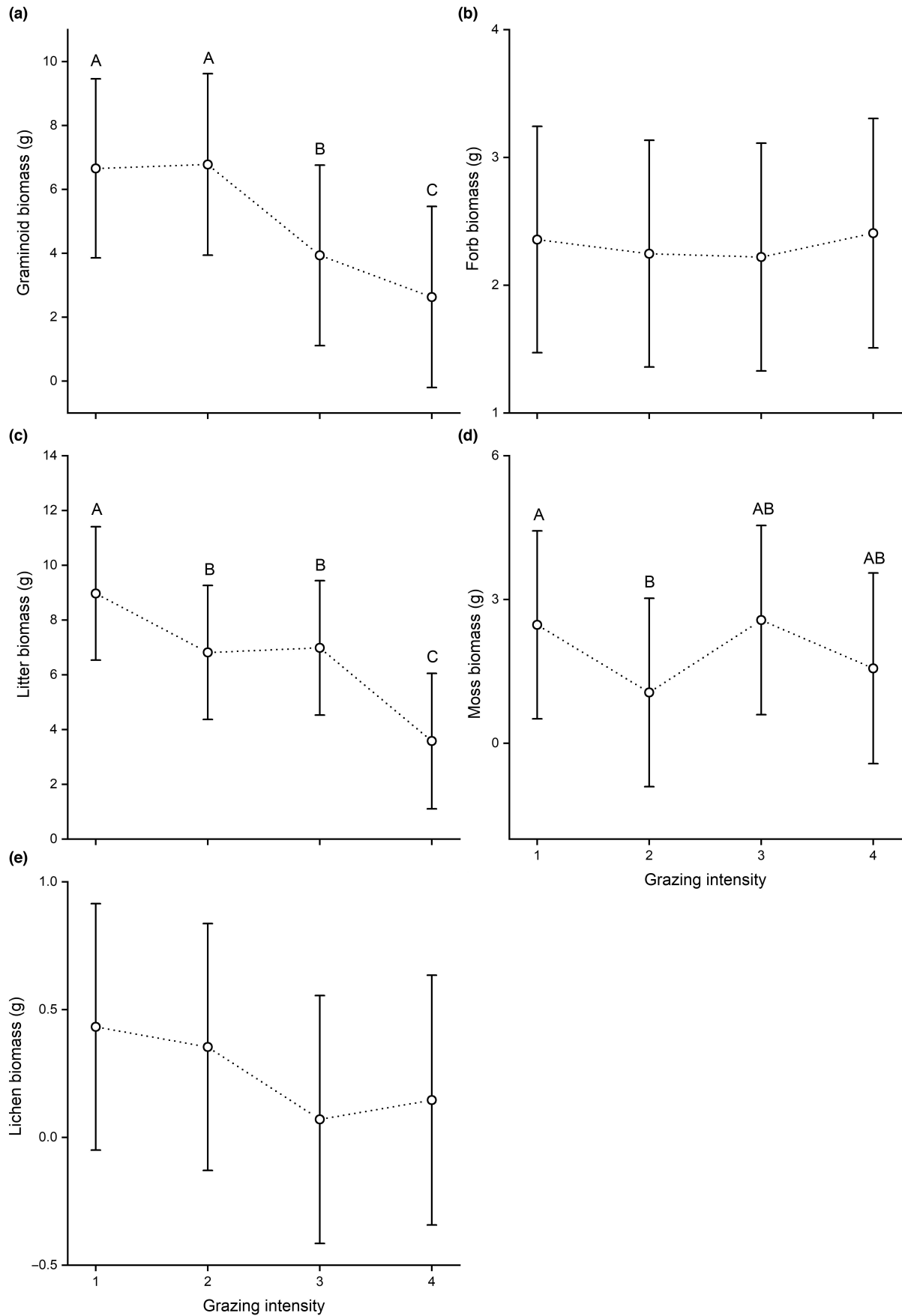


FIGURE 5 Change of biomass fractions along the grazing intensity gradient. Significant differences are denoted by different letters (estimated mean \pm SE, GLMM and least significant differences).

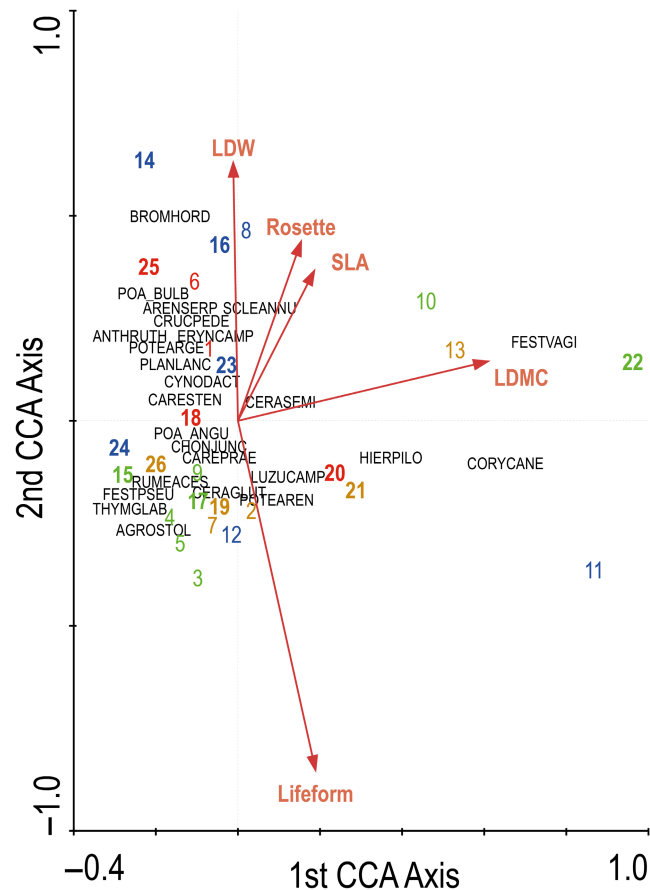


FIGURE 6 Relationship of vegetation composition and traits in grazed sand grasslands. Canonical correspondence analysis (CCA) was based on species abundance matrix averaged for sample areas, and the trait variables were added based on weighted averages. Variables were selected with forward selection (Monte-Carlo permutation test on full model with 499 unrestricted random permutations, only significant variables were added, $p < 0.05$). Eigenvalues for the first and second axes are 0.579 and 0.414, respectively. Notations: site codes are shown in Appendix S1; 1–13, sheep-grazed sites; 14–28 (boldface), cattle-grazed sites. Grazing intensity: 1, green; 2, blue; 3, light brown; 4, red. Abbreviations of the traits are detailed in Table 1. Species abbreviations include the first four letters of genus and species, and should be interpreted as follows: AGROSTOL, *Agrostis stolonifera*; ANTHRUTH, *Anthemis ruthenica*; ARENSERP, *Arenaria serpyllifolia*; BROMHORD, *Bromus hordeaceus*; CAREPRAE, *Carex praecox*; CARESTEN, *Carex stenophylla*; CERAGLUT, *Cerastium glutinosum*; CERASEMI, *Cerastium semidecandrum*; CHONJUNC, *Chondrilla juncea*; CORYCANE, *Corynephorus canescens*; CRUCPEDE, *Cruciata pedemontana*; CYNODACT, *Cynodon dactylon*; ERYNCAMP, *Eryngium campestre*; FESTPSEU, *Festuca pseudovina*; FESTVAGI, *Festuca vaginata*; HIERPILO, *Hieracium pilosella*; LUZUCAMP, *Luzula campestris*; PLANLANC, *Plantago lanceolata*; POA_ANGU, *Poa angustifolia*; POA_BULB, *Poa bulbosa*; POTEAREN, *Potentilla arenaria*; POTEARGE, *Potentilla argentea*; RUMEACES, *Rumex acetosella*; SCLEANNU, *Scleranthus annuus*; THYMGLAB, *Thymus glabrescens*.

perennials and typically have low LDW, SLA and rosette formation. In heavily grazed sites, the decrease in the CWMs of LDW and the increase in SLA and rosette formation are in line with the

decreasing trend of graminoid biomass (Figures 4a and 5a). This intensity-dependent decrease of LDW was also validated by Díaz et al. (2001). LDMC values peaked at the first and second intensity levels, then decreased (Figure 4c). This decrease is likely due to the consumption of taller plants having high LDMC and slow growth, which does not counterweight stronger disturbance (Fischer et al., 2019). Our results suggest that shorter plants with prolonged flowering and high likelihood of rosette formation can be better suited to sites with high grazing intensity. Similar patterns were also found by Török et al. (2016b) in alkali grasslands. The reasons for fluctuations in the CWM of lifeforms (Figure 3b) are likely driven by the highly fluctuating proportion of annuals at the higher intensity levels (Díaz et al., 2001; Klimešová et al., 2008), the foraging of highly palatable perennials at low intensities (Díaz et al., 2006; Magnano et al., 2019) and the grazing-tolerant perennials (Matějková et al., 2003) or short-lived plants at the third and fourth intensity levels. Plots of plant height and lifeform showed a similar pattern (Figure 3a,b). At the first level of intensity, the large, perennial competitors, while at the third level of intensity, disturbance-tolerant perennial species represented by larger individuals could contribute to higher values for both plant height and lifeform (Teuber et al., 2013).

5 | CONCLUSIONS

Our findings suggest that gap colonisers might be a key factor in the vegetation changes affected by grazing intensity in sand grasslands. Heavily grazed sites are essential in order to enable gap colonisers to establish their populations. In the future, we need to examine how the amount of weedy species changes along an intensity gradient in order to draw conclusions about how to arrange frequently grazed sites (e.g., watering and resting places which are more sensitive to infestations by weedy species). For this, we need to divide forbs and graminoids into smaller groups (e.g., perennial forbs, perennial graminoids, short-lived forbs, and short-lived graminoids). These goals are underpinned by the outcomes obtained for biomass and for leaf traits (e.g., SLA). Multi-trait indices may have an important role in the detection of the functional changes in vegetation caused by change in the intensity of grazing. However, most of these indices showed no clear and/or significant trends in our study. The main reason is likely that different traits display different patterns along the intensity gradient and these opposing trends combined in multitrait indices might cause the absence of clear and/or significant trends. We suggest therefore the simultaneous use of single-trait metrics. In conclusion, our results imply two important considerations for the future: (i) besides stocking rates expressed in LU/ha, further factors (e.g., duration of grazing, paddock arrangement, type of grazing) are needed in the evaluation of grazing effects on vegetation, which should be clearly defined for decision-makers; and (ii) well-defined, long-term experiments studying different livestock and habitat types along an intensity gradient are essential to formulate recommendations for practical nature conservation.

AUTHOR CONTRIBUTIONS

Péter Török and Béla Tóthmérész conceived the research idea; all authors collected data; Péter Török and Béla Tóthmérész performed statistical analyses with the contributions of Gergely Kovacsics-Vári. Gergely Kovacsics-Vári wrote the paper with contributions from Judit Sonkoly, Béla Tóthmérész and Péter Török; all authors discussed the results and commented on the manuscript. Péter Török revised and edited the final version of the manuscript.

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DATA AVAILABILITY STATEMENT

The authors will provide underlying species abundance data of grazed pastures upon request.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Characteristics of the sampling sites in the Nyírség region, East Hungary.

Appendix S2. Soil properties of the selected sites.

Appendix S3. Traits used in the analyses.

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