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Vegetation responses to long-term grazing along a pasture digression gradient in the semi-dry grasslands of the Dniester Canyon, Ukraine

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Keywords: species diversity, long-term grazing, pasture digression, destruction coefficient, phytoindication, life forms, Dniester Canyon

Ključne besede: vrstna pestrost, dolgotrajna paša, poškodovanje pašnika, koeficient uničenja, fitoindikacija, življenske oblike, kanjon Dnestra

Abstract

Understanding grazing effects on semi-dry grasslands is important for their conservation and management. We analysed vegetation change along a pasture-digression gradient in Podilski Tovtry National Nature Park, Ukraine, using 80 1 m² plots from three sites under long-term cattle grazing. Pasture digression was quantified by the destruction coefficient (Kd), based on the proportional cover of destructor species. Increasing Kd was associated with declining graminoid and hemicryptophyte dominance and increasing legumes and therophytes. Diversity and evenness showed non-linear responses, increasing towards intermediate Kd values and declining slightly at the upper end of the gradient, while dominance showed the opposite pattern. Phytoindication demonstrated shifts towards species associated with moister and more nitrogen-rich conditions and lower light and continentality values. Overall, pasture digression caused marked compositional restructuring rather than a simple decline in local diversity.

Izvleček

Ker je razumevanje učinkov paše na polsuha travišča pomembno za njihovo ohranjanje in gospodarjenje, smo analizirali vegetacijske spremembe vzdolž gradienta poškodovanosti pašnikov v Narodnem naravnem parku Podilski Tovtry na 80 ploskvah površine 1 m² s treh območij z dolgotrajno pašo. Poškodovanost pašnikov smo ocenili z koeficientom uničenja (Kd) na osnovi deleža pokrovnosti vrst, značilnih za poškodbe. Povečanje Kd je bilo povezano z upadom dominance graminoidnih vrst in hemikriptofitov ter povečanjem deleža metuljnic in terofitov. Diverziteta in vrstna enakomernost imata nelineraen odziv, s povečanjem proti vmesnim vrednostim Kd in rahlim upadanjem na zgornjem delu gradienta, medtem pa dominanca kaže obraten vzorec. S fitoindikacijo smo pokazali premik k vrstam, značilnim za vlažna in z dušikom bogatejša rastišča in nižjimi vrednostmi za svetlobo in kontinentalnost. Na splošno je intenzivnost paše povzročila spremembe v vrstni sestavi in ne samo preprosto zmanjšanje vrstne pestrosti.

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Introduction

Semi-dry grasslands are among the most species-rich habitats in Europe and play an important role in carbon storage, as well as in hydrological and biogeochemical processes (Dengler et al., 2014; Conant et al., 2017; Bengtsson et al., 2019; Norderhaug et al., 2023). At the same time, they are highly vulnerable to land-use change and inappropriate management. Both overgrazing and grazing abandonment may lead to vegetation change, biodiversity loss, and reduced ecosystem functioning (Dengler et al., 2014; Bardgett et al., 2021; Török et al., 2018, 2020, 2024).

The effects of grazing on grassland vegetation are complex and depend on grazing intensity, duration, local environmental conditions, and the adaptive traits of plant species. Under appropriate management, grazing can help maintain open grassland habitats and support plant diversity, whereas excessive grazing may promote soil disturbance, ruderalization, and community degradation (Pykälä, 2003; Papanikolaou et al., 2011; Liang et al., 2021; Reutimann et al., 2023). For this reason, the assessment of vegetation change along grazing gradients remains an important task in grassland ecology and conservation.

In Ukraine, dry grasslands are concentrated mainly in the Steppe zone, but most of their former area has been transformed by ploughing and intensive land use, and only a small proportion of natural grasslands remains (Burkovskyi et al., 2013). In other natural zones, semi-dry and dry grasslands occur more sporadically and often persist as fragmented remnants. Previous studies in Ukraine have addressed the transformation of grassland ecosystems under grazing and other anthropogenic factors, including both classical works on steppe digression and more recent studies from different natural zones (Tkachenko, 1973; Balashov, 1988, 1991; Kuzemko, 2006, 2008a,b, 2012; Kuzemko et al., 2016; Vynokurov, 2018).

The Dniester Canyon in Podillia is one of the regions where valuable remnants of semi-dry grassland vegetation have been preserved. In the study area, these communities belong to the class *Festuco-Brometea* and are represented by the alliance *Fragario viridis-Trifolion montani* (Korotchenko & Didukh, 1997; Abduloieva & Didukh, 1999; Abduloieva, 2002; Korotchenko, 2004). These grasslands are of high conservation value because they contain distinctive plant communities and numerous rare, endemic, relict, and Red Data Book species, including *Astragalus monspessulanus, Cytisus podolicus, Poa versicolor, Sesleria heufflerana, and Thymus moldavicus* (Abduloieva, 2002; Korotchenko, 2004; Onyshchenko, 2009; Didukh & Vasheniak, 2018; Vasheniak et al., 2021). However, despite their conservation importance, local studies on the effects of grazing on semi-dry grasslands in the Dniester region remain limited.

In this study, we investigated semi-dry grasslands in the Dniester Canyon within Podilski Tovtry National Nature Park, Ukraine. The study aimed to assess how plant species diversity and community structure vary along a gradient of pasture digression under long-term grazing.

Materials and methods

Study area

The study was conducted in the Dniester Canyon within Podilski Tovtry National Nature Park, Khmelnytskyi Region, western Ukraine. The study sites were located near three settlements on the right bank of the Dniester River (Figure 1).

The Dniester Canyon lies on the southwestern margin of the Podolian Upland and is characterized by steep valley slopes and a strongly dissected relief. In the study area, fragments of semi-dry and dry grasslands occur both on steep canyon slopes and on adjacent flat upland areas.

The area has a mild, moderately continental climate and lies in the southern part of the temperate zone of Europe. Owing to local topographic conditions, the canyon has relatively warm mesoclimatic conditions compared with surrounding areas. The mean temperature is about 19°C in July and –6°C in January, and mean annual precipitation is approximately 550 mm (Lipinskyi et al., 2003; Denysyk, 1996, 2006; Didukh et al., 2015).

The Dniester Canyon lies at the transition between the broadleaf forest and forest-steppe zones (Loidi et al., 2022, 2023), which contributes to the high diversity and mosaic structure of its vegetation. Natural vegetation in the area includes forests, shrublands, meadows, meadow steppes, rocky communities, forest edges, and riparian vegetation. Our study focused on semi-dry and dry grasslands of high conservation value within Podilski Tovtry National Nature Park. The sampled plots were located in the protected zone of the park, where grazing is carried out only by cattle.

Field data sampling

Field sampling was carried out in July-August 2022 and 2023 at three sites near the villages of Subych, Kalachkivtsi, and Ustia (Figure 1). The selected sites represented the same general semi-dry grassland habitat type and had all been subjected to regular cattle grazing for at least the previous ten years, typically from late March to October.

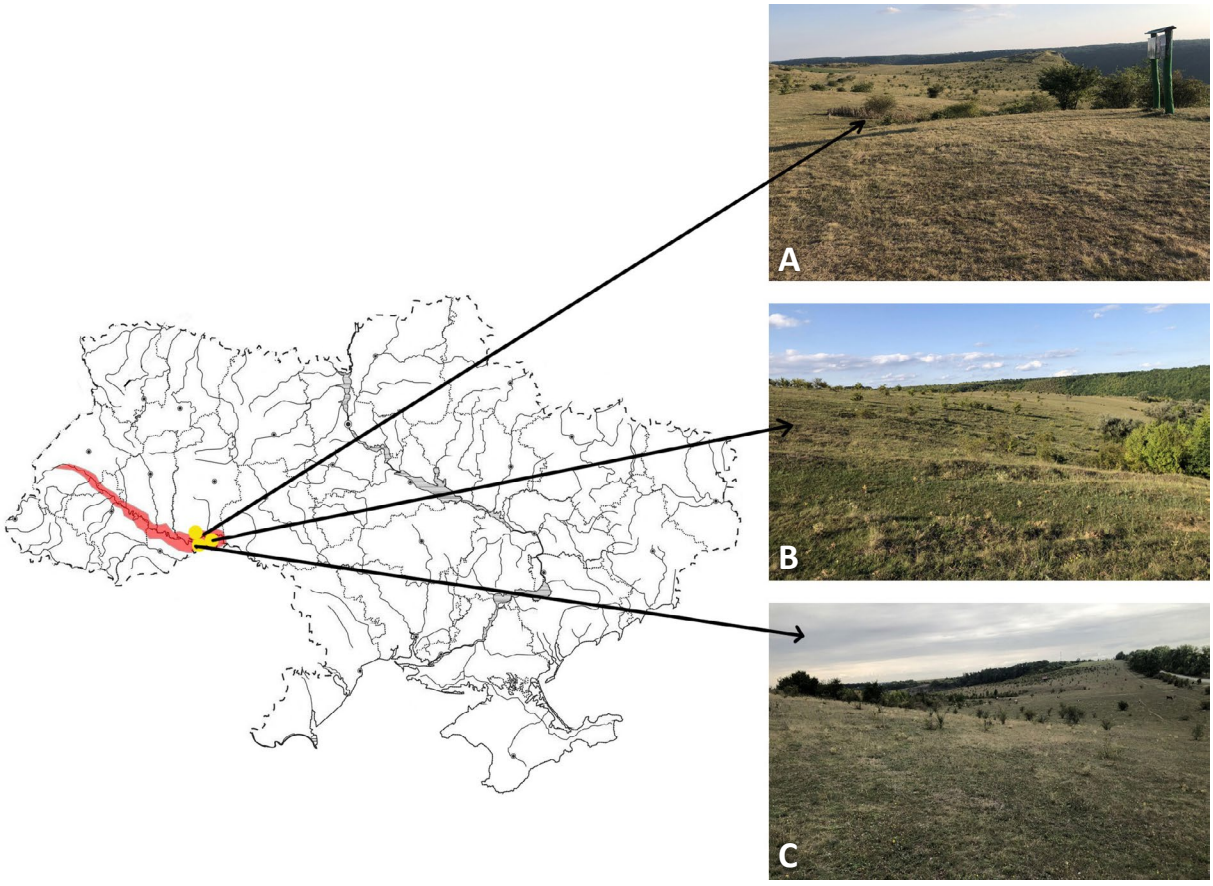


Figure 1: Study area and research sites. A – Subych village (48.585256, 26.826928); B – Kalachkivtsi village (48.604875, 26.875167); C – Ustia village (48.583420, 26.644595) (Khmelnytskyi Region, western Ukraine). The Dniester Canyon is shown in red.

Slika 1: Preučevano območje in preučevani pašniki. A – vas Subych (48.585256, 26.826928); B – vas Kalachkivtsi (48.604875, 26.875167); C – vas Ustia (48.583420, 26.644595) (regija Khmelnytskyi, zahodna Ukrajina). Kanjon Dnestra je prikazan z rdečo barvo.

Cattle grazed regularly at all three sites during the grazing season, but grazing pressure was spatially uneven, and different parts of the grassland patches were used with different intensity. They were chosen to capture variation in grazing-related disturbance within comparable habitat conditions, rather than to compare separate regional units.

The sampled grassland patches extended for up to ca. 1.5 km. All study plots were established on relatively flat upland surfaces rather than on the steep canyon slopes; therefore, slope inclination did not exceed 7° at the sampled locations. The plots were located on slopes with different aspects, including south-, south-west-, south-east-, east-, and west-facing slopes, as well as on the nearby flat plateau. The soils were shallow chernozems, often affected by erosion, and developed on calcareous parent material. Rocky outcrop vegetation was not included in the present study. According to local observations, the approximate number of grazing cattle was about 13 at the first site, 22 at the second site, and 17 at the third site (Table 1).

At each site, vegetation sampling was carried out along a transect established in the central part of the grazed grassland patch. Relevés were recorded at 30 m intervals using 1 × 1 m plots. In total, 80 monitoring plots were sampled. Bryophytes and lichens were not included in the analysis.

For each plot, we recorded total vegetation cover and species composition, with species abundance estimated as percentage cover. In addition, several visible indicators of grazing pressure were recorded, including minimum and maximum vegetation height, litter accumulation, dung occurrence, and soil surface condition. Geographic coordinates and elevation were recorded in the field using a mobile GPS application. These field observations were used to characterize local grazing conditions and to support field interpretation of vegetation change. However, the main analytical framework of the study was based on stages of pasture digression, which were treated as an in-

tegrated measure of plant community transformation under long-term grazing.

Truly ungrazed reference patches that would serve as control could not be identified within the studied grassland systems, because all sites were subject to long-term livestock influence. Therefore, the category "low grazing" should be interpreted as the least affected vegetation within the local grazing mosaic rather than as a true ungrazed control (Table 2, Figure 2). These plots were characterized by relatively dense and relatively tall vegetation, high vegetation cover, and greater litter accumulation. However, they were still occasionally used as cattle passage areas and thus cannot be considered fully free from grazing influence.

Table 1: Main characteristics of the three study sites.
Tabela 1: Glavne značilnosti treh preučevanih pašnikov.

Study site	Transect length (m) / area (ha)	Approximate cattle density (heads per ha)	Approximate number of grazing cattle	Number of sampled plots
Site 1 Subych	1368 / 8.87	1	~13	23
Site 2 Kalachkivtsi	1155/ 7.43	3	~22	40
Site 3 Ustia	1352/ 8.81	2	~17	17

Table 2: Field criteria used to distinguish relative grazing-pressure classes in the sampled grassland plots.
Tabela 2: Uporabljena merila za določitev razredov relativnega pritiska zaradi paše na vzorčenih travnikih.

Relative grazing - pressure class	Total vegetation cover	Herb-layer height range (cm)	Dung occurrence	Litter cover (%)	Open soil cover (%)
1 (low)	90–100%	30–50	absent	30	0
2 (moderate)	80–90%	20–30	present	20	0–10
3 (high)	60–80%	10–20	present	10	10–20
4 (very high)	<60	<10	present	<10	20–30

Data analyses

Vegetation data were stored in TURBOVEG (Hennekens & Schaminée, 2001). The nomenclature of vascular plants was standardized according to the Nomenclatural checklist of vascular plants of Ukraine (Mosyakin & Fedoronchuk, 1999), and syntaxon names followed the Prodromus of the Vegetation of Ukraine (Vynokurov, 2019).

Pasture digression in semi-dry grasslands was assessed using the destruction coefficient (Kd) following Kuzemko (2008a,b). This coefficient reflects the proportional contribution of destructor species to the summed cover of all species in a relevé. Following Kuzemko (2008b), destructor species were selected based on the synanthropic classification of Protopopova (1991), as synanthropic species indicative of anthropogenic disturbance, and included hemiapophytes, evapophytes, and adventive species, except agriophytes.

The destruction coefficient (Kd) was calculated as the proportional contribution of destructor species to the summed cover of all species in a relevé: $\mathbf{Kd = \sum Pdi / \sum Pi \times 100,}$ where ∑Pdi is the summed percentage cover of destructor spe-



Figure 2: Research plots representing different relative grazing-pressure classes: A – low grazing; B – moderate grazing; C – high grazing; D – very high grazing.

Slika 2: Preučevane ploskve, ki predstavljajo različne razrede relativnega pritiska zaradi paše: A – nizka intenzivnost paše; B – zmerna intenzivnost paše; C – visoka intenzivnost paše; D – zelo visoka intenzivnost paše.

cies and ∑Pi is the summed percentage cover of all species recorded in the relevé.

For descriptive purposes and stage-wise comparisons, relevés were assigned to four pasture-digression classes: Stage I (Kd < 20%), Stage II (20% ≤ Kd < 40%), Stage III (40% ≤ Kd < 60%), and Stage IV (Kd ≥ 60%). These stages represent an increasing degree of vegetation transformation associated with an increasing proportional contribution of destructor species. In addition to the categorical classification, Kd was retained as a continuous variable to analyse vegetation responses along the full pasture-digression gradient.

Species constancy across pasture digression stages was analysed in JUICE 7.0 (Tichý, 2002). Species occurring in at least 25% of relevés within a digression stage were treated as constant, and those occurring in at least 50% were considered highly constant (Appendix 1). Species with cover values of at least 50% were regarded as dominant.

All statistical analyses were performed in R 4.5.1 (R Core Team, 2025). Species richness was calculated as the number of species recorded in each relevé. Species diversity was assessed using the Shannon diversity index (Shannon, 1949), Simpson dominance index (Simpson, 1949), and Pielou's evenness index (Pielou, 1975). Shannon diversity and Simpson diversity were calculated using the *vegan* package (Oksanen et al., 2025). The *vegan* function returns Simpson diversity as 1 – D; therefore, Simpson dominance was calculated as D = 1 – (Simpson diversity). Pielou evenness was calculated as $\mathbf{J' = H' / \ln(S)}$, where H' is Shannon diversity and S is species richness. Differences in diversity indices among pasture-digression stages were tested using one-way analysis of variance (ANOVA), followed by Tukey's HSD post-hoc test for pairwise com-

parisons. Relationships between diversity metrics and the continuous pasture-digression gradient were analysed using generalized additive models (GAMs), with Kd treated as a continuous predictor. Shannon diversity was modelled assuming a Gaussian error distribution, whereas Simpson dominance and Pielou evenness, both bounded between 0 and 1, were analysed using beta-regression GAMs with a logit link. Smooth terms were fitted with a basis dimension of k = 5, and models were estimated using restricted maximum likelihood (REML). Model adequacy and the sufficiency of the selected basis dimension were evaluated using standard GAM diagnostic procedures. Modelled relationships were visualized using fitted GAM curves with 95% confidence intervals.

To evaluate changes in vegetation structure, species were assigned to three broad groups: legumes (*Fabaceae*), graminoids (*Poaceae* and *Cyperaceae*), and forbs (all remaining vascular plant species). For each relevé, the proportional participation of each group (Kgr) was calculated following the approach of Kuzemko (2008): **Kgr = Pgr / ∑Pi × 100,** where Pgr is the summed percentage cover of all species belonging to the target group and ∑Pi is the summed percentage cover of all species recorded in the relevé. Thus, the proportional contributions of legumes, graminoids, and forbs summed to 100% within each relevé.

Life-form affiliation was obtained from the UkrTrait database (Vynokurov et al., 2024) and classified according to the Raunkiær system into therophytes, hemicryptophytes, geophytes, chamaephytes, and phanerophytes. For taxa assigned to more than one life form, the first-listed life form was treated as the primary category. The proportional contribution of each life form was calculated separately for each relevé using the same cover-based approach as for the species groups. When a particular life form was absent from a relevé, its proportional contribution was assigned a value of zero. Mean proportional participation was subsequently calculated for each pasture-digression stage.

Changes in ecological conditions along the pasture-digression gradient were analysed using the synphytoindication method according to Didukh & Pluta (1994) and Didukh (2011). Ecological indicator values were assigned to individual plant species according to the ecological scales of Didukh (2011), and relevé-level values were calculated as cover-weighted mean indicator values of the informative species present in each relevé. Thus, species with greater percentage cover contributed proportionally more to the resulting relevé-level indicator value. Phytoindicator values do not represent direct environmental measurements but reflect the ecological affinities of the species composing the vegetation. The scales are ordinal and reflect species-specific ecological optima and amplitudes along environmental gradients. The following ecological indicators were analysed: **Hd** (soil moisture), **fH** (variability of soil moisture), **Rc** (soil acidity), **Sl** (salt regime), **Ca** (carbonate content), **Nt** (nitrogen availability), **Ae** (soil aeration), **Tm** (thermoregime), **Om** (ombroregime or climatic humidity/aridity), **Kn** (continentality), **Cr** (cryoclimate), and **Lc** (light availability). For each indicator, the mean value, standard deviation, minimum, and maximum were calculated for each pasture-digression stage (Appendix 2).

For analyses of vegetation groups, life forms, and phytoindication values, differences among pasture-digression stages were assessed using Kruskal–Wallis tests. When the overall test was significant, pairwise differences between stages were evaluated using Dunn's post-hoc tests with Holm adjustment for multiple comparisons. Relationships with Kd treated as a continuous variable were assessed using Spearman's rank correlation. For the phytoindication analysis, p-values of the overall Kruskal–Wallis tests and Spearman correlations were additionally adjusted across the 12 ecological indicators using the Holm method. Statistical effects were considered significant at $p < 0.05$.

Data processing, statistical analyses, and graphical visualization were performed primarily using the *vegan* (Oksanen et al., 2025), *mgcv* (Wood, 2011), *tidyverse* (Wickham et al., 2019), and associated R packages.

Results

Characteristics of pasture digression stages

Based on field observations and the calculated values of the destruction coefficient, four non-zero stages of pasture digression were recorded in the study area (Stages I-IV; Table 3). No plots with Kd = 0 were recorded, because truly ungrazed reference patches were absent within the studied grassland systems. Stage I was the most frequent, comprising 41 relevés with a mean Kd of 13.9%. Stage II included 23 relevés with a mean Kd of 28.5%, and Stage III comprised 11 relevés with a mean Kd of 46.0%. The most advanced stage, Stage IV, was represented by only five relevés and had a mean Kd of 69.2%. Thus, the majority of sampled plots belonged to the less transformed stages, whereas strongly transformed grassland patches were less frequent.

A synoptic table was used to examine changes in species constancy across pasture digression stages (Appendix 1). In total, 120 vascular plant species were recorded. Several

Table 3: Distribution of relevés among stages of pasture digression based on the destruction coefficient (Kd).
Tabela 3: Razdelitev popisov med posameznimi stopnjami poškodovanosti pašnikov na osnovi koeficienta uničenja (Kd).

Pasture digression stage	Number of relevés	Mean Kd (%)	Kd range (%)
I	41	13.9	6.98–19.5
II	23	28.5	20.4–39.5
III	11	46.0	40.0–58.1
IV	5	69.2	60.2–81.8

perennial species remained frequent throughout the pasture-digression gradient. For example, *Festuca valesiaca* occurred in 92.7% of relevés at Stage I and in all relevés at Stages III and IV, while *Eryngium campestre* increased in constancy from 68.3% at Stage I to 91.3% at Stage II and 100% at Stages III and IV.

Several species showed a consistent increase in frequency towards more advanced stages of pasture digression. The constancy of *Echium vulgare increased* from 17.1% at Stage I to 60% at Stage IV, *Trifolium arvense* from 2.4% to 40%, and *Carduus acanthoides* from 9.8% to 40%. *Eryngium campestre* also showed a progressive increase in constancy. Other species became particularly frequent at Stage IV, although their responses were less monotonic across the preceding stages. These included *Trifolium dubium* (14.6% at Stage I and 80% at Stage IV), *Astragalus onobrychis* (14.6% and 60%, respectively), *Centaurea stoebe* (36.6% and 80%), and *Plantago media* (63.4% and 100%). Some species that were absent or rare at the earlier stages occurred only or predominantly at the most advanced stage, including *Lactuca serriola, Lepidium campestre,* and *Trifolium campestre.*

In contrast, several species declined consistently along the pasture-digression gradient. The clearest decreases in constancy were observed for *Teucrium montanum*, from 43.9% at Stage I to complete absence at Stages III and IV; *Bothriochloa ischaemum*, from 58.5% to 20%; *Picris hieracioides*, from 31.7% to 0%; and *Scabiosa ochroleuca*, from 29.3% to 0%. These species therefore became progressively less frequent as the contribution of destructor species increased.

Changes in mean species cover showed an even clearer restructuring of the vegetation. The strongest decline was observed for *Festuca valesiaca,* whose mean cover decreased continuously from 55.8% at Stage I to 36.6% at Stage II, 13.7% at Stage III, and only 8.2% at Stage IV. *Bothriochloa ischaemum* also declined from 3.42% to 0.20%, while *Teucrium montanum* decreased from 2.59% at Stage I to complete absence at Stages III and IV.

In contrast, *Medicago lupulina* showed the strongest increase in mean cover, from 1.56% at Stage I to 5.87% at Stage II, 15.4% at Stage III, and 23.0% at Stage IV. *Elytrigia repens* similarly increased from 0.10% to 11.2%. Smaller increases were observed for *Lotus corniculatus* (1.93% to 9.0%), *Plantago lanceolata* (1.42% to 4.8%), *Plantago media* (0.95% to 3.0%), and *Eryngium campestre* (0.95% to 2.6%).

Changes in the proportional participation of selected species groups across pasture digression stages

The proportional participation of legumes and graminoids differed significantly among pasture digression stages (Kruskal-Wallis test: legumes, $H = 36.49$, $p < 0.001$; graminoids, $H = 33.60$, $p < 0.001$; Figure 3). In contrast, differences in forb participation among stages were not statistically significant ($H = 7.44$, $p = 0.059$).

Graminoids showed a marked decline from the least transformed vegetation towards the more advanced stages of pasture digression. Their proportional participation was highest at Stage I and substantially lower at Stages II–IV. Dunn's post-hoc test showed that Stage I differed significantly from Stages II, III, and IV, whereas no significant differences were detected among Stages II–IV. This pattern was also evident along the continuous destruction gradient, with graminoid participation showing a strong negative correlation with Kd (Spearman's $\rho = -0.649$, $p < 0.001$).

Legumes showed the opposite response. Their proportional participation was lowest at Stage I and increased markedly in the subsequent stages. Stage I differed significantly from Stages II, III, and IV, while no significant pairwise differences were detected among Stages II–IV. Along the continuous gradient, legume participation

showed a strong positive relationship with Kd (Spearman's ρ = 0.729, p < 0.001).

Forbs showed a weaker and more variable response across the four discrete pasture-digression stages, with considerable overlap among stages and no significant overall stage effect. Nevertheless, when Kd was analysed as a continuous variable, forb participation showed a weak but significant positive correlation with increasing pasture digression (Spearman's ρ = 0.301, p = 0.0066).

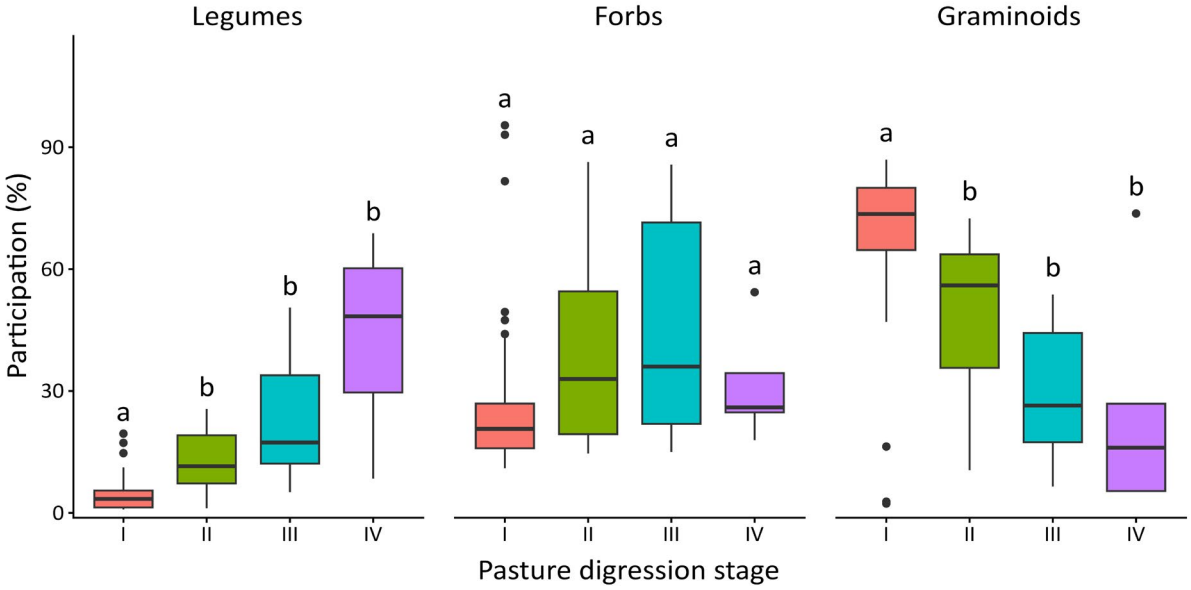


Figure 3: Variation in the proportional participation of legumes, forbs, and graminoids across pasture digression stages. Boxplots show the distribution of proportional participation (%) within Stages I–IV. Boxes represent the interquartile range, horizontal lines indicate medians, whiskers extend to 1.5 × IQR, and points represent outliers. Different lowercase letters indicate significant differences among pasture digression stages based on Dunn's post-hoc test with Holm adjustment following a Kruskal-Wallis test (p < 0.05).

Slika 3: Variabilnost deleža metuljnic, zelišč in graminiodnih vrst v različnih stopnjah intenzivnosti paše. Škatle z brki prikazujejo delež (%) v stopnjah I–IV. Škatle predstavljajo medkvartilni razpon, vodoravna črta mediano, brki razpon 1.5 × IQR in točke osamelce. Različne črke nakazujejo značilne razlike med stopnjami intenzivnosti paše, testirane z Dunn post-hoc testom s prilagoditvijo po Holmu in Kruskal-Wallis testom (p < 0.05).

Species diversity across pasture digression stages

Species diversity differed significantly among pasture digression stages (Figure 4). Mean Shannon diversity increased from 1.42 at Stage I to 1.99 at Stage II and 2.19 at Stage III, followed by a slight decline to 2.13 at Stage IV (ANOVA: F = 19.96, p < 0.001). Tukey's HSD test showed that Stage I differed significantly from Stages II, III, and IV, whereas no significant differences were detected among Stages II-IV. Pielou evenness showed a similar pattern, increasing from 0.49 at Stage I to 0.67 at Stage II and 0.75 at Stage III, followed by a decrease to 0.67 at Stage IV (ANOVA: F = 24.53, p < 0.001). Stage I differed significantly from all subsequent stages, whereas Stages II-IV did not differ significantly. Simpson dominance showed the opposite response, decreasing from 0.47 at Stage I to 0.26 at Stage II and reaching its lowest mean value at Stage III (0.18), followed by a slight increase to 0.24 at Stage IV (ANOVA: F = 22.53, p < 0.001). As for the other diversity metrics, Stage I differed significantly from Stages II-IV, whereas no significant differences were detected among the latter three stages.

When Kd was analysed as a continuous predictor, all three diversity metrics showed strong non-linear relationships with pasture digression (Figure 4). Shannon diversity increased towards intermediate Kd values and declined at higher levels of vegetation transformation (Gaussian GAM: edf = 2.89, F = 23.4, p < 0.001), with the model explaining 51.8% of deviance. Simpson dominance showed the opposite non-linear pattern (beta-GAM: edf = 3.04, χ^2 = 81.28, p < 0.001; 56.3% deviance explained), whereas Pielou evenness increased towards intermediate Kd values and declined at high Kd (beta-GAM: edf = 3.13, χ^2 = 94.44, p < 0.001; 58.9% deviance explained).

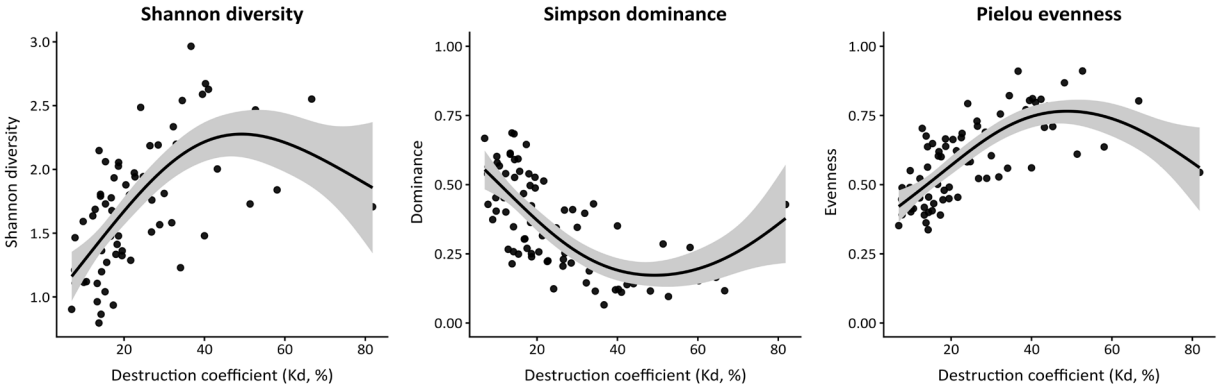


Figure 4: Non-linear relationships between the destruction coefficient (Kd) and species diversity metrics: (A) Shannon diversity, (B) Simpson dominance, and (C) Pielou evenness. Points represent individual relevés, solid lines show fitted generalized additive model (GAM) relationships, and shaded areas indicate 95% confidence intervals.

Slika 4: Nelinearna povezava med koeficientom uničenja (Kd) in različnimi metrikami vrstne pestrosti: (A) diverziteta (Shannon), (B) dominanca (Simpson) in (C) vrstna enakomernost (Pielou). Točke predstavljajo posamezne popise, polna črta predstavlja prilagojeni posplošeni aditivni model (GAM), zasenčeno območje prikazuje 95% interval zaupanja.

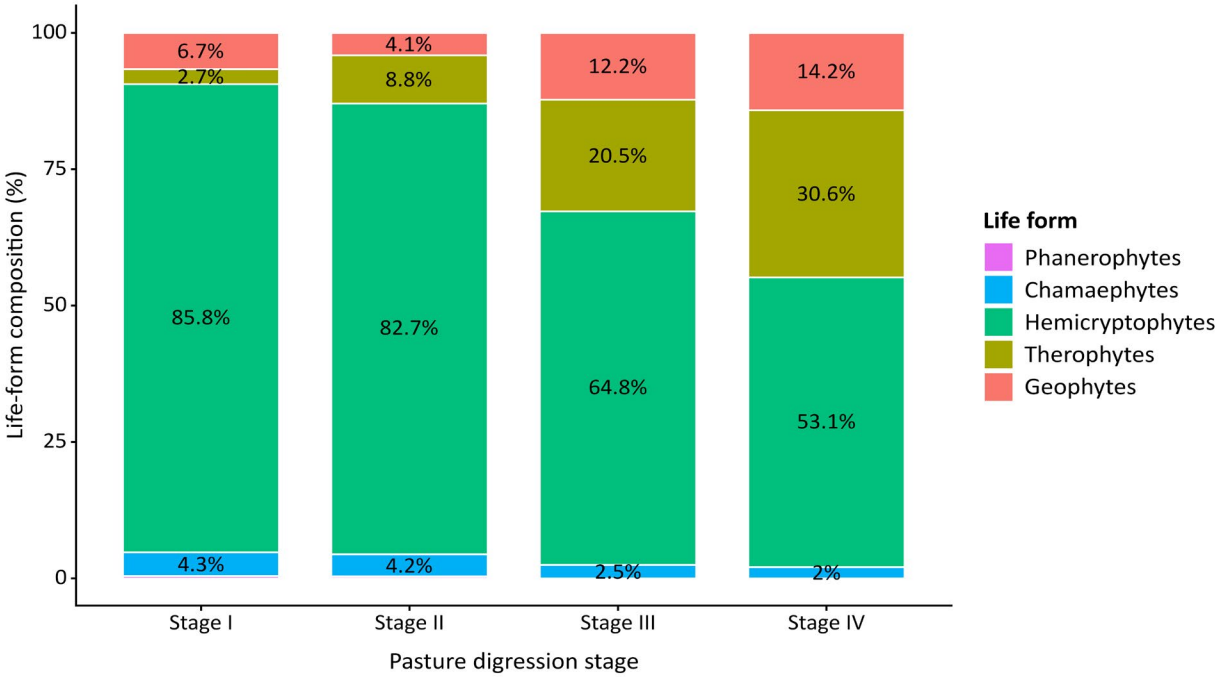


Figure 5: Mean proportional composition of Raunkiær's life-form groups across pasture digression stages. Each stacked column represents one pasture digression stage (I–IV) and shows the mean proportional participation of phanerophytes, chamaephytes, hemicryptophytes, therophytes, and geophytes. The proportions within each stage sum to 100%.

Slika 5: Povprečen delež življenskih oblik po Raunkierju med stopnjami intenzivnosti paše. Stolpec predstavlja posamezno stopnjo (I–IV) in prikazuje delež fanerofitov, hamefitov, hemikriptofitov, terofitov in geofitov. Skupna vsota deležev je 100%.

Changes in life-form composition across pasture digression stages

Life-form composition changed across pasture digression stages (Figure 5). Hemicryptophytes remained the dominant life-form group at all stages, but their mean proportional participation decreased from 85.8% at Stage I to 82.7% at Stage II, 64.8% at Stage III, and 53.1% at Stage IV. Differences among stages were significant (Kruskal-Wallis test: $H = 20.1$, $p < 0.001$). Dunn's post-hoc test showed significant differences between Stage I and Stages III and IV, whereas the remaining pairwise comparisons were not significant. The same trend was evident along the continuous gradient, with hemicryptophyte participation showing a significant negative correlation with Kd (Spearman's $\rho = -0.458$, $p < 0.001$).

Therophytes showed the opposite pattern, increasing from 2.7% at Stage I to 8.8% at Stage II, 20.5% at Stage III, and 30.6% at Stage IV. Their proportional participation differed significantly among pasture-digression stages ($H = 28.6$, $p < 0.001$). Stage I differed significantly from Stages II, III, and IV, whereas no significant differences were detected among Stages II–IV. Therophyte participation also showed a strong positive correlation with continuous Kd (Spearman's $\rho = 0.623$, $p < 0.001$).

Geophytes showed a weaker and non-monotonic stage-wise pattern. Their mean proportional participation was 6.7% at Stage I, decreased to 4.1% at Stage II, and then increased to 12.2% at Stage III and 14.2% at Stage IV. Differences among stages were significant ($H = 15.1$, $p = 0.0018$). Post-hoc comparisons showed significant differences between Stages I and III and between Stages II and III, whereas the remaining contrasts were not significant. Despite the non-monotonic pattern across the discrete stages, geophyte participation showed a significant positive correlation with continuous Kd (Spearman's $\rho = 0.371$, $p < 0.001$).

Chamaephytes remained a minor component of the vegetation and showed no significant differences among pasture-digression stages ($H = 3.96$, $p = 0.266$) and no significant relationship with continuous Kd (Spearman's $\rho = -0.160$, $p = 0.156$).

Phanerophytes were also scarce throughout the gradient, with mean proportional participation decreasing from 0.44% at Stage I to 0.15% at Stage II and being absent from Stages III and IV. The overall Kruskal–Wallis test indicated a weak stage effect ($H = 8.15$, $p = 0.043$), but no pairwise comparison remained significant after Holm correction. However, phanerophyte participation was negatively correlated with continuous Kd (Spearman's $\rho = -0.403$, $p < 0.001$).

Nitrogen availability (Nt) also increased along the gradient, from 4.73 at Stage I to 4.88, 5.24, and 5.60 at Stages II–IV, respectively ($H = 30.5$, Holm-adjusted $p < 0.001$). Stage I differed significantly from Stages II, III, and IV, and Stage II also differed from Stage IV. Nt was positively correlated with continuous Kd ($\rho = 0.616$, Holm-adjusted $p < 0.001$).

Cryoclimate values (Cr) increased from 8.06 at Stage I to 8.32 at Stage II and 8.55 at Stage III, followed by a slight decrease to 8.42 at Stage IV ($H = 21.6$, Holm-adjusted $p < 0.001$). Stage I differed significantly from Stages II and III, whereas Stage IV did not differ significantly from any other stage. Cr was positively associated with continuous Kd ($\rho = 0.497$, Holm-adjusted $p < 0.001$).

In contrast, continentality (Kn) and light (Lc) decreased with increasing pasture digression. Mean Kn declined from 10.5 at Stage I to 9.87 at Stage II, 9.47 at Stage III, and 9.09 at Stage IV ($H = 34.4$, Holm-adjusted $p < 0.001$). Stage I differed significantly from all subsequent stages, and Kn showed a strong negative correlation with continuous Kd ($\rho = -0.633$, Holm-adjusted $p < 0.001$). Light values showed a similar decline, from 7.87 at Stage I to 7.77, 7.66, and 7.57 at Stages II–IV ($H = 34.3$, Holm-adjusted $p < 0.001$), with Stage I differing significantly from all later stages and a strong negative relationship with Kd ($\rho = -0.666$, Holm-adjusted $p < 0.001$).

The salt-regime indicator (Sl) decreased from 9.10 at Stage I to 8.83 at Stage II and 8.71 at Stage III, with a slight increase to 8.74 at Stage IV ($H = 16.9$, Holm-adjusted $p = 0.005$). Stage I differed significantly from Stages II and III, whereas Stage IV did not differ significantly from any other stage. Sl was negatively correlated with continuous Kd ($\rho = -0.452$, Holm-adjusted $p < 0.001$).

No significant stage-wise differences remained after correction for multiple testing for soil aeration (Ae), carbonate content (Ca), soil acidity (Rc), humidity (Om), thermal climate (Tm), or variability of soil moisture (fH). These indicators also showed no significant relationships with continuous Kd after Holm correction, although Ca and fH showed weak positive tendencies.

Discussion

Semi-dry grasslands in the study area currently persist within a heterogeneous land-use mosaic shaped by both reduced agricultural use and continued local grazing. On the one hand, declining livestock numbers and the abandonment of traditional agricultural practices favour shrub and tree encroachment, including *Crataegus leiomonogyna*, *Rosa canina*, *R. corymbifera*, *R. rubiginosa*, *Prunus spinosa*, *Elaeagnus angustifolia*, *Malus sylvestris*, and *Pyrus communis*. On the other hand, the remaining cattle

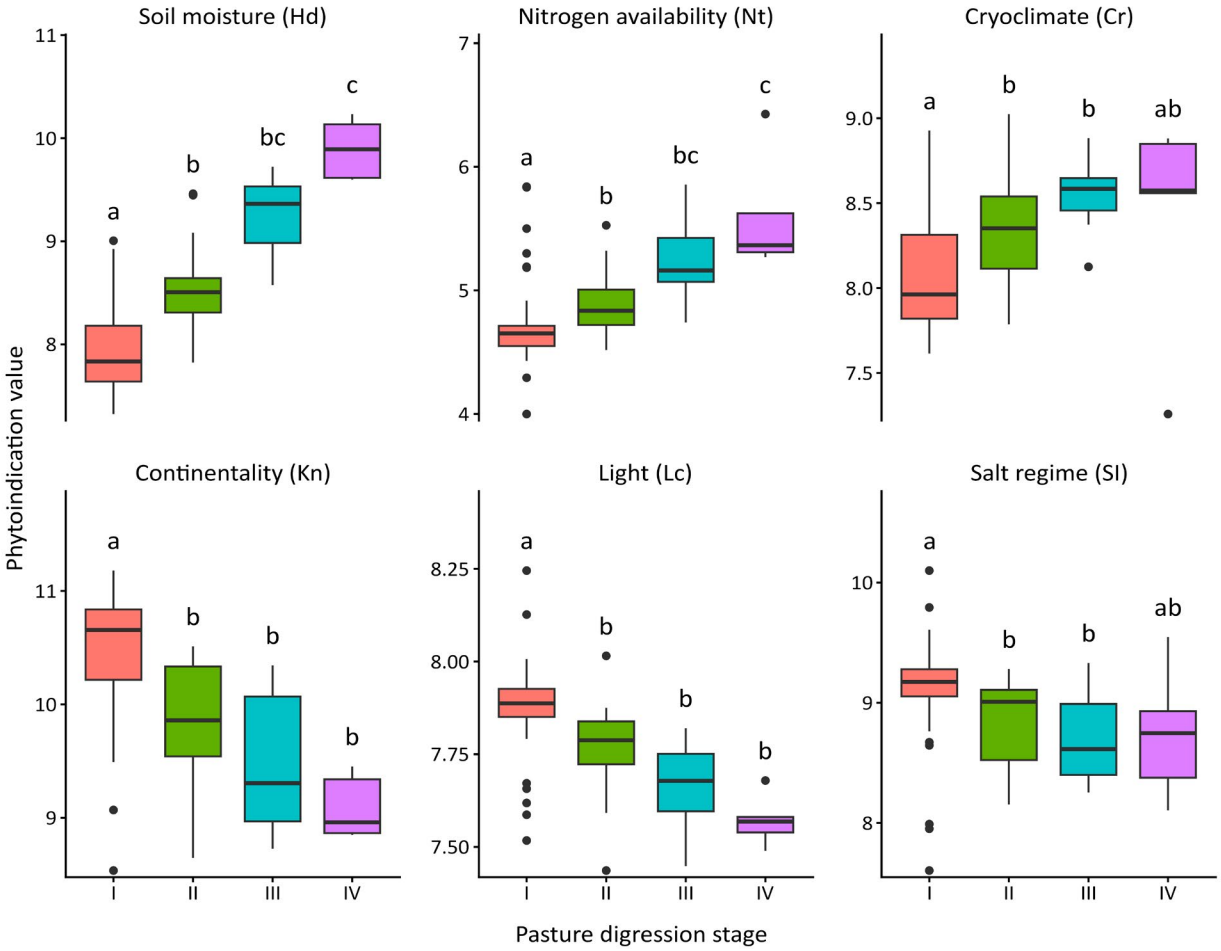


Figure 6: Cover-weighted phytoindication values across pasture-digression stages for soil moisture (Hd), nitrogen availability (Nt), cryoclimate (Cr), continentality (Kn), light (Lc), and salt regime (Sl). Boxes represent the interquartile range, horizontal lines indicate medians, whiskers extend to 1.5 × IQR, and points represent outliers. Different lowercase letters indicate significant differences among stages according to Dunn's post-hoc test with Holm adjustment ($p < 0.05$).

Slika 6: Fitoindikacija z upoštevanjem pokrovnosti v različnih stopnjah intenzivnosti paše za vlažnost tal (Hd), razpoložljivost dušika (Nt), krioklimo (Cr), kontinentalnost (Kn), svetlobo (Lc) in slanost (Sl). Škatle predstavljajo medkvartilni razpon, vodoravna črta mediano, brki razpon 1.5 × IQR in točke osamelce. Različne črke nakazujejo značilne razlike med stopnjami intenzivnosti paše testirane z Dunn post-hoc testom s prilagoditvijo po Holmu in Kruskal-Wallis testom ($p < 0.05$).

grazing maintains open grassland patches and creates spatial variation in disturbance intensity. Grazing therefore should not be viewed simply as a negative pressure. It is also one of the key processes preventing rapid succession towards shrub-dominated vegetation and maintaining structural heterogeneity in semi-dry grasslands. Similar dual effects have been reported for semi-natural grasslands, where low to moderate grazing may support plant diversity and maintain open vegetation, whereas both abandonment and excessive disturbance may lead to undesirable vegetation change (Pykälä, 2003; Alados et al., 2005; Alrababah et al., 2007; Papanikolaou et al., 2011; Liang et al., 2021; Török et al., 2024).

In the present study, vegetation change was analysed along a gradient of pasture digression rather than through direct comparison with ungrazed reference vegetation. This distinction is important because all sampled plots were located within grassland systems affected by long-term livestock use. Consequently, Stage I represents the least transformed vegetation within the local grazing system rather than an undisturbed reference state. Within this framework, the destruction coefficient was useful for expressing the increasing proportional contribution of destructor species and for describing vegetation transformation along a continuous gradient. Most relevés belonged to the earlier stages of pasture digression: 64 of 80 plots

were assigned to Stages I and II, whereas only 16 plots represented Stages III and IV. The relatively small number of Stage IV plots indicates that highly transformed vegetation was less frequent within the sampled grasslands.

Species-level responses indicate substantial floristic and structural restructuring along the pasture-digression gradient rather than a simple disappearance of perennial grassland species. One of the clearest examples was *Festuca valesiaca*. Its constancy remained very high throughout the gradient, reaching 100% in Stages III and IV, whereas its mean cover declined sharply from 55.8% at Stage I to only 8.2% at Stage IV. Thus, the species persisted within the vegetation but progressively lost its dominant structural role. Similar decreases were observed for *Bothriochloa ischaemum* and *Teucrium montanum*. In contrast, *Medicago lupulina* and *Elytrigia repens* increased strongly in cover towards the advanced stages, while species such as *Echium vulgare*, *Trifolium arvense*, *Carduus acanthoides*, and *Eryngium campestre* became progressively more frequent. These patterns indicate increasing compositional turnover and a weakening of vegetation strongly dominated by perennial meadow-steppe species.

Such restructuring is consistent with the effects of biomass removal and trampling, which alter competitive relationships, reduce vegetation closure, and create open microsites for establishment. In the earlier stages, dense perennial vegetation probably imposed stronger competitive constraints, whereas increasing disturbance opened space for additional species, including short-lived and disturbance-tolerant taxa. Similar processes have been described in other grazed grasslands, where low or moderate disturbance can increase small-scale heterogeneity and facilitate coexistence, while stronger disturbance leads to progressively greater compositional change (Alados et al., 2005; Alrababah et al., 2007; Dostálek & Frantík, 2008; Dengler et al., 2014; Silva et al., 2019). Trampling and biomass removal may additionally modify the soil surface and facilitate the establishment of species tolerant of repeated disturbance (Pykälä, 2003; Reutimann et al., 2023).

A central result of our study is that species diversity did not respond monotonically to increasing pasture digression. Shannon diversity and Pielou evenness increased from the least transformed vegetation towards intermediate values of Kd and declined again at the upper end of the observed gradient, whereas Simpson dominance showed the opposite pattern. The GAM analyses confirmed that these relationships were non-linear and explained approximately 52–59% of the deviance in the three diversity metrics. Similar non-linear relationships between grazing-related disturbance, vegetation productivity, and local plant diversity have been reported from other grassland systems (Köhler et al., 2005; Ruprecht et al., 2010; Dengler et al., 2014).

The diversity maximum at intermediate pasture digression should not, however, be interpreted simply as evidence of an optimal disturbance level in the sense of the Intermediate Disturbance Hypothesis. Although the observed pattern is consistent with an intermediate-disturbance-like response, our study does not directly test the mechanisms assumed by this hypothesis (Hanke et al., 2014). Instead, the increase in diversity coincided with pronounced compositional transformation, including declining dominance of perennial graminoids, increasing participation of legumes and therophytes, and a greater contribution of destructor species. Short-lived and disturbance-tolerant species can establish rapidly in newly created microsites and under changing local conditions associated with grazing disturbance (Pykälä, 2003; Dostálek & Frantík, 2008; Papanikolaou et al., 2011; Silva et al., 2019; Török et al., 2024). Thus, increasing local diversity partly reflected the addition of such species to a vegetation matrix in which characteristic perennial grassland species were losing dominance.

This distinction is important from a conservation perspective. High local species richness does not necessarily indicate favourable conservation status when it is accompanied by substantial changes in dominance structure and increasing synanthropization. In our data, Stage III combined relatively high diversity with already pronounced compositional restructuring, while the slight decline in diversity at Stage IV occurred in vegetation with the highest mean destruction coefficient. Similar threshold-like or state-transition responses have been described for ecosystems in which gradual changes in disturbance eventually produce substantial shifts in vegetation structure and composition (Bestelmeyer, 2006; Caravelli & Staniczenko, 2016). Because only five relevés represented Stage IV in our study, the exact shape of the response at the most advanced end of the gradient should be interpreted cautiously. Nevertheless, the overall pattern clearly shows that increasing pasture digression cannot be described as a simple monotonic decline in species diversity.

The life-form analysis supports this interpretation. Hemicryptophytes remained the dominant life-form group throughout the gradient, but their proportional contribution declined markedly from 85.8% at Stage I to 53.1% at Stage IV. Therophytes showed the opposite response, increasing from 2.7% to 30.6%, and their proportional participation was strongly positively related to continuous Kd. This shift indicates an increasing role of short-lived species under stronger grazing-related disturbance, probably associated with the creation of open microsites through trampling, biomass removal, and re-

duced vegetation closure. Similar increases in annual and short-lived life forms under grazing disturbance have been reported in other grassland systems (Papanikolaou et al., 2011; Kadhum et al., 2021). At the same time, the continued dominance of hemicryptophytes even at Stage IV indicates that the perennial grassland matrix had not been completely replaced.

Geophytes showed a weaker and less monotonic response, with their mean proportional contribution increasing particularly at Stages III and IV. Their positive relationship with continuous Kd suggests that species with belowground renewal organs may persist or even become relatively more important under increasing disturbance, possibly because bulbs, tubers, and rhizomes provide resilience to repeated biomass removal and trampling. Similar shifts in life-form composition under grazing have been observed previously (Papanikolaou et al., 2011). Chamaephytes remained a minor component and showed no significant response, which is consistent with the variable response of this life form to grazing reported from other dry grassland systems (Noy-Meir & Oron, 2001; Papanikolaou et al., 2011; Kadhum et al., 2021).

Phanerophytes were also scarce throughout the gradient and showed a negative relationship with continuous Kd. Their very low contribution is consistent with the long-term use of all studied plots by livestock, because continued grazing and trampling can restrict woody establishment even in landscapes where abandonment of neighbouring grasslands promotes shrub encroachment. This supports the broader role of grazing in suppressing shrub and tree recruitment and maintaining open grasslands (Dostálek & Frantík, 2008; Papanikolaou et al., 2011; Silva et al., 2019; Török et al., 2024).

The analysis of broad species groups revealed a parallel reorganization of vegetation. Graminoids declined strongly with increasing pasture digression, whereas legumes showed a pronounced positive response. Forbs showed a weaker pattern: their proportional participation did not differ significantly among the four discrete stages, although it was weakly positively associated with continuous Kd. The decline of graminoids reflects the weakening of the perennial grass matrix, particularly the marked loss of dominance of *Festuca valesiaca*. In contrast, the increasing contribution of legumes was associated with species such as *Medicago lupulina*, *Lotus corniculatus*, *Medicago falcata*, *Onobrychis arenaria*, *Trifolium arvense*, and *Trifolium dubium*. This response may reflect their tolerance of grazing-related disturbance and may also be favoured by local conditions associated with livestock activity (Kuzemko, 2008b; Aboling et al., 2008; Silva et al., 2019; Ciavattini et al., 2023; Török et al., 2024).

The increase in legumes is also consistent with the phytoindication results, which showed a shift towards species associated with higher nitrogen availability. However, this relationship should be interpreted cautiously. Phytoindication values describe the ecological affinities of the species composing the vegetation rather than directly measured soil properties. Thus, increasing Nt indicates a greater contribution of species associated with relatively nitrogen-rich conditions and may be compatible with local nutrient enrichment from livestock excreta, but direct soil measurements would be required to confirm this mechanism.

Phytoindication provided further evidence that pasture digression was accompanied by systematic changes in the ecological composition of the vegetation. The strongest response was observed for the soil-moisture indicator (Hd), which increased markedly along the gradient and showed a strong positive relationship with continuous Kd. Nitrogen availability (Nt) also increased, whereas light (Lc), continentality (Kn), and salt-regime values (Sl) declined; cryoclimate values (Cr) showed a weaker positive shift. Other ecological indicators showed no significant overall response after correction for multiple testing.

The increase in Hd suggests a shift towards species associated with relatively moister ecological conditions. This should not be interpreted as evidence of a direct increase in soil moisture, because phytoindication values reflect the ecological affinities of the species composing the vegetation rather than direct measurements of environmental conditions (Didukh & Pluta, 1994; Didukh, 2011). One possible explanation is the decreasing contribution of xerophytic and steppe-associated species and their replacement by more mesophilous, disturbance-tolerant, and synanthropic taxa.

A similar interpretation may apply to the decline in Lc and Kn. Many characteristic steppe species are associated with open, highly illuminated habitats and relatively continental conditions. Their decreasing contribution along the pasture-digression gradient could therefore lower community-weighted light and continentality values. Thus, the simultaneous increase in Hd and decline in Lc and Kn may reflect a gradual weakening of the original xerophytic and continental steppe component rather than direct changes in local light conditions or regional climate.

The increase in Nt indicates a greater contribution of species associated with more nutrient-rich conditions. This pattern may be consistent with local nutrient enrichment associated with livestock activity and with the increasing participation of legumes along the pasture-digression gradient (Ciavattini et al., 2023).

Overall, the phytoindication results support the interpretation that increasing pasture digression was accompa-

nied by a gradual shift in floristic composition away from the original semi-dry steppe assemblage towards species with different ecological affinities.

From a conservation and management perspective, these results reinforce the need to distinguish between the presence of grazing and its local intensity. Continued grazing remains important for preventing shrub encroachment and maintaining open semi-dry grasslands, but spatially concentrated or excessive grazing can promote advanced pasture digression and substantial compositional transformation. Management should therefore aim to maintain grazing as a conservation tool while avoiding prolonged concentration of livestock pressure in particular patches and, where necessary, combining grazing with measures aimed at controlling woody encroachment.

Conclusions

The study showed that long-term livestock grazing is associated with non-linear changes in semi-dry grassland vegetation. Along the pasture digression gradient, increasing transformation was accompanied by substantial restructuring of vegetation composition and dominance, including a decline in graminoids and hemicryptophytes and an increasing contribution of legumes, therophytes, and disturbance-tolerant and synanthropic species. Species diversity and evenness increased towards intermediate levels of pasture digression and declined slightly at the upper end of the observed gradient, while dominance showed the opposite pattern. Thus, higher local diversity under grazing did not necessarily indicate a more favourable conservation state, because it was accompanied by increasing compositional transformation and weakening of the original perennial grassland structure.

Phytoindication results further suggested a shift in the ecological composition of the vegetation, with increasing representation of species associated with relatively moister and more nitrogen-rich conditions and decreasing representation of species associated with higher light availability and continental conditions.

Despite the long history of grazing in the region, the recent decline in livestock numbers has led to fragmentation of grazing areas and increasing spatial heterogeneity of grazing pressure. As a result, semi-dry grasslands are currently affected by two opposing processes: local underuse, which favours shrub and tree encroachment, and locally intensive grazing, which promotes advanced pasture digression and vegetation transformation.

From a conservation perspective, these results indicate that grazing should be maintained as an important management process for preserving open semi-dry grasslands, but its spatial distribution and intensity should be regulated to avoid advanced pasture digression. At the same time, woody encroachment should be controlled where necessary by appropriate management measures.

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Research Data Availability

The data supporting this study are available from the corresponding author upon reasonable request.

Conflict of Interest

The authors declare no conflicts of interest relevant to the content of this manuscript.

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Appendix 1. Species constancy across the four pasture-digression stages. Species occurring in at least 25% of relevés within a stage were considered constant (light grey), and those occurring in at least 50% were considered highly constant (dark grey). Species are sorted by decreasing constancy; bold type indicates destructor species according to Protopopova (1991).

Pasture digression stage	**1**	**2**	**3**	**4**
Number of relevés	41	23	11	5
Picris hieracioides	32	22	18	0
Scabiosa ochroleuca	29	17	9	0
Bupleurum falcatum	27	9	9	20
Phalacroloma annuum	24	22	45	20
Cichorium intybus	17	13	36	20
Centaurea scabiosa	0	4	27	0
Ranunculus repens	0	9	27	0
Nonea pulla	12	13	27	20
Trifolium dubium	15	22	18	80
Astragalus onobrychis	15	9	9	60
Onobrychis arenaria	10	4	9	40
Dipsacus sylvestris	0	4	0	40
Torilis arvensis	2	4	0	40
Carduus acanthoides	10	13	18	40
Thymus pulegioides ag.	10	9	0	40
Trifolium arvense	2	13	18	40
Teucrium montanum	44	30	0	0
Pilosella officinarum	41	22	9	40
Centaurea stoebe	37	22	18	80
Pimpinella saxifraga	20	48	27	20
Securigera varia	12	43	36	20
Galium album	22	30	73	0
Teucrium chamaedrys	17	26	18	40
Elytrigia repens	10	17	45	40
Potentilla incana	59	52	18	60
Bothriochloa ischaemum	59	43	27	20
Thymus marschallianus	39	17	27	100
Convolvulus arvensis	29	30	36	20

Taraxacum officinale ag.	27	35	27	20
Centaurea jacea	24	39	36	40
Echium vulgare	17	26	36	60
Festuca valesiaca	93	96	100	100
Achillea submillefolium	80	83	91	60
Plantago lanceolata	78	70	73	100
Lotus corniculatus	73	74	64	80
Eryngium campestre	68	91	100	100
Plantago media	63	43	45	100
Galium verum	61	74	73	80
Elytrigia intermedia	51	43	55	60
Agrimonia eupatoria	49	61	45	40
Medicago lupulina	46	70	91	80
Euphorbia cyparissias	46	26	27	40
Asperula cynanchica	46	57	36	60
Potentilla argentea	46	35	55	40
Fragaria viridis	39	52	55	40
Poa angustifolia	37	61	36	80
Achillea setacea	32	43	82	60
Lathyrus tuberosus	0	4	9	20
Lepidium campestre	0	0	0	20
Koeleria cristata	10	4	0	20
Vicia sativa	7	17	0	20
Medicago falcata ag.	5	0	0	20
Lactuca serriola	0	0	0	20
Trifolium campestre	0	0	0	20
Inula ensifolia	5	9	9	20
Poa compressa	2	4	9	20
Bromopsis inermis	0	4	9	20
Trifolium pratense	5	22	18	20
Leontodon hispidus	12	9	9	20
Artemisia absinthium	12	9	0	0
Seseli annuum	10	22	0	0

Consolida regalis	0	9	0	0
Capsella bursa-pastoris	2	9	0	0
Daucus carota	5	9	0	0
Lappula squarrosa	0	9	0	0
Campanula glomerata	0	13	0	0
Arabidopsis thaliana	0	4	0	0
Pyrus communis	2	4	0	0
Ranunculus polyanthemos	0	9	0	0
Salvia pratensis	0	4	0	0
Allium paniculatum	0	4	0	0
Knautia arvensis	2	13	0	0
Lythrum hyssopifolia	0	9	0	0
Berteroa incana	5	9	0	0
Helichrysum arenarium	7	4	0	0
Carlina biebersteinii	0	4	0	0
Dactylis glomerata	2	4	0	0
Aster amellus	0	4	0	0
Astragalus glycyphyllos	0	4	0	0
Melilotus officinalis	0	4	0	0
Cerinthe minor	0	4	0	0
Sesleria heufleriana	2	4	0	0
Dianthus pseudarmeria	0	4	0	0
Cleistogenes serotina	0	4	0	0
Chamaecytisus albus	2	4	0	0
Onopordum acanthium	0	4	0	0
Viola ambigua	5	4	0	0
Bromus squarrosus	0	4	0	0
Veronica spicata	0	4	0	0
Vicia tenuifolia	0	4	0	0
Hypericum perforatum	0	9	0	0
Linaria vulgaris	2	0	0	0
Thymus moldavicus	2	0	0	0
Allium sphaerocephalon	0	0	9	0

Lepidium densiflorum	0	4	0	0
Astragalus monspessulanus	2	0	0	0
Centaurea arenaria	0	0	0	0
Torilis japonica	2	0	0	0
Chamaecytisus ruthenicus	0	0	0	0
Falcaria vulgaris	15	17	9	0
Ranunculus acris	0	0	9	0
Carex praecox	0	0	9	0
Eryngium planum	0	9	18	0
Veronica arvensis	0	0	18	0
Vicia cracca	0	0	9	0
Salvia nemorosa ag.	5	13	9	0
Erodium cicutarium	0	0	9	0
Potentilla reptans	10	0	9	0
Chamaecytisus austriacus	5	0	0	0
Rosa corymbifera	10	0	0	0
Glechoma hederacea	2	0	0	0
Artemisia austriaca	2	0	0	0
Trifolium medium	7	9	0	0
Salvia verticillata	10	9	0	0
Melampyrum nemorosum	2	0	0	0
Crataegus monogyna	10	4	0	0
Prunus spinosa	7	0	0	0
Rosa canina	2	0	0	0
Chenopodium album	2	0	0	0
Rosa spinosissima	2	0	0	0
Potentilla anserina	2	0	0	0
Adonis vernalis	2	0	0	0

Appendix 2. Cover-weighted phytoindication values of ecological factors along the pasture-digression gradient. For each of the four pasture-digression stages, mean (X), standard deviation (SD), minimum, maximum, and mean ± 2 SD are presented for each ecological indicator.

	Hd	fH	Rc	Sl	Ca	Nt	Ae	Tm	Om	Kn	Cr	Lc
1st STAGE GRASSLAND DIGRESSION												
X	7.95	6.81	8.68	9.1	8.01	4.73	5.53	9.37	10.19	10.47	8.06	7.87
SD	0.41	0.33	0.23	0.45	0.6	0.36	0.1	0.25	0.38	0.57	0.34	0.13
max	9.01	7.28	9.34	10.1	9.84	5.84	5.74	9.99	11.57	11.18	8.93	8.25
min	7.32	5.75	8.32	7.6	7.41	4	5.15	8.46	9.73	8.54	7.61	7.52
+2d	8.77	7.48	9.15	10.01	9.22	5.45	5.74	9.88	10.94	11.61	8.74	8.13
-2d	7.13	6.14	8.21	8.2	6.8	4.01	5.32	8.87	9.44	9.32	7.39	7.61
2nd STAGE GRASSLAND DIGRESSION												
X	8.55	6.85	8.66	8.83	8.05	4.88	5.55	9.3	10.49	9.87	8.32	7.77
SD	0.43	0.43	0.17	0.37	0.41	0.25	0.12	0.29	0.48	0.48	0.29	0.12
max	9.46	7.48	9.06	9.28	8.74	5.53	5.88	9.92	11.69	10.51	9.02	8.02
min	7.82	5.62	8.35	8.15	7.33	4.52	5.25	8.41	9.79	8.65	7.79	7.44
+2d	9.42	7.72	9	9.56	8.87	5.38	5.78	9.89	11.46	10.84	8.89	8.01
-2d	7.68	5.99	8.33	8.1	7.22	4.39	5.31	8.72	9.53	8.9	7.75	7.53
3rd STAGE GRASSLAND DIGRESSION												
X	9.26	7.13	8.82	8.71	8.23	5.24	5.48	9.24	10.4	9.47	8.55	7.66
SD	0.36	0.53	0.11	0.37	0.3	0.3	0.09	0.35	0.5	0.61	0.2	0.12
max	9.72	8.08	8.97	9.33	8.68	5.86	5.66	9.69	11.17	10.34	8.88	7.82
min	8.57	6.31	8.61	8.25	7.77	4.74	5.36	8.71	9.68	8.73	8.12	7.45
+2d	9.98	8.19	9.03	9.44	8.82	5.83	5.66	9.95	11.41	10.69	8.96	7.9
-2d	8.54	6.08	8.6	7.97	7.64	4.65	5.29	8.53	9.4	8.26	8.14	7.43
4th STAGE GRASSLAND DIGRESSION												
X	9.9	7.46	8.77	8.74	8.36	5.6	5.5	9.18	10.32	9.09	8.42	7.57
SD	0.29	0.72	0.16	0.55	0.5	0.48	0.25	0.44	0.43	0.28	0.67	0.07
max	10.23	8.55	8.96	9.55	9.18	6.43	5.84	9.62	10.84	9.45	8.88	7.68
min	9.6	6.63	8.57	8.1	7.97	5.27	5.21	8.46	9.83	8.85	7.26	7.49
+2d	10.48	8.9	9.09	9.85	9.37	6.56	5.99	10.07	11.19	9.66	9.76	7.71
-2d	9.31	6.01	8.45	7.63	7.36	4.63	5.01	8.29	9.46	8.53	7.09	7.43