








# Zoochory on and off: A field experiment for trait-based analysis of establishment success of grassland species

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## Abstract

**Aims:** We tested the establishment success of grassland species in the presence or absence of zoochory by livestock and identified the traits associated with successful establishment.

**Location:** Hortobágy National Park, Hungary.

**Methods:** In six restored species-poor grasslands we established two species-rich 4 m × 4 m source plots per site in 2013. One source plot was managed by extensive cattle grazing ("zoochory on"), the other one was fenced and protected from grazers ("zoochory off"). We monitored the vegetation development in the source plots (2014–2018), and the establishment success of sown species (2016–2018) in adjacent dispersal plots in four, 20-m-long strips per source plot in a total of 960 dispersal plots. We calculated community-weighted means of thirteen plant traits related to regeneration and competitive ability. The effect of grazing, year, distance from source plots, grazing–year and grazing–distance interactions on population and trait dynamics in the source and dispersal plots were analysed with generalized linear mixed-effect models.

**Results:** Although grazing reduced the cover and flowering success of sown species in the source plots, the number of successful establishment events was higher in dispersal plots next to grazed source plots. The sown species were the most abundant in plots adjacent to source plots, but occurred at all monitored distances. Zoochory favoured perennial plants with high specific leaf area (SLA), low leaf dry matter content (LDMC), short stature, light seeds, early flowering period, high clonal index and anemochory index.

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of regional seed propagation to Hungary (ProSeed)".

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**Conclusions:** We showed that species that can colonize the matrix with and without zoochory have contrasting trait syndromes. In grazing-adapted ecosystems, fencing source populations of target species does not always seem to be a good option. It was a good tool for increasing the cover and flowering success of the sown species in the short run, but it significantly decreased their chance to colonize the surrounding area in the long run.

#### KEYWORDS

alkaline grassland, dispersal success, epizoochory, establishment gaps, grassland restoration, grazing, loess grassland, plant trait, seed dispersal, seed sowing

## 1 | INTRODUCTION

Grasslands often require continuous or periodic disturbance to maintain their openness (Huston, 1979; Tälle et al., 2016). Grazing, which provides a spatially and temporally dynamic disturbance, is the most typical traditional management measure to maintain open habitats worldwide (Török et al., 2016a). Biomass removal by grazing animals reduces competition, prevents shrub encroachment and in combination with trampling leads to the creation of open surfaces; thus, it can maintain openness of the landscape and species diversity (Köhler et al., 2016; Tälle et al., 2016; Pulungan et al., 2019). Grazing animals are important vectors of both short- and long-distance seed dispersal (Manzano & Malo, 2006). Zoochory is a directed, non-random way of plant dispersal, which ensures long dispersal distances and high probability of reaching suitable microsites for establishment (Wenny, 2001; Manzano & Malo, 2006). Grazers can maintain connections between meta-populations by linking natural and semi-natural habitat patches in fragmented landscapes both by endozoochory and epizoochory (Couvreur et al., 2004, 2005). Grassland conservation and restoration projects often rely on grazers as seed dispersers of target species to overcome dispersal limitations and increase grassland plant diversity (Couvreur et al., 2004; Öster et al., 2009; Purschke et al., 2012; Kovácsné Koncz et al., 2020).

The presence of plant species in a habitat is determined both by their colonization (i.e. the ability of species to disperse to and establish at unoccupied patches) and persistence (i.e. the duration of species in a community before local extinction occurs) abilities. Colonization ability is especially important in early stages of succession and restoration. Dispersal ability is a crucial factor during colonization. It can be predicted by the growth form, height, seed mass, seed number and seed morphology of the species (Thomson et al., 2011; Tamme et al., 2014). In addition, the most successful species are those having persistent seeds and rapid, high germination potential under a wide range of environmental conditions (Pywell et al., 2003). At the later stages, as the sward closes, competitive ability becomes increasingly important (Pywell et al., 2003; Kiss et al., 2021). According to Grime (1977) good competitors have high relative growth rate, large biomass, and tall stature. The ability for clonal growth also provides a key advantage in the competition for open microhabitats (Saiz et al., 2016).

Grazing herbivores shape the vegetation composition and along with it have major impact on the trait distribution of the grassland vegetation (Díaz et al., 2007). Stahlheber and D'Antonio (2013) found that grazing increases the cover of grasses and species richness of forbs. Similarly, when comparing trait distributions between grazed and mown sites, Stammel et al. (2003) found that grazing favoured grasses, especially tiller-forming ones, and grasses and forbs with fast-spreading stolons. Among plant traits plant height, architecture and leaf characteristics are reliable predictors of plant species' responses to grazing (Díaz et al., 2001, 2007). In general, short, rosette-forming species respond positively to grazing (Stammel et al., 2003; Díaz et al., 2007; Deák et al., 2017). Species with these traits benefit from the increased light availability and decreased competition, and are able to avoid defoliation by leaves positioned at ground level (Stammel et al., 2003; Díaz et al., 2007; Janečková et al., 2017). A positive response to grazing is also associated with small seed weight (Dainese et al., 2015; Tóth et al., 2018), persistent seed bank (Dupré & Diekmann, 2001) and high specific leaf area (SLA), which is an indicator of high relative growth rate (Wright & Westoby, 2000; Díaz et al., 2001). Short-lived and ruderal species are also favoured by the presence of grazing (Pakeman, 2004; Díaz et al., 2007).

There is a rich literature on the effect of livestock grazing on grassland vegetation, but the mechanisms driving vegetation change are usually not separated. Hence, we have limited knowledge on the relative importance of zoochory and other effects of grazers, such as biomass removal, trampling and manuring. To fill this knowledge gap, we designed an experiment for testing the relative importance of zoochory by livestock. We tested the establishment success of grassland plant species under two settings: "zoochory on" (zoochory by livestock is possible) and "zoochory off" (zoochory by livestock is not possible) in an experimentally manipulated field trial. For this purpose, we experimentally introduced 35 grassland species that formerly did not occur in the species-poor pastures, into fenced and grazed experimental plots (source plots; Valkó et al., 2016). We evaluated the establishment success of the introduced grassland species originating from grazed and fenced source plots into the surrounding species-poor grassland. This sampling design enabled us to compare the establishment success of grassland species from grazed and ungrazed propagule sources to the surrounding pastures with zoochory

(from the grazed source plots) and without zoochory (from the fenced source plots) by livestock. Since the surrounding grasslands were uniformly managed by grazing, this experimental setup allowed to separate the effect of zoochorous dispersal from the other effects of livestock grazing (trampling, biomass removal, manuring) on the establishment success of grassland species. We asked the following questions: (a) are there differences in the development of grazed and fenced source plots; (b) how do the settings “zoochory on” and “zoochory off” affect the establishment of the sown grassland species in the surroundings of the source plots; and (c) which traits support the successful establishment of grassland species?

## 2 | METHODS

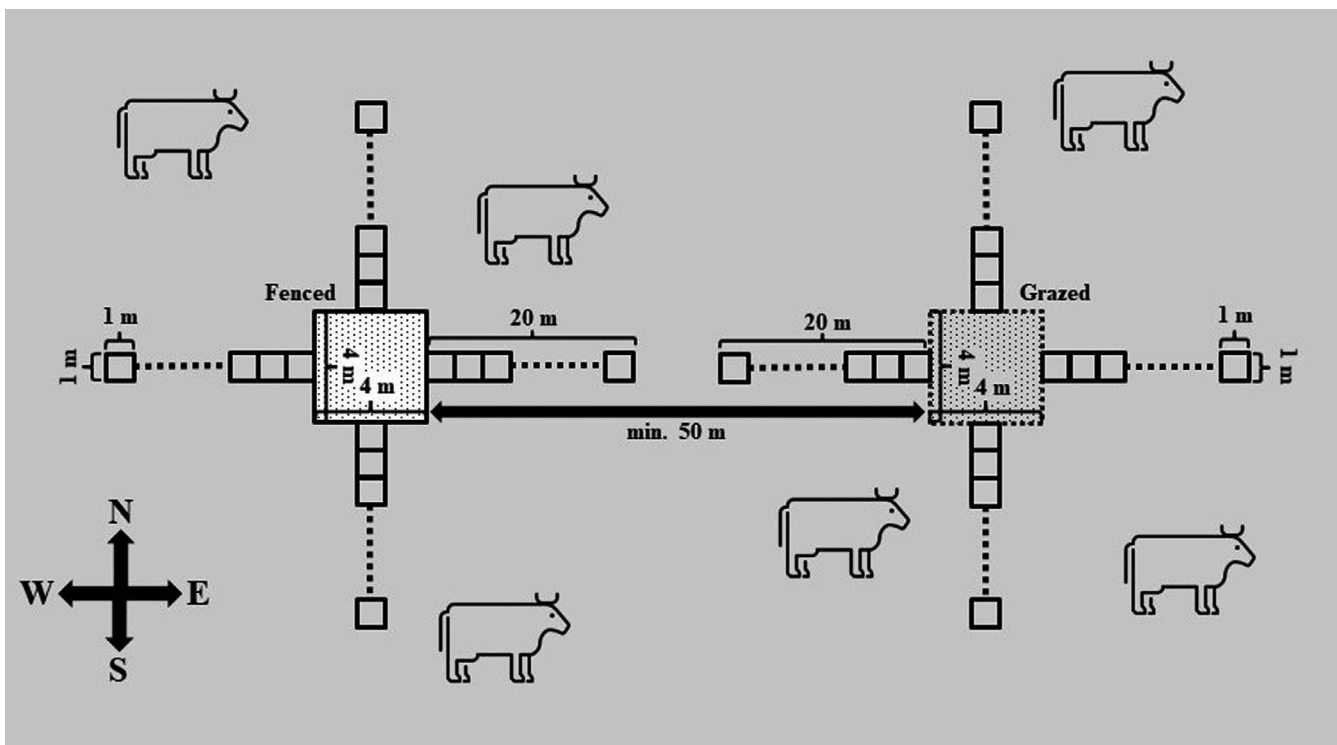
### 2.1 | Study sites

The study sites are situated in species-poor restored alkaline and loess grasslands in the Hortobágy National Park (East-Hungary), near the settlements Egyek and Tiszafüred. The study area is situated at 88–92 m a.s.l. and is characterized by a continental climate (550 mm mean annual precipitation and 9.5°C mean annual temperature, Lukács et al., 2015). Many stands of natural loess grasslands (*Festucion rupicolae*), alkaline meadows (*Beckmannion eruciformis*) and alkaline dry grasslands (*Artemisio-Festucetalia pseudovinae*) which were typical to the historical landscape of the region (Deák et al., 2014) have been ploughed since the 19th century (Török et al., 2010; Valkó et al., 2016). After the cessation of arable farming, the area

was restored in 2005 by sowing matrix grass species (*Bromus inermis*, *Festuca rupicola*, *Festuca pseudovina* and *Poa angustifolia*; Török et al., 2010). Post-restoration management consisted of mowing (2006–2008) and extensive cattle grazing (from 2009 to the present).

In October 2013, at six sites we established two 4 m × 4 m plots per site by soil disturbance. All source plots were sown with a high-diversity seed mixture containing propagules of species typical to loess and alkaline grasslands (35 species, 10 g/m<sup>2</sup>; Appendix S1, S2) to establish source plots that can serve as propagule sources for the colonization of the species-poor grassland (Valkó et al., 2016). We collected the seeds following the ENSCONET (2009) protocol; seeds originated from multiple mother plants from three populations in the region. The source plots were installed at least 50 m apart from each other to minimize propagule dispersal between them (Figure 1). The feasibility of using source plots for increasing the biodiversity of species-poor grasslands from the restoration perspective is discussed in Valkó et al. (2016) and Kiss et al. (2021). Here we focus on the trait-based analysis of dispersal success of target species from the grazed and fenced source plots to the surroundings, which has not been discussed yet in our study system.

One of the source plots at each site was extensively grazed by cattle, with a stocking rate of 350 kg live weight per hectare (corresponding to 0.5 livestock units/ha), between April and October every year, the other one was fenced and protected from grazing. The size of the six sites ranged between 30 and 40 ha and in all sites, the same stocking rate was set in accordance with the management plan of the Hortobágy National Park. These stocking rates are characteristic for the six study sites at the large scale, but we did not have



**FIGURE 1** Sampling design showing the fenced and grazed source plots and the monitoring transects (dispersal plots). Dotted texture indicates sowing. Grey background and cows indicate livestock grazing, white background indicates the enclosure (fenced source plot)

fine-scale data on the spatial distribution of grazing pressure within the sites. Note that the fence excluded livestock and large game species, but small mammals and birds had access to the fenced source plots. We assume that sown species detected in the surroundings of the grazed or fenced source plots originate most probably from the closest source plot. We report a manipulated field experiment that was conducted under real-world conditions; thus, we cannot exclude the possibility that some individuals were dispersed from longer distances (e.g., by wind or zoochory), however, we assume that these potential confounding factors affect the surroundings of the differently managed source plots with similarly low probability.

## 2.2 | Sampling design

Between 2014 and 2018 percentage cover scores of sown plant species occurring in the source plots were recorded annually in late June. In three consecutive years (from 2016 to 2018), we monitored annually the dispersal success of the sown grassland species from the source plots to the surrounding species-poor grassland. We placed four 20-m-long transects running in the four main directions (north, east, south and west) from the source plots. Each transect contained twenty 1 m × 1 m-sized plots (dispersal plots). In each 1 m × 1 m plot, we recorded the individual number of sown species and the number of flowering shoots annually in July. In total, we sampled 960 dispersal plots per year. Original data can be found in Appendix S1.

We selected traits that reflect the colonization (dispersal ability and reproduction strategy), establishment and persistence abilities (reproduction strategy, stress- and disturbance avoidance, resistance and tolerance) of the sown species in the source plots and in the extensively grazed grassland. For the analyses, we used the following traits: life span, seed bank persistence, seed weight, specific leaf area (SLA), leaf dry matter content (LDMC), plant height, the start, end and length of the flowering period, presence or absence of a rosette, clonal index, anemochory and epizoochory ranking indices (Table 1). We collected trait data from Hungarian data sources (Table 1, Appendix S2) or if regional data were not available, we used international databases (TRY – Kattge et al., 2020; CLO-PLA – Klimešová et al., 2017; D3 – Hintze et al., 2013; Appendix S3). The mean of the indicated minimum and maximum values was calculated for plant height. A mean was calculated if SLA and LDMC traits had multiple records, and the highest reported value was considered for seed bank persistence.  $\ln(x+1)$  transformation was performed for SLA, LDMC, seed weight and plant height values.

## 2.3 | Statistical analyses

All data analyses were calculated in the R statistical environment (ver. 4.0.2; R Core Team, 2020). To study the effect of predictors on the dependent variables and to account for repeated measurements, we used generalized linear mixed-effect models (GLMMs) fitted by the *glmmTMB* function of the *glmmTMB* package (Brooks et al., 2017).

For pairwise comparisons, we used the *emmeans* function of the *emmeans* package (Russell, 2020).

We studied the development of sown species in source plots between 2014 and 2018. To test the effect of grazing (fenced/grazed; fixed factor), year (2014–2018; continuous predictor) and grazing–year interaction on the dependent variables (cover and number of sown species, number of sown flowering species and flowering shoots) GLMMs were fitted with Gaussian distribution for cover data and Poisson distribution for number of species. Cover data was  $\ln(x+1)$ -transformed.

To study the dispersal dynamics of sown species from the source plots to the surroundings, GLMMs with Poisson distribution were fitted. Grazing of the source plot (zoochory on/off) was the fixed factor and year (2016–2018), distance from source plot (1–20 m), and the interaction of grazing–distance and grazing–year were continuous predictors. The distance was  $\ln(x+1)$ -transformed for the analyses. Dependent variables were the number of established species and individuals, number of flowering species and number of flowering shoots.

The community-weighted means (CWMs) of continuous traits in the source plots and the dispersal plots were calculated using the *functcomp* function of the *FD* package (Laliberté & Legendre, 2010; Laliberté et al., 2014). CWMs were calculated using the cover scores of sown species in the source plots and the individual numbers of sown species in the dispersal plots. Cover and count data, as well as SLA, LDMC, seed weight and height values were  $\ln(x+1)$ -transformed before applying the *functcomp* function. CWMs were dependent variables both in source plots and dispersal plots. In the source plots predictors were grazing (fenced/grazed; fixed factor), year (2014–2018; continuous predictor) and the interaction of grazing–year. GLMMs were fitted with beta distributions (CWMs of perenniality, rosette, anemochory and epizoochory ranking index) and Gaussian (CWMs of all other traits) distributions. In the dispersal plots predictors were grazing (zoochory on/off; fixed factor), year (2016–2018), distance from source plot (1–20 m) (continuous predictors), as well as the interaction of grazing–distance and grazing–year. We used GLMM with beta (CWMs of perenniality, persistence, rosette, anemochory and epizoochory ranking index) and Gaussian (CWM of the rest) distributions.

For all repeated-measures analyses we used site as random factor. Autocorrelation between the years (in case of source plots and dispersal plots), and spatial autocorrelation between adjacent sampling plots (in case of dispersal plots) is suspected. To control for such autocorrelations, we used autoregressive first-order covariance structures (AR1) in the models to accounting for the fact that consecutive years, or neighbouring distances, may show higher similarities than distant ones. We used the Akaike Information Criterion (AIC) for model selection (Akaike, 1998) to select the model which explains our data best. We compared the two models (controlling for autocorrelation and not controlling for autocorrelation); if the difference between the models was significant, we selected the model with the lower AIC value. When the difference between the models was not significant, we selected the simpler model (i.e. without control for autocorrelation). In the source plots, AIC is indicated to

**TABLE 1** Function, variable type, possible values and measurement unit of the plant traits used in the analyses. Values for start and end of flowering period represent the months (i.e. 2 = February; 5 = May)

Trait	Function	Type	Values	Measurement unit	Data source
Life span	Persistence	Nominal (binary)	s = short-lived; p = perennial	-	Király (2009)
SLA (specific leaf area)	Stress and disturbance resistance	Numeric (continuous)	4.75–37.09	mm <sup>2</sup> /mg	E-Vojtkó et al. (2020), Kattge et al. (2020), Appendix S3
LDMC (leaf dry matter content)	Stress and disturbance resistance	Numeric (continuous)	129.5–588.9	mg/g	E-Vojtkó et al., 2020, Kattge et al., 2020, Appendix S3
Seed weight	Dispersal ability; persistence	Numeric (continuous)	0.081–32.133	g	Török et al. (2013; 2016b)
Height	Stress and disturbance avoidance; dispersal ability	Numeric (continuous)	12.5–100.0	cm	Király (2009)
Clonal index	Persistence; dispersal ability;	Numeric (discrete)	0, 3, 4, 5	-	Klimešová et al. (2017)
Start of flowering period	Reproduction; stress and disturbance avoidance	Numeric (discrete)	2, 5, 6, 7, 8	Months	Király (2009)
End of flowering period	Reproduction; stress and disturbance avoidance	Numeric (discrete)	6, 7, 8, 9, 10, 11	Months	Király (2009)
Length of flowering period	Reproduction; stress and disturbance avoidance	Numeric (discrete)	2, 3, 4, 5, 6, 7	Months	Király (2009)
Seed bank persistence	Persistence; stress and disturbance tolerance	Nominal (binary)	0 = transient; 1 = short- or long-term persistence	-	Csontos (2001), Czarapata (2005), Tóth and Hüse (2014)
Rosette	Stress and disturbance avoidance	Nominal (binary)	0 = absence of semi-rosette or rosette; 1 = presence of semi-rosette or rosette	-	Klimešová et al. (2017)
Anemochory ranking index	Dispersal ability	Numeric (continuous)	0.02–0.85	-	Hintze et al. (2013)
Epizoochory ranking index	Dispersal ability	Numeric (continuous)	0.05–0.96	-	Hintze et al. (2013)

Abbreviations: LDMC, leaf dry matter content; SLA, specific leaf area.

control for autocorrelation in the models of cover, number of flowering shoots, CWMs of seed weight, height, length of flowering period and anemochory ranking index. In the dispersal plots, both temporal and spatial autocorrelation was used in all studied variables except CWM of persistence, where only spatial autocorrelation was included in the model. AIC model selection was also used to decide whether to use models with a beta-distribution or Gaussian distribution when the CWM values ranged between 0 and 1 (CWM perennality, persistence, rosette, anemochory and epizoochory ranking index). To model convergence in models for the CWM of the anemochory ranking index in source plots and the number of flowering shoots in dispersal plots, we needed to rescale the continuous year variable (we subtracted the mean and divided by standard deviation). Principal components analysis (PCA) was calculated with the `prcomp` function using the CWMs of the traits of source plots and dispersal plots using data from the last year of the study (2018).

### 3 | RESULTS

#### 3.1 | Effect of management and year on the source plots

We found several significant differences in the vegetation and trait composition of grazed and fenced source plots (Appendices S4 and S5). The cover of sown species and the number of flowering shoots were lower in the grazed source plots. The species richness and the number of flowering sown grassland species did not differ between the two settings. Year had a significant effect on the number of flowering species, while the grazing–year interaction significantly affected the number of flowering shoots (Appendix S4).

The CWMs of perennality, SLA and anemochory ranking index were higher and the CWMs of LDMC, height, start of flowering period and epizoochory ranking index were lower in the grazed source plots compared to the fenced ones. The CWMs of perennality, clonal index, length of flowering period, persistent seed bank and anemochory ranking index increased, while the CWMs of seed weight, start of flowering period, rosette and epizoochory ranking index decreased over time (Appendix S4). Between-year differences and interaction effects are presented in Appendices S6, S7, S8. The PCA analysis (Appendices S9 and S10) of the source plots highlighted a moderately strong correlation for most studied traits with the first PCA axis. In total, the first two PCA axes explained 65.6% of the total variation.

#### 3.2 | Establishment of grassland species around the source plots

Out of the 35 species sown, 30 were able to establish at a distance of at least 1 m from the source plots, as five sown species (*Allium scorodoprasum*, *Atriplex littoralis*, *Bunias orientalis*, *Rapistrum perenne*, *Salvia verticillata*) were not recorded in any of the dispersal plots.

The number of established sown species and the number of their individuals was higher, and the number of flowering shoots was lower when the source plots were grazed (“zoochory on”; Table 2, Figure 2). Year had a significant positive effect on the number of flowering species. The effect of distance was significantly negative for the number of sown species, number of their individuals, number of flowering species and number of flowering shoots (Table 2, Appendix S11). The negative effect of the grazing–distance interaction was significant in the case of number of established individuals and number of flowering shoots; the negative effect of distance was more pronounced when source plots were grazed (Table 2, Appendix S11). The effect of the grazing–year interaction was significant and positive on the number of individuals and flowering shoots; their number was higher in consecutive years in grazed source plots than in fenced ones (Table 2, Appendix S12).

Management type of the source plots had a significant effect on the trait distribution in the surroundings (Table 2, Figure 2). The CWMs of SLA, clonality and anemochory ranking index were higher in the dispersal plots when the source plots were grazed (“zoochory on”), while in the same setting the CWMs of LDMC, seed weight, height and start of flowering period were lower (Figure 2). Variables not affected by grazing of the source plot are shown in Appendix S13.

The CWMs of SLA, end, and length of flowering period and epizoochory ranking index increased over the years (Table 2, Appendices S14 and S15), while the CWMs of LDMC, seed weight and clonality decreased. CWMs of LDMC, height, start, end and length of flowering period, and epizoochory ranking index decreased with distance, while CWMs of perennality, SLA and seed weight increased (Table 2, Appendix S11). The interaction between grazing of source plots and distance had mostly positive effects on CWMs (LDMC, start, end and length of flowering period, epizoochory ranking index); it had a negative effect only on CWMs of SLA and clonality. The CWMs of LDMC, flowering traits and epizoochory ranking index declined with distance under the “zoochory off” scenario. When the source plots were grazed the CWMs of these traits increased with distance, while those of SLA and clonality decreased.

The first two PCA axes (Figure 3) explained 67.3% of the total variation. A medium, positive correlation (Appendix S16) was found between the first PCA axis and the CWMs of length of flowering period and persistent seed bank, while a medium negative correlation was present in case of CWMs of seed weight and height.

### 4 | DISCUSSION

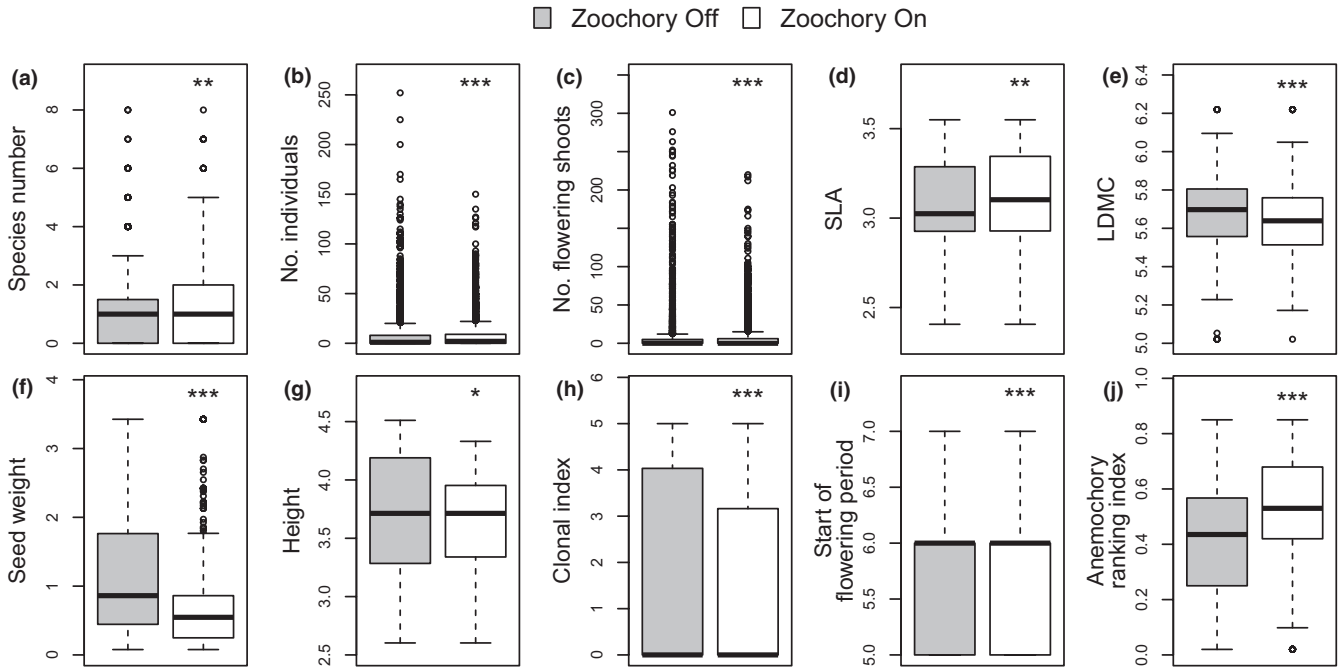
#### 4.1 | Development of grazed and fenced source plots

The sown grassland species could successfully establish in the source plots under both management types, and there was no difference in the number of established sown species between the developed grazed and fenced source plots. The similar species number of sown species in the two types of source plots indicates that neither grazing, nor its

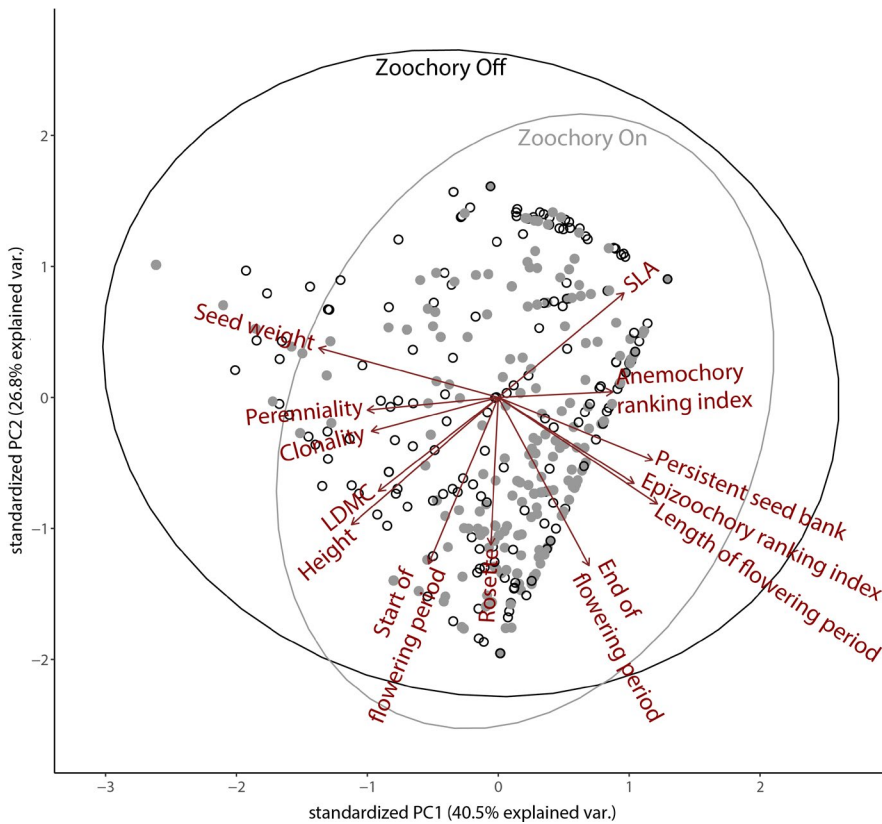
**TABLE 2** Effect of year (2016–2018), management of the source plot (grazed = “zoochory on”, fenced = “zoochory off”), distance from source plot (1–20 m), and interactions grazing–distance and grazing–year on the establishment of the sown species in the dispersal plots. Significant effects are marked in bold

	Intercept		Year		Grazing		Distance		Grazing–distance		Grazing–year	
	z	p	z	p	z	p	z	p	z	p	z	p
Species number	-1.202	0.229	1.208	0.227	3.216	<b>0.001</b>	-5.870	< <b>0.001</b>	-1.556	0.120	-	-
Number of individuals	0.869	0.385	-0.859	0.391	4.470	< <b>0.001</b>	-2.296	<b>0.022</b>	-16.323	< <b>0.001</b>	4.482	< <b>0.001</b>
Number of flowering species	-2.083	<b>0.037</b>	2.086	<b>0.037</b>	1.583	0.113	-5.858	< <b>0.001</b>	-0.568	0.570	-	-
Number of flowering shoots	5.044	< <b>0.001</b>	0.535	0.593	-3.513	< <b>0.001</b>	-2.796	<b>0.005</b>	-5.262	< <b>0.001</b>	25.709	< <b>0.001</b>
Perenniality	0.515	0.607	-0.513	0.608	1.957	0.050	3.853	< <b>0.001</b>	-1.874	0.061	-	-
SLA (specific leaf area)	-2.084	<b>0.037</b>	2.166	<b>0.030</b>	2.624	<b>0.009</b>	3.600	< <b>0.001</b>	-2.128	<b>0.033</b>	-	-
LDMC (leaf dry matter content)	2.728	<b>0.006</b>	-2.406	<b>0.016</b>	-5.575	< <b>0.001</b>	-3.098	<b>0.002</b>	5.030	< <b>0.001</b>	-	-
Seed weight	4.157	< <b>0.001</b>	-4.151	< <b>0.001</b>	-3.987	< <b>0.001</b>	3.474	< <b>0.001</b>	-0.512	0.608	-	-
Height	0.018	0.985	0.017	0.986	-2.424	<b>0.015</b>	-4.227	< <b>0.001</b>	1.825	0.068	-	-
Clonal index	2.302	<b>0.021</b>	-2.292	<b>0.022</b>	3.664	< <b>0.001</b>	0.542	0.588	-4.484	< <b>0.001</b>	-	-
Start of flowering period	1.781	0.075	-1.695	0.090	-3.352	< <b>0.001</b>	-6.279	< <b>0.001</b>	3.196	<b>0.001</b>	-	-
End of flowering period	-2.565	<b>0.010</b>	2.658	<b>0.008</b>	-0.759	0.448	-6.642	< <b>0.001</b>	3.947	< <b>0.001</b>	-	-
Length of flowering period	-5.018	< <b>0.001</b>	5.078	< <b>0.001</b>	0.960	0.337	-5.015	< <b>0.001</b>	3.153	<b>0.002</b>	-	-
Persistent seed bank	0.333	0.739	-0.295	0.768	0.176	0.860	-0.877	0.381	0.330	0.742	-	-
Rosette	1.411	0.158	-1.405	0.160	0.586	0.558	0.738	0.460	0.518	0.605	-	-
Anemochory ranking index	-1.365	0.172	1.363	0.173	5.132	< <b>0.001</b>	-0.862	0.389	-1.411	0.158	-	-
Epizoochory ranking index	-3.712	< <b>0.001</b>	3.719	< <b>0.001</b>	0.642	0.251	-3.510	< <b>0.001</b>	2.244	<b>0.025</b>	-	-

Abbreviations: LDMC, leaf dry-matter content; SLA, specific leaf area.



**FIGURE 2** Effect of grazing (“zoochory on/off”) on the establishment success of the sown species in the dispersal plots (panels a–c) and on the community-weighted means (CWMs) of the studied traits (panels d–j). Significant effects of the management type of the source plots are marked with asterisks (Tukey test: \*\*\*,  $p \leq 0.001$ ; \*\*,  $p \leq 0.01$ ; \*,  $p \leq 0.05$ ). Data originating from all plots in the surroundings were pooled by the type of source plot



**FIGURE 3** Principal components analysis (PCA) biplot of dispersal plots surrounding the grazed and fenced source plots, and the community-weighted means (CWMs) of the studied traits in the last year of study (2018). Observations from the four transects and six sites were summed within distance categories, represented here by circles. Grey circles = “Zoochory on”, white circles = “Zoochory off”. Ellipses represent 95% confidence intervals

absence hinder the establishment success of target grassland species in the short run. However, in the long run cessation of grazing can result in biomass accumulation, reduced light availability and decreased nutrient

content of the soil, which may lead to species loss and the dominance of few, highly competitive species in fenced source plots (Belsky, 1992; Rosenthal et al., 2012; Kelemen et al., 2013). Although the species





richness of sown grassland species did not differ between the two settings, we found that in the absence of grazing, the cover and flowering success of the sown species were higher than under grazed conditions over the study period.

We also found that plant trait composition was different in the grazed and fenced source plots, which is consistent with former studies. Increasing CWM of SLA and decreasing CWMs of LDMC and height indicate that fast-growing, shorter species are supported in grazed source plots (Stammel et al., 2003; Díaz et al., 2007; Jaurena et al., 2012; Niu et al., 2016). An earlier start of flowering may be a compensating response to grazing; early flowering ensures successful reproduction by grazing avoidance in time (de Bello et al., 2005; Peco et al., 2005).

Similarly to Peco et al. (2005), we observed an increasing CWM of perennality in grazed source plots. In both studies, one (in Peco et al., 2005) or two particular species (in this study) are responsible for the change. This implies that in such cases the observed differences of CWMs of traits may be due to differences in species composition of the plots for which they are calculated, not to the particular traits of the occurring species (Peres-Neto et al., 2017; Zelený, 2018). In our study, the two most abundant species were *Achillea collina* and *Centaurea solstitialis*, a perennial and a short-lived species, respectively. *Centaurea solstitialis* is a fast-growing biennial with a good defence mechanism. However, the young individuals are easily consumed by grazers (Wallace et al., 2008), so fenced source plots can provide more optimal habitats for them. In contrast, *Achillea collina* is favoured by grazing; it can develop better under open habitat conditions and it can successfully compensate defoliation by grazers by clonal growth.

#### 4.2 | Effect of “Zoochory On” and “Zoochory Off” on the colonization of sown species

We found that zoochory plays an important role in the dispersal and establishment of sown species, as they occurred in higher number outside the source plots under the “zoochory on” scenario despite their lower abundance and reproductive success in the grazed source plots. Grassland species in general have low dispersal abilities (Ozinga et al., 2005; Novák & Konvička, 2006), dispersal kernels peak near the mother plants (Wilson, 1993; Nathan et al., 2008). Grazing livestock tend to optimize the quantity and quality of the consumed forage (Couvreur et al., 2005; Soder et al., 2007) and hence in the studied homogeneous grassland they probably visit the source plots with high biomass and species richness. The high probability of livestock passing by the grazed source plots increases the chance of zoochorous dispersal of the sown species. In our study, colonization success of the sown species was largely determined by the presence of grazers. The trait composition of the vegetation was similar in the grazed source plots and in their surroundings, which highlights that in the studied system, the most successful species are those favoured by grazing.

The CWM of clonality tended to be higher in the dispersal plots next to the grazed source plots. Clonal integrity, i.e. the connection

of the ramets by stolons, rhizomes and roots of clonal plants, plays a major role in overcoming grazing pressure; intact ramets share resources with injured individuals and hence they can compensate for defoliation (Liu et al., 2007; Wang et al., 2017). Ability for clonal reproduction compensates for generative reproduction failure by allocating in vegetative dispersal (Vallejo-Marín et al., 2010). Besides, plants with clonal spreading ability can easily occupy free gaps created by grazers by effective lateral spread (Fahrig et al., 1994; Herben et al., 2018).

Many propagules have developed morphological adaptations to attach to grazers' fur (Couvreur et al., 2005; Albert et al., 2015), such as elongated seeds or seeds with appendages. In our study, we did not observe that species with such morphological adaptations would have performed better under grazed conditions than species without adaptations to epizoochory. On the contrary, our result supports the finding of Albert et al. (2015) and Horáčková et al. (2016), that species with simple seed morphology can also be dispersed by grazers, for example when mud functions as an adhesive for small seeds to attach to animals' fur and hoof. Purschke et al. (2012) also reported that species of open habitats with long grazing history are strongly and positively correlated with long-distance dispersal potential both by animals and wind. In our study, we also observed that small-seeded species were favoured by the “zoochory on” scenario. This suggests that small-seeded species benefit from multiple dispersal strategies; beside epizoochory they may also have higher chances to disperse by wind under grazed conditions. Grazing animals, besides being dispersal vectors, also open the vegetation and thus increase the chance for wind dispersal and also for the establishment of wind-dispersed species (Ozinga et al., 2005). The high CWM of the anemochory ranking index also supports this finding, as small seeds in general have low terminal velocity and good wind dispersal ability (Greene & Johnson, 1993).

The above-mentioned fact that seed dispersal usually peaks close to the mother plants, especially in the absence of dispersal vectors (Wilson, 1993; Nathan et al., 2008) explains our observation that most of the sown species and individuals were observed close to the source plots. The dispersal distance by epizoochory ranges from a few metres to several hundred kilometres (Mouissie et al., 2005; Manzano & Malo, 2006), dependent on the type of grazers, as seeds adhere to sheep's fur better and in higher numbers than to cattle, horses or donkeys (Mouissie et al., 2005; Couvreur et al., 2008; Kaligarič et al., 2016). Since our study sites were grazed by cattle, which have short and straight hair, the seed retention rates were most probably rather short (Couvreur et al., 2008).

Significant interactions between the effects of grazing and distance highlight the fact that the general effect of grazing was more pronounced close to the source plots and diminishes with increasing distance. Fast-growing species with high SLA and low LDMC characterized the close proximity of grazed source plots, but with increasing distance from grazed propagule sources their abundance decreased. The smaller SLA and larger LDMC suggest that slower-growing species with defence mechanisms and tough leaves that are not favoured by grazers, perform better (Wright & Westoby, 2000; Jaurena et al., 2012). Besides, these results also highlight that the effect of the

management type is the strongest close to the source plots that are often visited by grazers due to their richness in forb species.

The differences in trait composition of the vegetation under the “zoochory on” and “zoochory off” settings highlight the importance of grazing in the study system. By overcoming dispersal limitations and increasing connectivity between favourable habitats, the efforts needed for successful grassland restoration of extensively grazed sites can be considerably reduced. We showed that depending on the presence or absence of zoochory plant species with contrasting traits can colonize the surrounding homogeneous matrix. Communities that developed under zoochory were characterized by traits that are adaptive under grazed conditions, while communities that could not communicate with the source plots via zoochory were functionally different. This suggests a strong link of traits favouring zoochory and those supporting the survival of plants under grazing conditions.

In grazing-adapted ecosystems, fencing source populations of target species does not always seem to be a good option. We found that fencing increased the cover and flowering success of the sown species in the short run, but it significantly decreased their chance to colonize the surrounding area. Another negative effect of fencing in the long run is the accumulation of litter and related decrease in species richness. These problems might be overcome by targeted management of the fenced patches by mowing or by using mobile fences that can be temporarily removed; however, these practices should be tested in future studies. We suggest that in conservation and restoration projects fencing should be applied when the priority is the protection of a source population; however, when the goal is to facilitate the spread of target species, fencing is probably not a favourable option.

#### AUTHOR CONTRIBUTIONS

OV, BD, RK, BT, PT, AKi and ST conceived and designed the experiment; RK, OV, BD, KL, TM, KT, RS, GL, AKe, ZK, SB and SJ collected the data; RK analyzed the data; RK and OV wrote the manuscript; RK and OV revised the manuscript, all authors checked and approved the paper.

#### DATA AVAILABILITY STATEMENT

The data that support the findings of this study are given in Appendix S1.

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- Appendix S1.** Raw data of the study.
- Appendix S2.** List of the 35 grassland species sown and their trait values used in the analyses.
- Appendix S3.** Data sets and reference list used from the TRY database.
- Appendix S4.** Effect of years, grazing and grazing-year interaction on the studied variables within the source plots.
- Appendix S5.** Changes of the studied variables in the fenced and grazed source plots.
- Appendix S6.** Results of the pairwise comparison of the effect of years on the studied variables within the source plots.
- Appendix S7.** Changes of the studied variables in the source plots over the study years.
- Appendix S8.** Number of flowering species and number of flowering shoots in the differently managed source plots over the study years 2016–2018.
- Appendix S9.** Principal components analysis (PCA) biplot of source plots and the community-weighted means (CWMs) of the studied traits in the last year of study (2018).
- Appendix S10.** Correlation table of the community-weighted mean (CWM) of studied traits and the first two principal components analysis (PCA) axes in the last year of study (2018) in the source plots.
- Appendix S11.** Effect of distance and grazing:distance interaction on studied variables in the dispersal plots.
- Appendix S12.** Number of individuals and flowering shoots in the dispersal plots under the Zoochory On and Zoochory Off settings over the years.
- Appendix S13.** Variables not affected by the Zoochory On and Zoochory Off settings.
- Appendix S14.** Results of the pairwise comparison of the effect of years on studied variables in the dispersal plots.
- Appendix S15.** Changes of the studied variables in the dispersal plots surrounding the source plots over the years.
- Appendix S16.** Correlation table of the community-weighted means (CWMs) of studied traits and the first two principal components analysis (PCA) axes in the last year of study (2018) in the dispersal plots.

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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