

Mowing machinery and migratory sheep herds are complementary dispersal vectors for grassland species

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Abstract

Aim: We assessed the role of mowing machinery and endozoochory by migratory sheep as dispersal vectors in semi-natural grasslands by comparing the species compositions and traits of species found in the vectors to the regional above-ground vegetation and soil seed bank. Furthermore, we discuss how their interplay may affect the conservation of semi-natural grasslands.

Location: Rhön Mountains, central Europe.

Methods: Plant material from mowers ($n = 12$ from one date) and dung samples from migratory sheep ($n = 39$ from 13 dates) were collected and the dispersed plant species were determined using the emergence method. We compared the species compositions to the regional above-ground vegetation and seed bank using non-metric multidimensional scaling (NMDS) and indicator species analysis. Furthermore, we compared functional traits of the dispersed species to traits of non-dispersed species of the regional species pools by calculating log-response ratios and performing metaregressions.

Results: While 43 species were shared between the vectors, the vegetation compositions differed from each other. Mower samples were more similar to the above-ground vegetation whereas dung samples were more similar to the seed bank. Mowers and sheep endozoochory favoured the dispersal of species with different traits and phenologies. Species with small seed sizes were prevalent in both vectors. Mowers were less selective concerning most traits, but favoured high-growing grasses such as *Alopecurus pratensis* and *Trisetum flavescens*. Sheep dung samples contained less grasses and more palatable species, such as *Urtica dioica*. Mowers were most selective concerning phenology, whereas endozoochory by migratory sheep also included late-flowering species.

Conclusion: Sheep endozoochory and mowing machinery are complementary dispersal vectors favouring species with differing functional traits. Sheep endozoochory enables dispersal of species that have unfavourable traits (e.g. low releasing heights) or phenologies for dispersal by mowing machinery. To ensure the dispersal of a high

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number of plant species in semi-natural grasslands, the interplay of different vectors should be considered.

KEYWORDS

dispersal vector, endozoochory, grassland conservation, mowing machinery, plant traits, seed bank, seed dispersal, semi-natural grasslands

1 | INTRODUCTION

Semi-natural grasslands are among the most species-rich ecosystems in the world at small spatial scales (Wilson et al., 2012). They are severely threatened by both land abandonment and intensification (Bakker & Berendse, 1999) and the current distribution of high-nature-value grasslands in Europe is mostly restricted to remote landscapes or protected areas. Often, some remnants of species-rich grasslands occur within intensively used landscapes and are thus prone to the negative effects of isolation. This is why, despite considerable efforts, both the amount of well-preserved grasslands and the number of species associated with these habitats are continuously decreasing in many places (Dahlström et al., 2008).

The conservation of semi-natural grasslands strongly relies on the continuation of traditional low-intensity land use practices that originally led to the formation of these ecosystems over centuries (Pärtel et al., 2005), such as mowing and grazing. While site conditions and disturbance regimes induced by these practices are typically influenced by their timing and intensity (Vogt et al., 2019), the long-term conservation depends on additional factors that cannot be influenced at the local scale. These include for example airborne nitrogen deposition or the supply with seeds of characteristic grassland species from other sites (Bakker & Berendse, 1999). In particular, seed dispersal was strongly facilitated by traditional land use, e.g. by migratory sheep herding or application of hayseed (Babai, 2014), and is nowadays strongly restricted in many modern landscapes (e.g. Poschlod et al., 2005). Both the lower number and quality of seed sources and the discontinuation of dispersal vectors have led to seed dispersal limitation, which severely jeopardizes the success of conservation efforts (Eriksson, 2000).

Late mowing (typically after July 1) and low-intensity grazing are two of the most widely applied traditional land use practices in semi-natural grasslands (Kapfer, 2010). Both mowing machinery and grazing animals act as dispersal vectors that transport species within and between grasslands, although species with different traits are expected to benefit from each vector. Mowing machinery, i.e. a mowing unit mounted on the rear of a tractor, can carry plant material that remains attached after mowing between grassland patches managed by the same farmer. Mowing machinery favours the dispersal of plants that grow high, carry viable seeds at the time of mowing, and are abundant at the mown sites (Strykstra et al., 1997). Grazing leads to the dispersal of seeds by either epizoochory or endozoochory and can favour different species depending on grazing

preferences and size of the respective animal. Especially endozoochory is a rather selective mechanism favouring highly palatable species that carry high numbers of small seeds that resist decomposition in the gut (Janzen, 1984; Hattermann et al., 2019). This has led to the assumption that similar plant traits favour endozoochoric dispersal and allow the survival of seeds in the soil seed bank (Janzen, 1984; Kuiters & Huiskes, 2010), although it is unclear to what degree these species pools overlap in grasslands. For the planning of successful conservation management schemes in semi-natural grasslands, an improved understanding of the role of different dispersal vectors compared to the above-ground vegetation and the soil seed bank is needed (Török et al., 2018). However, comparative assessments of different dispersal vectors that include the regional soil seed bank are rare.

In our study, we assessed the role of two crucial dispersal vectors by comparing them to the local grassland species pool in the above-ground and seed bank vegetation of semi-natural grasslands in the nature reserve 'Lange Rhön', a protected central-European landscape. To this end, we analyzed the species composition of seeds attached to mowers and in dung of migratory sheep. We performed a combination of a compositional and a trait-based analysis to assess which species of the local grassland species pool (hereafter referred to 'above-ground vegetation') and the local grassland seed bank species pool (hereafter referred to 'seed bank vegetation') are dispersed and discuss how the interplay of both vectors affects the conservation of grasslands. Overall, our study aims at investigating the compositional and functional differences between the four investigated groups.

Additionally, we tested the following hypotheses:

1. Plants dispersed through endozoochory by migratory sheep are functionally more similar with plants prevalent in the local seed bank than with plants in the above-ground vegetation. Namely, plants with a high number of small seeds, a longer flowering duration, a high seed bank longevity and plants that are easily palatable (herbs with low leaf dry matter content [LDMC] and high Ellenberg indicator value for nutrients) have an increased probability to be dispersed by sheep.
2. Plants dispersed by mowing machinery are less constrained by their seed or dispersability traits compared to species dispersed by sheep endozoochory. However, species that have a higher abundance in the above-ground species pool and/or grow higher are more prone to be dispersed by mowing machinery.

2 | METHODS

2.1 | Study area

The study was conducted in the nature reserve "Lange Rhön" (50°26'–50°32' N, 09°54'–10°05' E) in central Germany. The nature reserve comprises an area of 32 km² and is situated between 600 m and 950 m a.s.l. The climate of the study area is characterized by a short growing season, with a mean annual temperature of 5.4°C and an annual precipitation of approx. 1,176 mm (means of 1980–2010 of Mt Wasserkuppe, 950 m a.s.l.; DWD, 2016). Basalt rocks form the bedrock in the study area. Although soils that develop on basaltic bedrocks are well supplied with base cations, high precipitation as well as land-use-induced nutrient removal have led to low nutrient availability and very low soil pH values in most of the area (Puffe & Zerr, 1988). Furthermore, calcareous soils can be found in small parts of the study area. Two thirds of the nature reserve (ca. 21 km²) is covered by species-rich semi-natural grasslands (e.g. Habitats Directive 92/43/EEC, habitat types 6520: mountain hay meadows, and 6230: species-rich *Nardus* grasslands) that are non-intensively used as meadows and pastures. These grasslands have a centuries-long land use history of mowing and pasturing with low nutrient inputs. Therefore, the nature reserve is of supraregional importance for the conservation of these habitat types in central Europe (Grebe, 1995).

In the study area, migratory sheep herding is carried out between April and October. Mostly Rhön sheep and Merino sheep are used in the area. Grazing may be carried out longer or shorter, depending on the weather conditions. Until August 15, sheep graze mainly on pastures that are not mown by machinery due to steep terrain or stoniness of the surface (although sheep herds move between different pastures, thus some grazing on other areas/roadsides may happen). After August 15, all of the study area may be used for pasturing, and aftermath grazing is carried out in mown areas. Different shepherds focus on different parts of the study area, but some overlap in grazed areas cannot be ruled out. Overall, which areas are grazed exactly depends on the decisions of the shepherds and local management may thus differ between years.

The mowing regime in the study area is based on contractual nature conservation, meaning farmers are subsidized to manage meadows in the study area. For the protection of ground-nesting birds, mowing is staggered based on different mowing dates between June 15 and August 1 and is not carried out on the respective areas before these dates. Apart from the mowing units, other haymaking machinery is employed in the area, such as tractor-mounted rakes (e.g. rotary rakes and wheel rakes) and a mobile baling press.

2.2 | Sampling

To analyze the endozoochoric dispersal, we took dung samples from three flocks of sheep (*Ovis aries*) weekly from July 4 to September 30, 2017. This resulted in 39 samples (three samples per week over

the course of 13 weeks). For each sample, 500 ml of several fresh droppings were randomly collected. Sheep of all sampled flocks are herded in the study area throughout the summer. While the shepherds of three flocks of sheep focus on managing different parts of the study area (Flock 1, consisting of 800 Merino sheep, in the north, Flock 2, consisting of 350 Merino sheep, in the centre, and Flock 3, 800 Rhön sheep, in the south), the flocks often move several kilometres per day and both pastured areas and pens are frequently relocated. Due to this and as the retention times in the sheep gut can vary depending on the digested biomass and seed traits (Cosyns et al., 2005b), the collected dung samples could not be linked directly to grazing sites.

On July 4, 2017, under dry weather conditions, 12 samples of mowing machinery were taken. The chosen mowing date represented the most common mowing date in the study area, with ~60% of the area being mown after this date. The sampling was performed in the central part of the study area, and samples were taken from nine disc mowers and from three sickle bar mowers. Before the first sampling, we cleaned the mowers from adherent plant material. Afterwards, the farmers mowed the corresponding meadows as they would normally do. After mowing, when leaving the meadow, they usually elevate the mowing unit on-site ('transport mode') and move to the next meadow. To not overestimate the plant material that could potentially be transported, sampling was carried out after the mower was put into transport mode once and lowered again. For each of the 12 meadows, we then collected all plant material from all parts of the mowers. The amount of sampled plant material varied between meadows and ranged from 1 to 5 L per sample. Seeds were extracted from excess plant material by threshing before further handling.

All samples were stored in a refrigerator at 4°C until germination in the greenhouse from the end of September 2017. The amount of germinable seeds was determined using the emergence method (Roberts, 1981). To this end, samples were spread in a layer of 1–2 mm on a 3–4 cm layer of a 2:1 sterile garden soil (Fruhstorfer Erde LD80 Archut[®])–sand mixture in styrofoam trays of 18 cm × 28 cm size. In the greenhouse, the trays were exposed to controlled diurnally alternating temperatures (day: 18–24°C, night: 12–18°C), light (>10,000 lx from 6:00 a.m. to 10:00 p.m.), and humidity (<70%) conditions and were watered every three days. From December 2017 to March 2018, the samples were cold-wet-stratified under outdoor conditions. After stratification, the trays were moved to the greenhouse, where germination was observed until August 2018. We added ten control trays containing sterile garden soil only to account for wind-borne seeds. Species germinating from these trays were excluded from both groups (mowers and sheep dung).

To represent the local grassland species pool, we carried out vegetation surveys on 72 study plots (size: 5 m × 5 m) from the three most abundant grassland types (mesic and wet mountain hay meadows as well as species-rich *Nardus* grasslands) in 2016. We estimated plant species abundance following the approach of Braun-Blanquet (1964) and transferred the classes to percentage values ($r = 1\%$, $+ = 2\%$, $1 = 3\%$, $2 = 13\%$, $3 = 38\%$, $4 = 68\%$, $5 = 88\%$). The invasive

legume *Lupinus polyphyllus* can be found frequently in the above-ground vegetation of the study area and was present in most of the plots (Otte & Maul, 2005; Klinger et al., 2019).

For the local grassland seed bank species pool, soil samples were taken from the same plots used for the vegetation surveys in September 2015. For each plot, we pooled nine soil cores (0–10 cm depth, 2.8 cm diameter) resulting in 0.554 L of soil volume for each of the 72 plots. We removed plant remains, litter and roots immediately after sampling. Seed bank samples were kept in the refrigerator under similar conditions as the dung and mower samples. In the greenhouse, samples were spread on the same styrofoam trays and were kept under the same controlled conditions as the dung and mower samples. We identified all emerging seedlings from October to December 2015. From December 2015 to March 2016, the samples were cold-wet-stratified under outdoor conditions. After stratification, samples were transferred to the greenhouse again and germination was observed until July 2016, when no more seeds germinated. More information on the vegetation and seed bank sampling can be found in Ludewig et al. (2021). Plant nomenclature follows Jäger (2017). A full list of all species found in the four groups and their abundances can be found in Appendix S1.

We focused on seed and plant traits that have been identified as relevant for the dispersal through the two vectors by other studies (e.g. Strykstra et al., 1997 for mowers; Albert et al., 2015a for sheep endozoochory). Explicitly, we looked at the traits LDMC as indicator for palatability and plant resource use, maximum releasing height (RH_{max}) as trait relevant for the seed uptake both by animals and mowers, and seed longevity as indicator for how long a seed can survive in the soil seed bank or in the animal gut (as taken from the LEDA Database; Kleyer et al., 2008). Furthermore, we included seed volume (seed length * width * height) as proxy for seed size, as smaller seed sizes are associated with high seed production and high seed dispersability, and flowering duration as phenological parameter (from the Bioflor Database; Kühn et al., 2004). For missing trait values, we calculated the mean trait value of the genus. For 5.7% of trait values, there were no data available, mainly concerning seed longevity. Furthermore, as the most prevalent functional groups, we included the proportion of herbs and grasses (including grasses, sedges, and rushes) of each sample. Additionally, we included the Ellenberg indicator value for nutrients (EIV-N; Ellenberg, 1991) as indicator for palatability as well as plant resource accumulation capability. The effective number of species, calculated as the exponent of the Shannon entropy (Jost, 2006), was included as diversity index in the analysis. Additionally, we considered sampling week as explanatory variable in the analysis of the sheep samples.

2.3 | Data analysis

For the statistical analyses, we calculated relative species abundances. To this end, we set the sum of all species abundances/seedling numbers for each sample to 100% and calculated the relative abundance of each species in each sample. We examined

species-sampling relationships for the four groups separately using species accumulation curves (see Appendix S2). All data analyses were carried out using R 3.6.1 (R Core Team, 2019).

To identify species indicative for each of the four groups (above-ground, seed bank, sheep, and mowers), we performed an indicator species analysis (ISA) for the single groups and all possible two-way and three-way group combinations using the package *indicspecies* (Cáceres et al., 2010; Dufrene & Legendre, 1997). The ISA combines both abundance and frequency of tested species independently for each species in the assemblage and creates an indicator value (IV) ranging from 0 to 100.

To compare the species compositions of dung and mower samples to the local above- and below-ground grassland species pools, we performed a NMDS ordination using the *vegan* package (Oksanen et al., 2019). We applied Bray–Curtis distances to create a dissimilarity matrix and calculated the NMDS based on 20 random starts and three dimensions (determined by a stress plot). We grouped the sample points according to the four groups: sheep, mowers, above-ground vegetation, seed bank vegetation. The same ordination method was applied to assess compositional differences between sheep samples; in this case the samples were grouped by sheep flock. We fitted the average, abundance-weighted trait values to the ordination plot using the *envfit* function. Differences in the vegetation composition of the different groups were tested using a PerMANOVA with 999 permutations (*adonis* function) followed by pairwise group comparisons (results see Appendix S3).

We compared the dispersed species' traits to the traits of the above- and below-ground species pools. We focused on the relative trait differences between the groups by calculating the log ratios (according to Hedges et al., 1999) of the unweighted mean trait values or the proportions of herbs and grasses. For the species' traits, we compared the mean trait values of each dung and mower sample (dispersed species) to the mean trait values of the species that were present in the respective species pool, but not in the dispersal vector (non-dispersed species). Log-response ratios greater than zero indicate higher trait values or higher percentages of herbs and grasses in the two vectors (sheep, mower) compared to the respective species pool, while values below zero indicate lower trait values or lower percentages of herbs and grasses. We used fixed-effects metaregressions (Viechtbauer, 2010) to test for significant differences in trait values between dispersed and non-dispersed species. In the metaregression, we treated the three sheep flocks as single studies while the mower samples were treated as one study. The metaregressions were performed using the *metafor* package (Viechtbauer, 2010).

3 | RESULTS

3.1 | Species composition

We found a total of 3,041 seedlings of 52 species in the sheep dung. The number of species per sample ranged between 2 and 11 species and mean effective species richness per litre dung was six.

The species with the highest seedling numbers in the dung samples was *Urtica dioica*, which made up 56% of the total number of seedlings and was present in 28 of 39 samples, followed by *Juncus effusus* (13% of seedlings) and *Poa trivialis* (13% of seedlings). Furthermore, *Stellaria media* and *Scirpus sylvaticus* were strongly associated with sheep dung samples according to the ISA (Table 1). The sheep samples shared 34 species (66%) with the above-ground vegetation while 37 species (71%) found in the sheep dung were also present in the seed bank.

In the mower samples, we found 19,175 seedlings of 102 species, ranging between 35 and 61 species and averaging 15 effective species per sample. *Cerastium holosteoides* (16.8% of seedlings), *Holcus lanatus* (8%) and *Poa trivialis* (6.4%) had the highest number of seedlings in the mower samples. Furthermore, there were several indicator species for mowers, e.g. a number of grasses such as *Alopecurus pratensis*, *Trisetum flavescens* or *Festuca pratensis*, or herbs like *Veronica arvensis*, *Silene flos-cuculi*, and *Taraxacum* spp. (Table 1). The mower samples shared 72 species (71%) with the above-ground vegetation and 63 species (62%) with the seed bank vegetation. Two species were strongly associated with both dispersal vectors: *Juncus effusus* and *Plantago media* (Table 1).

The above-ground vegetation consisted of 146 species. Species associated with the above-ground vegetation, but not with the dispersal vectors, were for example *Bistorta officinalis*, *Sanguisorba officinalis* or *Rhinanthus minor*, but also the non-native *Lupinus polyphyllus* (Table 1). The seed bank consisted of 106 species, and typical

species associated with the seed bank were e.g. *Luzula luzuloides*, *Carex pilulifera*, and *Stellaria alsine*.

The NMDS of the dung samples revealed no major differences between the three flocks (Figure 1). The first dimension mainly showed differences associated with sampling week, LDMC, and flowering duration, while the second dimension was mainly associated with differences in the effective number of species and EIV-N. This indicates a phenological shift in species composition during the sampling period. Samples collected later during the vegetation period contained species with lower LDMC (Figure 1). Compared to the other groups, sheep dung samples had higher community weighted EIV-N, higher longevity and longer flowering durations. Furthermore, species compositions of seed bank samples and dung samples were more similar than those of above-ground vegetation and sheep dung (Figure 2).

While sheep dung and mowers shared a high number of species (43), the vegetation composition of samples of both vectors differed strongly from each other (as indicated by a mean Bray-Curtis dissimilarity of 0.821, Figure 2). Along the first dimension, the NMDS clearly differentiated the samples according to the four groups (Figure 2). The above-ground vegetation, seed bank, and mower samples were located relatively close to each other. In the above-ground vegetation, effective species numbers were highest of all samples and species with larger seed volumes were more prevalent. The soil seed bank consisted of species with smaller seeds and higher longevity compared to the above-ground vegetation. While

TABLE 1 Indicator species for the groups above-ground, seed bank, sheep dung, and mower as well as for group combinations 'sheep dung + mower' and 'sheep dung + mower + seed bank' with indicator value (IV), frequency, and *p*-value

Above-ground				Seed bank			
Indicator species	IV	Freq.	<i>p</i> -value	Indicator species	IV	Freq.	<i>p</i> -value
<i>Bistorta officinalis</i>	89.5	90.2	0.001	<i>Luzula luzuloides</i>	73.3	75.8	0.001
<i>Lupinus polyphyllus</i>	88.9	96.4	0.001	<i>Carex pilulifera</i>	64.9	97.7	0.001
<i>Sanguisorba officinalis</i>	86.4	84	0.001	<i>Stellaria alsine</i>	52.5	99.4	0.002
<i>Rhinanthus minor</i>	85.8	100	0.001	<i>Calluna vulgaris</i>	45.8	94.5	0.014
<i>Festuca ovina</i>	66.7	100	0.001	<i>Rumex acetosella</i>	45.5	99.4	0.004
Sheep				Mower			
Indicator species	IV	Freq.	<i>p</i> -value	Indicator species	IV	Freq.	<i>p</i> -value
<i>Urtica dioica</i>	83.1	96.2	0.001	<i>Alopecurus pratensis</i>	97.1	94.3	0.001
<i>Stellaria media</i>	39.1	99.6	0.001	<i>Trisetum flavescens</i>	95.6	91.3	0.001
<i>Scirpus sylvaticus</i>	32	100	0.021	<i>Cerastium holosteoides</i>	91.9	84.5	0.001
				<i>Festuca pratensis</i>	76.7	70.6	0.001
				<i>Silene flos-cuculi</i>	72.1	56.7	0.001
Sheep dung + mower				Sheep dung + mower + seed bank			
Indicator species	IV	Freq.	<i>p</i> -value	Indicator species	IV	Freq.	<i>p</i> -value
<i>Poa trivialis</i>	77.3	95.3	0.001	<i>Agrostis capillaris</i>	80.3	96.7	0.001
<i>Plantago media</i>	37.0	100	0.001	<i>Juncus effusus</i>	77.3	94.3	0.001

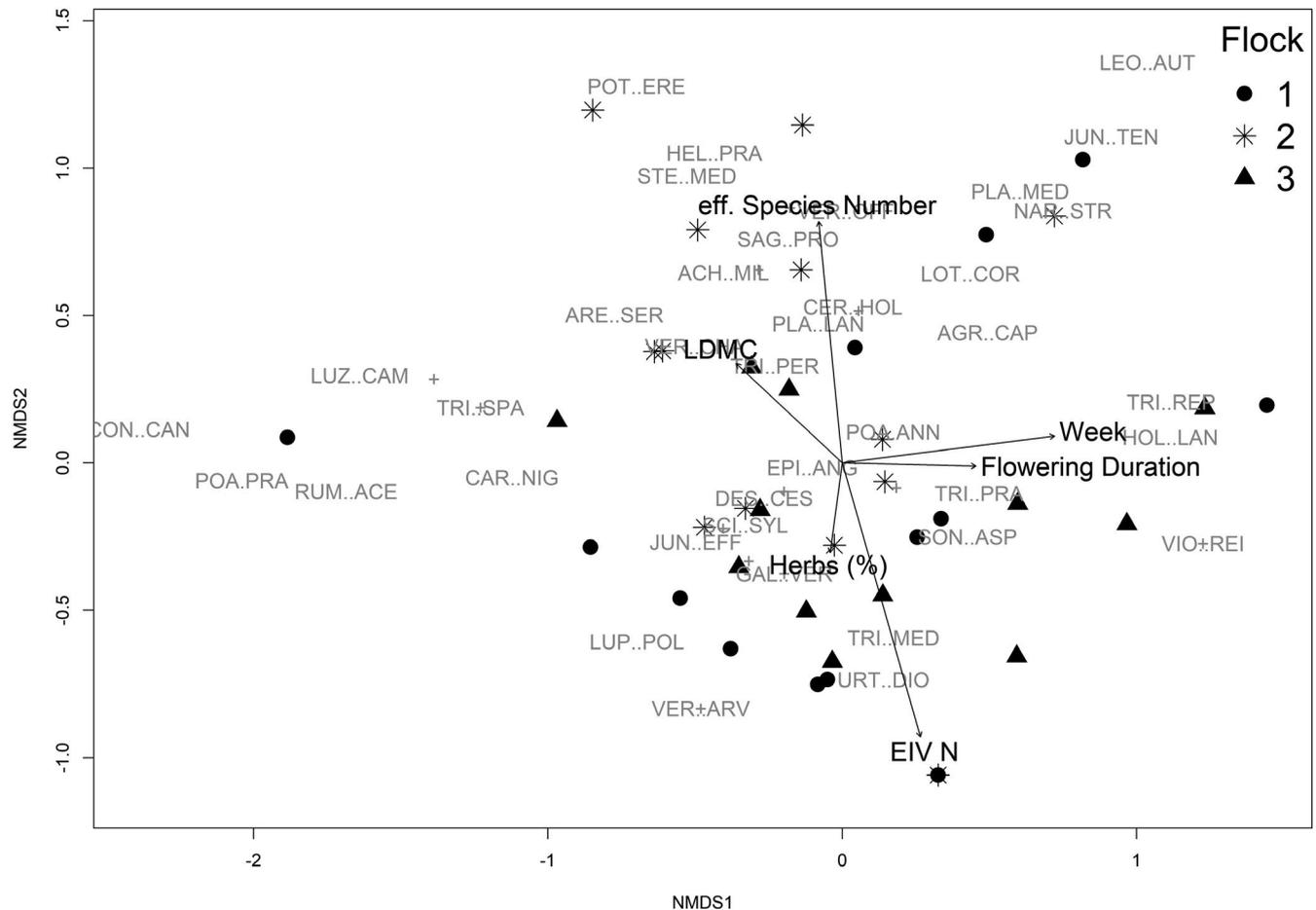


FIGURE 1 Non-metric multidimensional scaling (stress level: 0.131) of the vegetation composition found in sheep dung of three sheep herds between July and September, 2017. We observed a shift in species composition during the sampling period

above-ground vegetation and mower samples showed little dispersion along the first two dimensions, seed bank and sheep dung samples were more scattered. Looking at the first and third dimension of the ordination, there was an overlap between the mower samples and the seed bank, while sheep samples overlapped marginally with the seed bank (Figure 2b).

3.2 | Trait comparison

Sheep dung samples contained 44% less grasses; sheep-dispersed species had slightly (8%) longer flowering durations than the above-ground vegetation and had approx. 90% lower seed sizes than non-dispersed species from both species pools. Furthermore, the species dispersed by sheep usually had high longevity values (+103% compared to the above-ground vegetation and +47% compared to the seed bank; Figure 3). Overall, sheep-dung-dispersed species had similar maximum releasing heights compared to non-dispersed species of the above-ground vegetation (Figure 3a). They contained 25% less herbs and similar percentages of grasses compared to the seed bank (Figure 3b). Concerning palatability, there were no large differences in mean LDMC values of dispersed and non-dispersed species, but EIV-N was significantly higher in

sheep-dispersed species compared to non-dispersed species of both species pools.

Mower samples were less clearly differentiated from the other groups concerning their traits, although they had lower seed sizes and contained more grasses than both species pools. Compared to the above-ground vegetation, they were characterized by 38% smaller seeds and 56% more grass species per sample (Figure 3c). Contrastingly, releasing heights and percentages of herbs in the samples were similar to those of non-dispersed species of the above-ground vegetation. Compared to the seed bank vegetation, species found in mower samples had 62% smaller seeds and 11% higher releasing heights (Figure 3d). Furthermore, the percentage of herbs was 25% lower than in seed bank samples and the percentage of grasses was strongly increased by 130% in mower samples compared to seed bank samples. Longevity of species was 80% higher in the mower samples compared to the non-dispersed species of the above-ground vegetation.

4 | DISCUSSION

The first hypothesis could be partially confirmed: while the number of shared species was only marginally higher between sheep and seed bank than between sheep and above-ground vegetation,

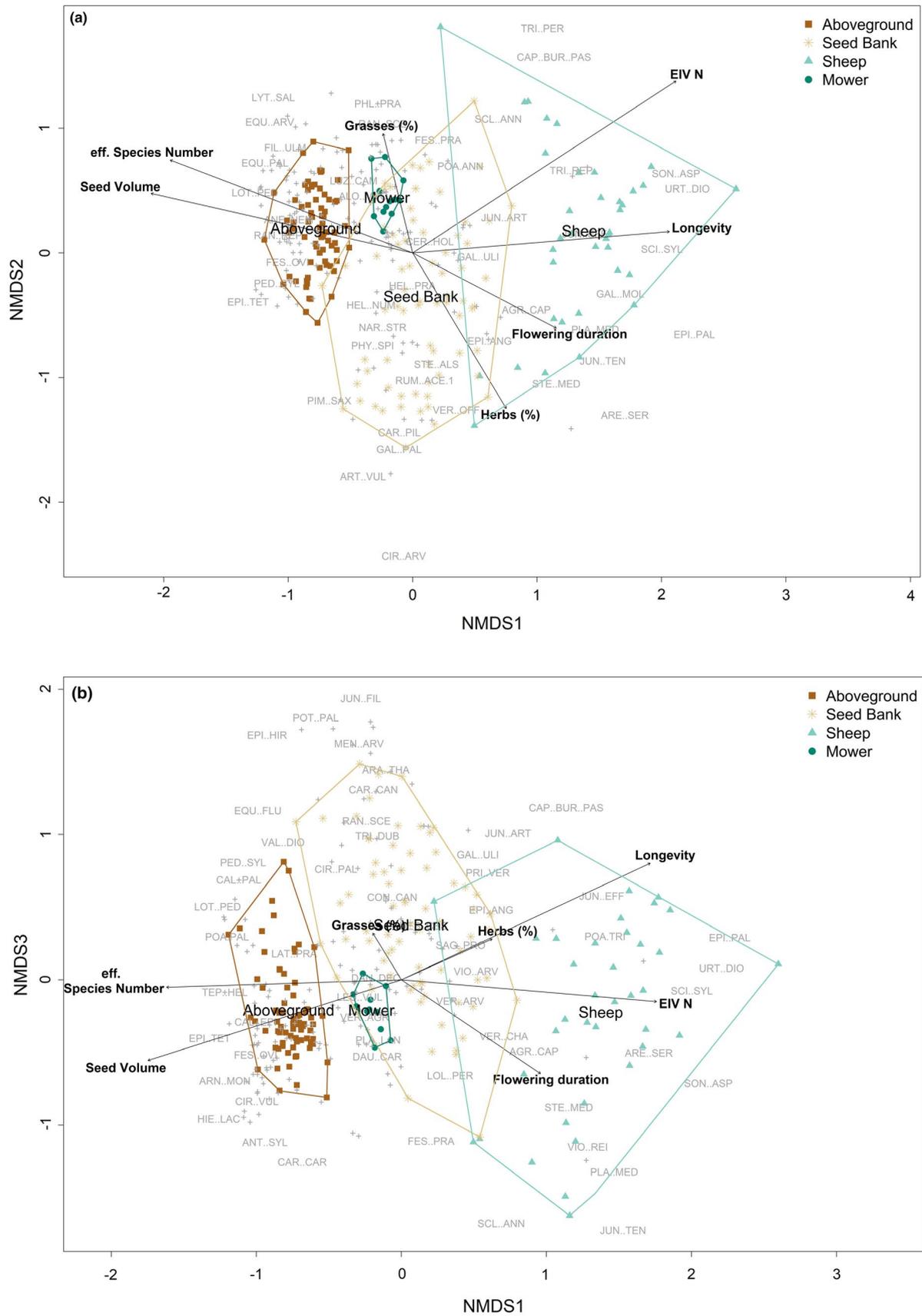


FIGURE 2 Non-metric multidimensional scaling (stress level: 0.151) axes (a) one and two and (b) one and three of the above-ground vegetation and seed bank vegetation compared to species compositions found in the dispersal vectors sheep dung and mowing machinery

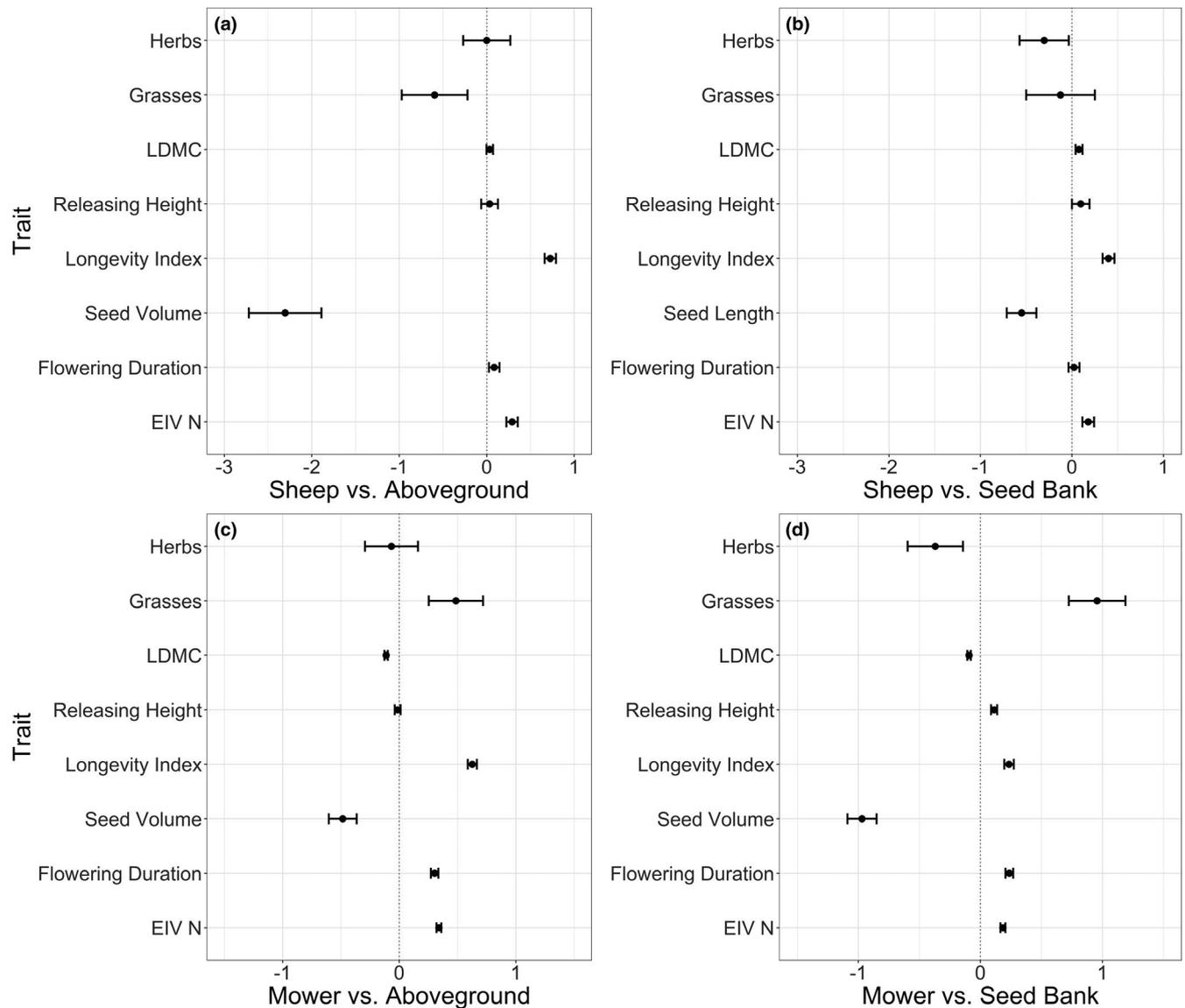


FIGURE 3 Log-response ratios dispersal vectors vs species pools (a) sheep vs above-ground, (b) sheep vs seed bank, (c) mower vs above-ground, (d) mower vs seed bank. Zero indicates the mean value of the non-dispersed species from the respective species pool, bars show mean log-response ratios \pm confidence intervals. No overlap between bars and zero line thus indicates significant differences in mean trait value between the respective dispersal vector and species pool. Note the different scaling of the x-axes

samples of sheep and seed bank were more similar concerning species composition and some of the observed traits. Many different species were found in sheep dung; however, most species were found in very low frequencies. The most common sheep-dispersed species were typical roadside or field border species. A large fraction of seedlings emerging from sheep dung consisted of *Urtica dioca*, which is rarely found in the grasslands of our study area, but which is prevalent on road verges or field borders. This is most likely due to the species' high palatability (Cosyns et al., 2005a; Kuiters & Huiskes, 2010). We found relatively low abundances of typical grassland species in sheep dung, which is contradictory to other findings on ungulate endozoochory (Auffret & Cousins, 2013). This may be due to the grazing management in the study area, where from mid-August on, aftermath grazing is carried out on meadows that have been mown

when most typical grassland species carry viable seeds. In the course of the sampled period (July to September), we observed a shift in the species dispersed via endozoochory. As expected, this shift was mainly associated with phenological traits, such as flowering time.

Seeds dispersed by endozoochory were on average one order of magnitude smaller than seeds of non-dispersed species of both species pools. This is probably due to the fact that small seed sizes are related to shorter retention times of seeds in the animal's gut, which strongly increases the probability of the seed surviving the gut passage (Janzen, 1984). Furthermore, small-seeded species are often characterized by high seed production, which increases the number of ingested seeds and thus the probability that some seeds survive the gut passage (Bruun & Poschold, 2006). Contrary to these results, species with large and round seeds had the highest

survival rates when ingested by Kazakh sheep in another study (Wang et al., 2017). Sheep dung contained less grasses than the above-ground vegetation. Low survival rates of grasses in sheep dung have been reported by other authors (Wang et al., 2017) and this finding may partially be explained by sheep preferring herbs over grasses. Furthermore, the relatively high releasing heights of typical grasses in our species pools may lead to reduced seed ingestion, as low releasing heights (<20 cm) may increase the seed intake of grazers (Albert et al., 2015b) and plants with lower releasing heights may be more resistant to grazing pressure due to an increased ability to resprout (Díaz et al., 2001). However, in our study, species dispersed by sheep had similar releasing heights compared to non-dispersed species of both species pools. This was due to the fact that the high-growing *Urtica dioica* and *Juncus effusus* were found in most sheep dung samples. Legume seeds were not more common than herbs or grasses in sheep dung (being absent from half of the dung samples and thus not considered in the trait analysis). This was unexpected, as hardseededness, a trait common in legumes, was found to increase the probability of the seeds surviving the gut passage (Russi et al., 1992; Wang et al., 2017), but is in line with findings by other studies (e.g. Karimi et al., 2018). Additionally, species found in sheep dung had higher longevity values, which may be associated with small seed sizes. Sheep preferred species with higher EIV-N, which indicates selective feeding on plants of higher palatability. However, there were no major differences concerning leaf dry matter content compared to both species pools, probably due to the fact that LDMC decreases during the grazing season (Kleinebecker et al., 2011). Compared to non-dispersed species of the above-ground vegetation, species dispersed by sheep had longer flowering durations. This may be due to migratory sheep herding taking place during all of the vegetation period and thus enabling the dispersal of species with late/long flowering periods. Overall, sheep endozoochory dispersed many different species, but nonetheless seems to be rather selective concerning some traits. While some species and traits are indeed similar to traits of species commonly found in the seed bank, the grazing preferences of the animals and herd management lead to differing species compositions. Furthermore, some of the differences may be observed because the soil seed bank represents the past vegetation rather than the present one (Bakker et al., 1996). Additionally, epizoochory, i.e. seed dispersal via animal fur or hoofs, is estimated to transport high numbers of seeds and may favour species with different traits compared to endozoochory, such as higher-growing plants or species producing seeds with appendages (Albert et al., 2015a). Furthermore, seed dispersal by epizoochory also depends on animal characteristics, such as hair length (Couvreux et al., 2005). Thus, epizoochory complements endozoochory and enables more species with different traits to be dispersed by sheep.

Our second hypothesis could be confirmed: overall, the species composition of mower samples was similar to the composition of the above-ground vegetation (with a shift towards small-seeded species that may also be found in the seed bank) and mowers contained a high number of typical grassland species. This is probably

due to the mowing taking place around July 1, which allows most species in central-European semi-natural grasslands to have produced (and still carry) viable seeds, but may disadvantage some species with unfitting phenology (Leng et al., 2011). Obviously, only species that carry viable seeds by the time of mowing can be dispersed, and mowing is thus strongly selective concerning phenological traits. In our data set, the underrepresentation of some of the more common grassland species, such as *Bistorta officinalis*, *Sanguisorba officinalis* or *Filipendula ulmaria* gives evidence of this, as they are characterized by late flowering and fruiting compared to the analyzed mowing date around July 1. However, as there are different mowing dates in our study area, these species may be dispersed between meadows that were not sampled in our study. In the mower samples, species that were more abundant or frequent in the above-ground vegetation had a higher probability to be dispersed than rare species. Similar results have been reported by Strykstra et al. (1997), but in a study on seed dispersal by manure and motor vehicles, typical grassland species were less abundant in mud attached to motor vehicles (Auffret & Cousins, 2013). The favouring of locally abundant species by mowing machinery may lead to the homogenization of mown grassland patches (Lepš, 2014) and mowing may have negative effects both on the richness of the above-ground vegetation and the seed bank (Klaus et al., 2018). In our study, mowers were selective towards several traits, although to a lesser degree than sheep, and favoured small-seeded species, in particular grasses. This favouring of smaller seeds was also found by other authors, e.g. for *Panicum miliaceum* in Canada (McCanny & Cavers, 1988). Furthermore, smaller seeds are potentially dispersed over longer distances by mowing machinery (Bullock et al., 2003). Compared to the non-dispersed species found in the seed bank, tall-growing species had a higher probability to be dispersed, as they are more prone to getting caught in the mowing unit (Strykstra et al., 1997). However, there were no differences between releasing heights of mower-dispersed and non-dispersed species of the above-ground vegetation in our study. Overall, our results suggest that mower samples are functionally more similar to the above-ground vegetation than sheep dung samples.

Our study revealed that mowing machinery and sheep endozoochory are complementary dispersal vectors for grassland species, while some of the observed differences among the four groups may be due to the samples being related to different areas: the above-ground vegetation and seed bank were bound to the same plots, species composition in mower samples depends on the size of the respective meadows, whereas the composition of sheep samples is related to the area grazed by the respective flock. However, we showed that many different species can be transported and species with different traits are favoured by each vector. Thus, the interplay of both vectors may be crucial for sustaining high plant diversity. Overall, sheep endozoochory is a more selective ecological filter, favouring easily palatable species with very small seeds. Mowers, although also favouring small-seeded species, were less selective concerning most of our analyzed traits, but in general favoured high-growing grasses and species that were abundant in the above-ground

vegetation. As tall-growing vegetation may be able to autonomously disperse seeds further than small-growing plants (Thomson et al., 2011), these species may be less reliant on dispersal vectors to sustain populations. On the one hand, due to their grazing preferences, sheep may disperse some unwanted species, such as *Urtica dioca*. On the other hand, migratory sheep herding enables the dispersal of species that are underrepresented in mower samples due to their phenology, or may allow dispersal in years that are characterized by early or late fruiting compared to the mowing date. Both vectors provide “directed dispersal” (Fischer et al., 1996), as mowing machinery and sheep herds move between suitable habitats, lowering competition by reducing the biomass and creating microsites with open soil. In the case of sheep dung, these microsites are nutrient-rich, but may expose the seed to drought (Eichberg et al., 2007). Thus, germination or seedling survival in sheep dung may be increased, as found in legumes by Russi et al. (1992), or decreased, as found in species of the *Koelerion glaucae* association (Eichberg et al., 2007).

Overall, our results show that the long-term conservation of the high species diversity in semi-natural grassland is reliant on the interplay of different dispersal vectors and the seed bank, as the availability of several modes of dispersal facilitates the seed dispersal of species (Ozinga et al., 2004). Thus, the combination of mowing and migratory herding that has traditionally been carried out in many meadows of central Europe (Kapfer, 2010) is highly desirable to ensure the long-term conservation of semi-natural grasslands, particularly in fragmented landscapes. Furthermore, spatial and temporal variations in management, such as different mowing dates and migratory sheep herding throughout the vegetation period, enable the dispersal of a higher number of species and are thus to be recommended.

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AUTHOR CONTRIBUTIONS

KL, AO, and RLE conceived of the research idea; YK, KL and WH collected data, YK and WH with help from TK and RLE performed statistical analyses; YK with contributions from KL, RLE and TK wrote the paper; all authors discussed the results and commented on the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available in the Supplementary Material of this article.

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SUPPORTING INFORMATION

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

Appendix S1. Species abundances per sample

Appendix S2. Species accumulation curves

Appendix S3. Permanova results

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