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Which vegetation and seed-bank changes are induced by the disturbance regime of livestock trails in open sand ecosystems?

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Abstract. In many grazed grassland systems livestock trails form distinct stripe-shaped structures. Focussing on sheep trails in dry sandy grasslands (northern upper Rhine valley, Germany), we investigated their spatial structure and their floristic composition in the above-ground vegetation and the soil seed bank. We generated sheep-trail maps in the field on the basis of high resolution CIR aerial photographs, made relevés on trail and control plots and analysed the seed bank of both plot types using the seedling emergence method (soil layer 1: 1-6 cm depth and soil layer 2: 11-16 cm depth).
The spatial extent of sheep trails in the study system was considerable (2-3 km total length on a 4-ha paddock, representing ca. 1 % of the paddock area). The development of trail systems is driven by the spatial distribution of essential resources (food, water, salt) and requisites (shade-producing structures). In the above-ground vegetation, cover-abundance of 11 of the altogether 78 identified plant taxa was significantly affected by sheep trails (7 annual taxa benefited, 4 perennial taxa were repressed). With respect to presence, another 20 taxa showed a tendency towards increase (13 taxa, mainly annuals) or decrease (7 taxa, mainly perennials) (differences of more than 20 percentage points between trail and control plots). Concerning the soil seed bank there was no significant trail effect on the level of plant community; on the species level, however, two annual taxa showed higher seed densities in the topsoils of sheep trails (*Chenopodium album* agg., *Veronica verna*). This indicates a high "robustness" of the studied seed banks.
In an extensively grazed open sand ecosystem, sheep trails form microhabitats with high plant species diversity and regressive successional tendencies in the above-ground vegetation, promoting mainly annual, habitat-typical plant species.

Zusammenfassung. Wie wirkt sich das Störungsregime von Weidepfaden auf die Vegetation und die Diasporenbank von offenen Sandökosystemen aus?
In vielen Grasland-Systemen bilden Weidepfade abgegrenzte lineare Strukturen. Wir untersuchten am Beispiel von Schaf-Weidepfaden in trockenem Sand-Grasland der nördlichen Oberrheinebene (Deutschland) ihre räumliche Struktur und die floristische Zusammensetzung der aktuellen Vegetation und der Diasporenbank. Wir fertigten Karten von Schaf-Weidepfaden auf der Basis hochauflösender CIR-Luftbilder an und analysierten jeweils auf Weidepfad- und Kontrollflächen die oberirdische Vegetation (Vegetationsaufnahmen) und die Diasporenbank (Keimlings-Auflaufmethode; Bodenschicht 1: 1-6 cm Tiefe und Bodenschicht 2: 11-16 cm Tiefe).

Die räumliche Ausdehnung der Schaf-Weidepfade war im untersuchten System beträchtlich (2-3 km Gesamtlänge auf einer 4-ha-Koppel; dies entspricht etwa 1 % der Koppelfläche). Die Entwicklung von Weidepfad-Systemen wird durch die räumliche Verteilung essentieller Ressourcen (Nahrung, Wasser, Salz) und Requisiten (Schatten-spendende Strukturen) bestimmt. In der oberirdischen Vegetation zeigten sich für 11 von insgesamt 78 identifizierten Taxa signifikante Unterschiede in der Artmächtigkeit im Vergleich der Weidepfad- und Kontrollflächen (7 annuelle Taxa wurden auf Pfaden

gefördert, 4 perenne Taxa auf den Kontroll-Flächen). Im Hinblick auf die Stetigkeit zeigten weitere 20 Taxa eine Tendenz entweder zur Zunahme auf Weidepfaden (13 Taxa, v.a. Annuelle) oder zur Abnahme (7 Taxa, v.a. Perenne) (Unterschiede von mehr als 20 Prozentpunkten zwischen Weidepfaden und Kontrollen in der Stetigkeitstabelle). Bezüglich der Diasporenbank im Boden gab es keinen signifikanten Weidepfad-Effekt auf der Ebene der Pflanzengesellschaft, jedoch auf der Ebene der Pflanzenarten zeigten zwei einjährige Taxa höhere Diasporendichten in der oberen Bodenschicht der Weidepfade (*Chenopodium album* agg., *Veronica verna*). Dies spricht für die hohe Robustheit der untersuchten Diasporenbanken.

In einem extensiv beweideten, offenen Sandökosystem repräsentieren Schaf-Weidepfade Mikrohabitate mit hoher Pflanzenarten-Diversität und regressiven Sukzessionstendenzen in der oberirdischen Vegetation, wobei vor allem einjährige, Habitat-typische Pflanzenarten profitieren.

1 Introduction

Extensive livestock grazing in grassland systems normally results in the development of distinctive vegetation patterns (e. g., BAKKER et al. 1983, BERG et al. 1997). Generally, there are more intensively grazed patches comprising plant species of high forage quality and neglected patches with inedible plant species or species of low forage quality. Besides the spatial distribution of forage resources, places supplying water, salt or shade are important pasture components affecting livestock movement and, as a consequence, the development of vegetation patterns. It is well known that livestock species, e. g. sheep, develop a good spatial knowledge of their home range (PORZIG & SAMBRAUS 1991). They create an infrastructure of trails, which connect places supplying food, water or shade (PORZIG & SAMBRAUS 1991). The spatial use of a given grazing area by livestock species can be controlled by the placement of water and salt sources (PORZIG & SAMBRAUS 1991, GANSKOPP 2001). This is of relevance for conservation as well as economic aims of habitat management. Especially in arid regions the zones around water points (piospheres; from Greek “pios”: to drink) are characterised by a dense radial system of livestock trails (LANGE 1969, SQUIRES 1974).

In the dry open inland sand ecosystem studied here water is a very limited resource. This system represents an environmental gradient of highly endangered sand vegetation in the northern upper Rhine valley (Germany), where pioneer vegetation is characterized by base-rich sand and more consolidated areas by slightly acidic conditions in the upper soil layer. Pioneer stands mainly belong to the threatened *Koelerion glaucae* alliance, slightly acidic stands mainly to the threatened *Armerio-Festucetum trachyphyllae* community. Both types are classified as “priority habitats” according to the European Fauna-Flora-Habitat Directive (SSYMANK et al. 1998). We already published some initial results on the topic “livestock trails” (SCHWABE et al. 2004), but meanwhile we have increased our knowledge.

We hypothesized that sheep trails are micro-habitats with regressive development and high soil seed-bank dynamics, representing an earlier successional stage than the surrounding vegetation and soil seed bank. Specifically, we asked the following questions: 1. Which spatial structure do sheep trails have on extensive sand grassland paddocks, and how great an area do they cover? 2. What are the floristic and structural differences between sheep trails and control plots, and are these differences dependent on vegetation type? 3. What are the differences between the soil seed bank of sheep trails and that of control plots?

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One of the most important topics of Fred Daniëls' scientific work are *Koelerio-Corynephoretea* vegetation complexes, their fine-scale pattern and the successional pathways of such complexes. Therefore we dedicate this paper to him on the occasion of his 65th birthday; livestock trails in dry grasslands may be an interesting example of a close interrelation between pattern and process.

2 Study site

The study site was the nature reserve "Ehemaliger August-Euler-Flugplatz von Darmstadt" (71 ha, 8°35'E/49°51'N) which is located in the northern upper Rhine valley region. Under slightly subcontinental climatic influences (650 mm precipitation a^{-1}, 9.9°C mean annual temperature) and historically varied use by man (a relatively long period of military use ceased in the early 1990's; since 1999 grazing has been employed as a conservation measure) a mosaic of sand grassland types developed in the plane area. Pioneer stands of the *Koelerion glaucae* (K) are characterized by pH values (measured in 0.01 mol l^{-1} $CaCl_2$ solution) of 7.4 ± 0.02 (mean ± SE; n = 11 grid points; distance between grid points: 65 m) in the upper soil layer (0-10 cm), mid-successional stages mainly belong to the *Armerio-Festucetum trachyphyllae* (A; pH 6.7 ± 0.2; n = 6 g. p.); transitional stages have also developed (*Koelerion glaucae*/*Armerio-Festucetum*: KA; pH 7.2 ± 0.1; n = 11 g. p.). Ruderalized stands of the *Armerio-Festucetum* (AR) occur in one part of the area (former fields). Four paddocks were investigated with respect to the described vegetation types; productivity increases in the following order: K, KA, A, AR (Tables 1 and 2).

3 Methods

3.1 Grazing regime

The studied livestock trails resulted from the following grazing regime: on relatively large paddocks (2-13 ha) a stock of 169-450 sheep grazed for a short period (a few days to weeks per year; Tab. 1). Sheep grazed the paddocks as long as an adequate food supply could be guaranteed. Water tanks and salt/mineral licks were supplied together at one point in each paddock, shade was available at one or more other paddock areas.

3.2 Spatial structure and extent of sheep trails

We generated sheep-trail maps in the field for three paddocks (K, KA, AR) by plotting the trails on colour-infrared (CIR) aerial photographs with very high resolution (pixel size 7.5 cm; see SCHWABE et al. 2004 and SÜSS et al. 2007). To a large extent the original trails could be distinguished on the photographs. The field maps were digitised and integrated in a GIS (Geomedia Professional 5.1) to calculate total trail length per paddock. The aerial photographs were made in the course of a project funded by the "German Ministry of Research and Technology" (BMBF, No. 01LN0003). On paddock AR we measured a trail width of 15.3 ± 0.2 cm (mean ± SE; n = 100). This value was used to calculate the trail areas within the three paddocks (trail width in the studied system varies only slightly).

3.3 Vegetation relevés

In May-July 2002, we made relevés on trail and control plots in three paddocks before the grazing period had started. We documented the effects of two (KA: 2000-2001) or three (K, A: 1999-2001) consecutive years with almost identical paddock boundaries (portable electric fences). Generally, the trails are used for several years, if the spatial arrangement of fences and "attraction places" (water, salt, shade) is not changed. We carried out a side-by-side comparison with elongated plots that are 4.5-5.3 m x 0.1 m in size. One relevé was made in the centre of a trail segment and one on a control plot oriented in parallel (0.5 m distance; paired plots). Seven replicates, distributed over the whole trail system, were sampled per paddock. We used the cover-abundance scale of BARKMAN et al. (1964). Later, the original relevés were arranged as presence columns (in %), representing the trail relevés and control relevés for each paddock.
Additionally, we carried out a census of the number of individuals on each plot for the threatened (KORNECK et al. 1996) annual species *Silene conica* and *Phleum arenarium.*

3.4 Soil seed-bank analysis

In March 2004, five trail segments 10 m in length and five parallel control plots of the same size (distance between trail and control plots: 0.5 m) were sampled on paddock KA (the paired plots were distributed over the whole trail system) (BOES 2006). The investigated trails (potentially) had been used by sheep in the years 2000-2002 (almost identical spatial arrangement of fences and "attraction places"). From each plot 100 individual soil samples were taken at a standard distance of 10-cm apart, by means of an Eijkelkamp "liner sampler". They were subdivided into layer 1 (1-6 cm depth) and layer 2 (11-16 cm depth). Every tenth individual sample was bulked to give a composite sample. Consequently, each layer of each plot is represented by 10 composite samples. The sampled area for each plot was 0.1735 m^2. We used the seedling emergence method and exposed the samples (sheltered by gauze and a transparent roof) outdoors in the botanical garden of Darmstadt on a platform 0.9 m above the soil for 18 months (for further details, see EICHBERG et al. 2006).

3.5 Nomenclature

The nomenclature follows WISSKIRCHEN & HAEUPLER (1998) for phanerogams, KOPERSKI et al. (2000) for bryophytes and SCHOLZ (2000) for lichens.

3.6 Statistical analyses

3.6.1 Vegetation

Differences between sheep trails and control plots were tested by the Wilcoxon rank test for matched pairs (SPSS 6.1) for the following dependent variables: plant species diversity, cover of bryophytes, cover of litter, cover of bare ground, cover-abundance indices of all individual plant species and individual numbers of *Silene conica* and *Phleum arenarium*. Cover-abundance indices were transformed to a 9-rank scale prior to analysis.

3.6.2 Soil seed bank

Mixed linear models (SAS 9.1, Proc Mixed, LITTELL et al. 2000) were calculated in order to analyse the influence of the independent variables sheep trail and soil depth on the following dependent variables: total number of plant species, total number of seeds, number of seeds of all individual species. The seedling numbers of the ten composite samples of each plot and layer were pooled and log (x + 1) transformed prior to analysis. We regard it as extremely unlikely that soil layer 2 should be influenced by an impact of three short-duration grazing periods, for two reasons: (i) in the study system, there is evidence that the depth to which seeds are buried by sheep trampling is much less than 11 cm (EICHBERG et al. 2005), and (ii) downward movement of seeds through soil is a slow process (VAN TOOREN 1998). Instead, we argue that an effect of trail use should be restricted to layer 1 and thus result in a significant trail x soil layer interaction. That is, if both soil layers of a trail plot are found to be different in the same direction in comparison to those in the control plot, we would regard this as a result of inter-plot differences prior to our study.

4 Results

4.1 Spatial structure and extent of sheep trails

Fig. 1 shows the spatial distribution of sheep trails developed within three sand grassland paddocks. The spatial dimension of the trails is summarized in Tab. 1. A 4-ha paddock comprises about 2-3 kilometres total trail length, representing nearly one percent of the paddock area. On all paddocks there was a radial pattern of trails around the point of water and mineral supply and around larger shady places (dependent on the fence lines). On paddocks KA and AR the occurrence of non-radial (tangential) trails was an exception; on paddock K the trail pattern was more erratic. The example of paddock AR shows that among the places supplying shade those preferred by the sheep are large enough to be used by the whole flock.

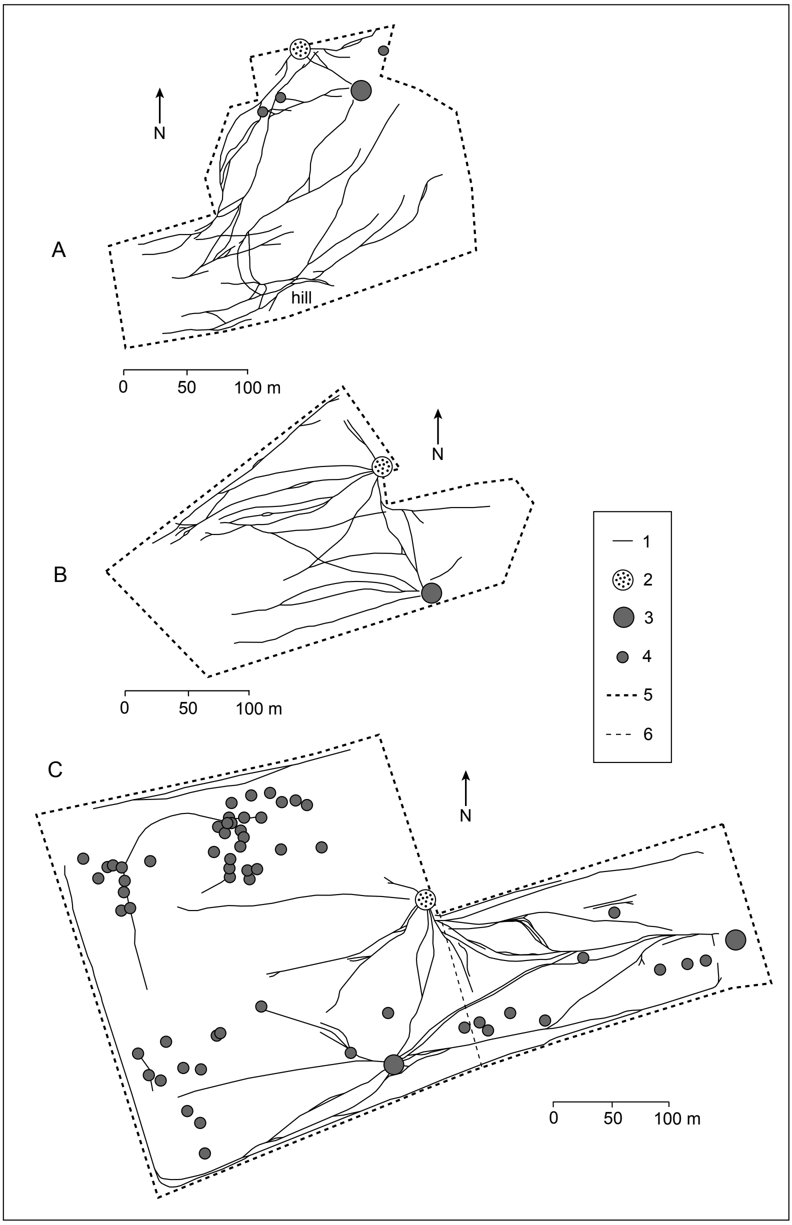

Fig. 1: Sheep trails on three paddocks of the investigated sand grassland nature reserve:
A) *Koelerion glaucae* complex (paddock K), **B**) *Koelerion glaucae/Armerio-Festucetum trachyphyllae* transitional stage (paddock KA), **C**) ruderalized *Armerio-Festucetum trachyphyllae* (former field; paddock AR).
Labels: **1**: sheep trail, **2**: water tank + salt and mineral licks, **3**: larger shady area (e. g., a part of a forest or a group of trees), suitable as a resting place for the whole sheep flock, **4**: smaller shady area (mostly single trees), suitable only for parts of the flock, **5**: paddock boundary (portable electrical fence), **6**: paddock boundary during the first two grazing days of paddock AR; the paddock part on the right hand of the thin dotted line is an enlargement area that had been added to the left part to enhance forage supply (grazing time of the enlarged paddock: three days).

Tab. 1: Spatial dimensions of the investigated sheep-trail systems and paddocks

K: *Koelerion glaucae* complex, KA: *Koelerion glaucae*/*Armerio-Festucetum* transitional stage, AR: ruderalized *Armerio-Festucetum trachyphyllae* (former field). Succ. stage: successional stage.

PT = Productivity types: I ≤150 g aboveground dry matter/m², II >150-300 g dm/m², III >300 g dm/m²; peak standing crop data according to SÜSS et al. (2007). Data on the grazing regime: grazing period prior to trail mapping. The standing crop on paddock AR was restricted in the grazing period prior to trail mapping because the paddock had previously been used by sheep within the same vegetation period.

*: trail area = total trail length x 0.153 m (see Section 3.2).

Paddock	Succ. stage	PT	Paddock size (ha)	Previous grazing regime		Total trail length (m)	Total trail area (m²)*	% area of paddock
				Duration (days)	No. of sheep			
K	early	I	4.5	9	169	2712	415	0.92
KA	early-mid	I-II	4.1	17	169	2295	351	0.86
AR	mid	III	13.1	5	450	5553	850	0.65

4.2 Vegetation of sheep trails and control plots

Only in paddock KA was plant species diversity (including cryptogams) significantly higher on trails compared to controls (p=0.018, Wilcoxon test); in paddocks K and A there was no significant difference (Tab. 2). Cover of bryophytes and litter was significantly lower, cover of bare ground significantly higher on the trail plots for all three paddocks (p<0.05, Wilcoxon test; Tab. 2).

Paddock	K	K		KA	KA		A	A	
Plot type	Trail	Control	*p*	Trail	Control	*p*	Trail	Control	*p*
Productivity type		I			I-II			II-III	
Cover of bryophytes (%)	66 ± 18	93 ± 4	*	34 ± 13	76 ± 7	*	42 ± 20	91 ± 4	*
Cover of litter (%)	2 ± 1	3 ± 1	*	4 ± 1	6 ± 1	*	10 ± 5	27 ± 7	*
Cover of bare ground (%)	24 ± 17	2 ± 1	*	45 ± 13	5 ± 3	*	46 ± 17	2 ± 1	*
Total number of plant species	31.9 ± 2.2	32.4 ± 1.9	ns	26.3 ± 2.0	21.6 ± 2.7	*	26.9 ± 2.7	23.1 ± 3.0	ns
Ch, d: K									
Poa bulbosa	100	100		.	.		.	.	
Veronica praecox	71	100		.	.		.	.	
Senecio vernalis	86	86		.	.		.	.	
Koeleria glauca	43	29		.	.		.	.	
Euphorbia cyparissias	29	29		.	.		.	.	
Chenopodium album agg.	14	.		.	.		.	.	
Ch, d: K+KA									
Saxifraga tridactylites	100	100		100	100		.	.	
Phleum arenarium	100	100		14	14		.	.	
Psyllium arenarium	100	100		57	43		.	.	
Conyza canadensis	100	100		57	43		.	.	
Helichrysum arenarium	29	43		43	57		.	.	
Salsola kali ssp. tragus	100	86		43	.		.	.	
Erophila verna	71	86		57	.		.	.	
Setaria viridis	86	71		29	.		.	.	
Corynephorus canescens	86	71*		14	.		.	.	
Silene otites	86	71		14	.		.	.	
Ch, d: KA+A									
Poa angustifolia	.	14		14	14		86	86	
Koeleria macrantha	.	.		100	100		100	100	
Festuca brevipila+ovina agg.	.	.		100	100*		100	100	
Trifolium arvense	.	.		57	29		43	57	
Potentilla argentea agg.	.	.		14	14		29	14	
Ch, d: A									
Medicago falcata	.	.		.	29		86	57	
Armeria maritima ssp. elongata	.	.		.	.		86	86	
Agrostis capillaris	.	.		.	.		71	71	
Vicia angustifolia	.	.		.	.		29	29	
Plantago lanceolata	.	.		.	.		43	14	
Cerastium arvense	.	.		.	.		57	29	
Achillea millefolium	.	.		.	.		43	29	
Hieracium pilosella	.	.		.	.		43	57	
Elymus athericus	.	.		.	.		86	100*	
Agrostis vinealis	.	.		.	.		.	29	
Ch, d: Koelerio-Corynephoretea									
Medicago minima	100	100		100*	100		86*	29	
Arenaria serpyllifolia agg.	100	100		100*	100		100	100	
Bromus tectorum	100	100		29	57		57	43	
Cerastium semidecandrum	100	100		100	86		100*	100	
Sedum acre	100	100		57	57		14	29	
Silene conica	100*i	100		43	14		71	29	
Veronica verna	100	100		100	86		86	71	
Vulpia myuros	100	100		100	57		86*	57	
Vicia lathyroides	43	57		100	100		86	100	
Myosotis stricta	43	57		57	43		71	29	
Erodium cicutarium	71	86		86	71		86*	14	
Petrorhagia prolifera	43	43		43	14		57	57	
Rumex acetosella s.l.	100	71		29	29		71	57	
Geranium molle	43	29		57	.		100	100	
Trifolium campestre	100*	.		100	86		100*	43	
Echium vulgare	14	14		29	.		14	.	
Holosteum umbellatum	14	14		.	.		71	57	
Carex praecox	.	.		14	14		.	.	
Myosotis ramosissima	.	.		.	.		14	14	
Scleranthus perennis	.	.		.	.		14	14	

Other species						
Veronica arvensis	57	71	100*	57	100	86
Carex hirta	57	43	57	57	71	71
Ononis repens	29	57	71	71	14	.
Crepis capillaris	14	29	.	.	.	14
Elymus repens	.	.	14	14	.	14
Bromus hordeaceus	.	.	14	.	71	86
Arabidopsis thaliana	14	.	.	14	.	.
Cynodon dactylon	29	29	.	.	.	.
Oenothera biennis s.l.	14	.	.	.	.	14
Tragopogon dubius	.	.	14	14	.	.
Bromus sp. (tectorum/ hordeaceus), seedling	.	.	.	.	57	14
Thymus pulegioides s.l.	.	.	.	.	14	14
Papaver dubium	.	14	.	.	.	.
Artemisia campestris	.	.	29	.	.	.
Hypochaeris radicata	.	.	14	.	.	.
Sisymbrium altissimum	.	.	14	.	.	.
Asparagus officinalis	.	.	14	.	.	.
Carduus nutans	.	.	.	.	14	.
Cynoglossum officinale	.	.	.	.	14	.
Verbascum phlomoides	.	.	.	.	14	.
Berteroa incana	.	.	.	.	.	14
Cryptogams						
Hypnum cupressiforme var. lacunosum	100	100*	100	100*	100	100*
Cladonia furcata+rangiformis	86	100	100	100	14	43
Peltigera rufescens	57	86	43	43	.	14
Tortula ruraliformis	100	100	100	100	.	.
Cetraria aculeata	86	100	14	14	.	.
Brachythecium albicans	57	86	86	100	.	.
Bryum argenteum	.	.	.	14	.	.
further Acrocarpi	14	14	.	.	.	.

Tab. 2: Presence of plant species on sheep trails and control plots in three sand paddocks of the investigated nature reserve
values: % occurrence on plots (n = 7 for all columns).
K: *Koelerion glaucae* complex, KA: *Koelerion glaucae*/*Armerio-Festucetum* transitional stage, A: *Armerio-Festucetum trachyphyllae*.
Productivity types see Tab. 1. Cover of bryophytes, litter and bare ground and total number of plant species: mean values ± mean absolute deviations from the mean.
Ch: characteristic species, d: differential species. In boxes: occurrence >20 percentage points higher on trails as compared to controls; underlined: occurrence >20 percentage points higher on controls. */*i: p<0.05 (*: based on a 9-rank scale; *i: based on individual numbers), ns: not significant (Wilcoxon test). The position of the asterisk indicates where a species has a significantly higher mean cover-abundance index or a significantly higher mean individual number: on trails or controls.

Tab. 3: Number of seeds detected in soil seed banks of sheep trails and control plots located on paddock KA

KA: *Koelerion glaucae/Armerio-Festucetum trachyphyllae* transitional stage. Dots: zero values.

Plot number	1	2	3	4	5	mean	1	2	3	4	5	mean	1	2	3	4	5	mean	1	2	3	4	5	mean
Soil depth (1: 1-6 cm, 2: 11-16 cm)	1	1	1	1	1	1	1	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2	2	2
Sheep trail (T)/ control (C)	T	T	T	T	T	T	C	C	C	C	C	C	T	T	T	T	T	T	C	C	C	C	C	C
No. of plant taxa	18	22	22	19	28	22	22	21	19	26	27	23	5	9	7	5	11	7	5	8	5	12	10	8
Individuals recorded	175	252	234	289	418	274	164	181	157	570	532	321	15	37	18	14	49	27	26	41	26	68	51	42
Seeds m^{-2}	1009	1452	1349	1666	2409	1577	945	1043	905	3285	3066	1849	86	213	104	81	282	153	150	236	150	392	294	244
Present on trail plots and control plots																								
Chenopodium album agg.	24	9	10	12	13	13.6	4	5	.	13	15	7.4	11	23	5	6	21	13.2	20	29	5	25	25	20.8
Arenaria serpyllifolia agg.	13	19	73	30	15	30.0	12	8	36	29	59	28.8	.	.	1	1	3	1.0	2	.	5	3	3	2.6
Saxifraga tridactylites	85	106	44	153	194	116.4	69	46	28	306	244	138.6	1	2	3	.	12	3.6	.	.	.	15	14	5.8
Conyza canadensis	4	57	17	38	5	24.2	7	47	20	60	9	28.6	1	4	1	.	1	1.4	.	1	4	.	.	1.0
Sedum acre	10	6	5	14	26	12.2	13	6	3	22	20	12.8	1	.	.	.	4	1.0	.	1	.	1	3	1.0
Cerastium semidecandrum	9	3	11	2	14	7.8	4	6	7	9	16	8.4	.	.	.	.	.	0	.	2	.	1	1	0.8
Herniaria glabra	2	2	1	10	3	3.6	4	.	.	24	5	6.6	.	.	.	3	1	0.8	2	.	.	17	.	3.8
Verbascum phlomoides	3	11	18	2	2	7.2	3	9	19	6	.	7.4	.	.	5	.	.	1.0	.	.	8	.	.	1.6
Veronica arvensis	4	10	1	1	17	6.6	3	4	2	4	29	8.4	.	.	.	.	1	0.2	.	.	.	.	.	0
Setaria viridis	.	2	.	4	.	1.2	5	3	1	5	4	3.6	1	.	.	3	.	0.8	.	5	.	1	.	1.2
Erodium cicutarium	5	.	6	1	52	12.8	22	7	5	50	48	26.4	.	.	.	.	2	0.4	.	.	.	.	.	0
Medicago minima	.	.	.	3	15	3.6	2	1	3	6	22	6.8	.	.	.	.	1	0.2	1	.	.	1	.	0.4
Erophila verna	3	2	1	6	1	2.6	4	6	1	5	2	3.6	.	.	.	.	.	0	.	.	.	.	.	0
Potentilla argentea agg.	.	1	.	2	23	5.2	.	1	1	1	5	1.6	.	.	.	1	1	0.4	.	.	.	.	.	0
Festuca brevipila+ovina agg.	2	4	2	.	1	1.8	1	1	.	2	3	1.4	.	.	.	.	.	0	.	1	.	.	.	0.2
Rumex acetosella s.l.	.	4	.	.	1	1.0	3	16	.	.	2	4.2	.	.	.	.	.	0	.	.	.	1	1	0.4
Myosotis ramosissima+stricta	2	.	3	1	2	1.6	.	.	1	.	4	1.0	.	1	.	.	.	0.2	.	.	.	.	.	0
Polygonum aviculare agg.	1	.	.	.	.	0.2	2	.	.	10	1	2.6	.	.	.	.	.	0	.	1	.	.	1	0.4
Vicia lathyroides	1	.	3	.	3	1.4	.	.	3	.	2	1.0	.	.	1	.	.	0.2	.	.	.	.	.	0
Koeleria macrantha	.	1	2	.	.	0.6	1	1	.	1	5	1.6	.	.	.	.	.	0	.	.	.	.	.	0
Holosteum umbellatum	.	1	.	.	1	0.4	.	1	.	1	1	0.6	.	1	.	.	.	0.2	.	.	.	.	.	0
Carex hirta	.	.	27	.	7	6.8	1	.	19	.	14	6.8	.	.	.	.	.	0	.	.	.	.	.	0
Corynephorus canescens	.	1	.	.	.	0.2	.	7	.	1	.	1.6	.	3	.	.	.	0.6	.	1	.	.	.	0.2
Veronica verna	3	2	2	.	4	2.2	.	.	.	.	2	0.4	.	.	.	.	.	0	.	.	.	.	.	0
Poa angustifolia	.	.	1	.	4	1.0	1	.	.	.	2	0.6	.	.	.	.	.	0	.	.	.	.	1	0.2
Cerastium arvense	.	.	.	.	1	0.2	.	1	1	.	4	1.2	.	.	.	.	.	0	.	.	.	.	.	0
Trifolium campestre	.	.	.	.	.	0	1	.	1	2	.	0.8	.	.	.	.	.	0	.	.	.	1	.	0.2
Trifolium arvense	.	.	.	.	4	0.8	.	2	.	.	4	1.2	.	.	.	.	.	0	.	.	.	.	.	0
Achillea millefolium	.	4	.	.	.	0.8	.	1	.	1	.	0.4	.	.	.	.	.	0	.	.	.	.	.	0
Echium vulgare	.	.	.	.	1	0.2	.	.	2	.	.	0.4	.	.	.	.	.	0	.	.	.	.	.	0
Diplotaxis tenuifolia	.	1	.	.	.	0.2	1	.	.	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0
Stellaria media	1	.	.	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	1	.	0.2
<u>Further taxa</u>																								
Further Dicotyledoneae	.	4	.	1	4	1.8	.	2	1	1	2	1.2	.	.	.	.	1	0.2	.	.	1	.	.	0.2
Veronica sp. (arvensis/praecox/verna)	.	.	.	1	1	0.4	.	.	2	1	4	1.4	.	.	.	.	.	0	.	.	.	.	.	0
Further Monocotyledoneae	1	.	1	.	.	0.4	.	.	.	.	1	0.2	.	.	.	.	.	0	.	.	.	.	.	0

Tab. 3 cont.

Only present on trail plots																								
Betula cf. pendula	.	.	.	2	.	0.4	.	.	.	.	.	0	.	1	.	.	.	0.2	.	.	.	.	.	0
Convolvulus arvensis	.	.	.	.	.	0	.	.	.	.	.	0	.	1	2	.	.	0.6	.	.	.	.	.	0
Geranium robertianum	1	.	.	2	.	0.6	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Agrostis capillaris	.	.	.	.	1	0.2	.	.	.	.	.	0	.	.	.	.	1	0.2	.	.	.	.	.	0
Psyllium arenarium	.	1	.	.	1	0.4	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Vulpia myuros	.	.	1	.	.	0.2	.	.	.	.	.	0	.	1	.	.	.	0.2	.	.	.	.	.	0
Cardamine hirsuta	.	.	2	.	.	0.4	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Asparagus officinalis	.	.	1	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Carex praecox	.	.	1	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Cerastium holosteoides	.	.	.	1	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Crepis capillaris	.	.	.	.	1	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Eragrostis minor	.	1	.	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Fragaria sp.	.	.	.	1	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Salix sp.	.	.	.	.	1	0.2	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
<u>Further taxa</u>																								
Cerastium sp. (arvensis/ holosteoides/semidecandrum)	1	.	1	2	.	0.8	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0
Only present on control plots																								
Dicotyledoneae sp.	.	.	.	.	.	0	.	.	.	1	.	0.2	.	.	.	.	.	0	.	.	.	1	.	0.2
Oenothera biennis s.l.	.	.	.	.	.	0	.	.	.	1	1	0.4	.	.	.	.	.	0	.	.	.	.	.	0
Silene conica	.	.	.	.	.	0	.	.	.	1	1	0.4	.	.	.	.	.	0	.	.	.	.	.	0
Asteraceae sp.	.	.	.	.	.	0	.	.	.	6	.	1.2	.	.	.	.	.	0	.	.	.	.	.	0
Solanum nigrum	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0	.	.	3	.	.	0.6
Amaranthus cf. retroflexus	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	1	0.2
Chenopodium cf. botrys	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	1	0.2
Digitaria sanguinalis	.	.	.	.	.	0	.	.	.	.	.	0	.	.	.	.	.	0	1	.	.	.	.	0.2
Medicago lupulina	.	.	.	.	.	0	.	.	.	1	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0
Rubus caesius	.	.	.	.	.	0	1	.	.	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0
Senecio vulgaris	.	.	.	.	.	0	.	.	1	.	.	0.2	.	.	.	.	.	0	.	.	.	.	.	0
<u>Further taxa</u>																								
Unidentified	.	.	.	.	.	0	.	.	.	.	1	0.2	.	.	.	.	.	0	.	.	.	.	.	0

When the cover-abundance indices of the individual species were considered, weakly significant ($p<0.05$, Wilcoxon test; * in Tab. 2) enhancements in the trail vegetation as compared to the control vegetation were found on paddock A for five annual species: *Medicago minima* (threatened species, KORNECK et al. 1996), *Trifolium campestre, Cerastium semidecandrum, Erodium cicutarium, Vulpia myuros*; on paddock KA for three annuals (*M. minima, Arenaria serpyllifolia* agg.*, Veronica arvensis*) and on paddock K for one annual (*T. campestre*). Four taxa showed significantly ($p<0.05$) lower cover-abundance on trails as compared to controls, all of which are perennials. One of those, the moss *Hypnum cupressiforme* var. *lacunosum*, showed a significant decrease on the trail plots on all paddocks; in addition, *Corynephorus canescens* (threatened species, KORNECK et al. 1996) decreased in cover-abundance on the trail plots in paddock K, *Festuca brevipila/ovina* agg. in paddock KA and *Elymus athericus* in paddock A.

Another 20 (in total: 25; including the species mentioned above) of the altogether 78 identified plant taxa (*Bromus* sp. seedlings and "further Acrocarpi" not considered) showed a tendency to decrease or increase in their degree of presence on trails (differences of more than 20 percentage points between trail and control plots in Tab. 2). Among those taxa 8 out of 10 (in total: 13 out of 15) annual species were positively affected by trail occurrence, whereas half of the perennial species (5 taxa, including the cryptogams *Brachythecium albicans*, *Cladonia furcata+rangiformis* and *Peltigera rufescens*) showed reduced presence on trail plots as compared to control plots. One further species, *Medicago falcata*, showed increased or decreased presence on trail plots, depending on vegetation type.

The census of plant individuals for two threatened species demonstrated that numbers of *Silene conica* increased significantly on trail plots in paddock K (365 ± 150 individuals on trails versus 163 ± 103 i. on controls, mean ± mean absolute deviation from the mean; $p=0.028$, Wilcoxon test) while there was no significant difference for *Phleum arenarium*.

Overall, the results indicate a regressive successional trend in the vegetation on sheep trails.

4.3 Soil seed bank of sheep trails and control plots

The soil seed-bank data are shown in Tab. 3. As expected, the seed banks of the upper soil layer show clearly higher values of species diversity and seed density than the seed banks of the lower soil layer (Tables 3 and 4). On the level of plant community, for species number and total seed density no trail effect was found (Tab. 4). On the species level, two taxa, *Chenopodium album* agg. and *Veronica verna*, showed significantly increased seed densities in trail topsoils compared to control-plot topsoils; since this was not true for the subsoils, there was a significant interaction between trail and soil depth (Tab. 5; for interpretation of trail effects see Section 3.6.2).

Tab. 4a: Mean species numbers and seed densities per soil layer with mean absolute deviations from the mean (n = 5).

Tab. 4b: Tests of fixed effects on soil seed-bank data (species numbers, seed numbers) of the data set of 4a by mixed linear models (SAS 9.1, Proc Mixed). Significant results (p<0.05) are displayed in bold. Nd.f.: numerator degrees of freedom, Dd.f.: denominator degrees of freedom.

a)	Number of species		Seeds m^{-2}	
Soil layer (cm)	1-6	11-16	1-6	11-16
Sheep trail	22 ± 3	7 ± 2	1577 ± 368	153 ± 76
Control	23 ± 3	8 ± 2	1849 ± 1061	244 ± 79

b)			Number of species		Number of seeds	
	Nd.f.	Dd.f.	F value	p	F value	p
Sheep trail	1	12	0.70	0.4203	2.86	0.1167
Soil depth	1	12	185.75	**<0.0001**	183.69	**<0.0001**
Sheep trail x soil depth	1	12	0.08	0.7856	2.34	0.1521

Tab. 5a: Mean seed densities per soil layer (with mean absolute deviations from the mean; n = 5) for plant species which show significant effects with respect to the interaction term "sheep trail x soil depth". T: sheep trail, C: control.

Tab. 5b: Tests of fixed effects on seed numbers of the data set of 5a by mixed linear models (SAS 9.1, Proc Mixed). Significant results (p<0.05) are displayed in bold type. Nd.f.: numerator degrees of freedom, Dd.f.: denominator degrees of freedom.

a)		Seeds m^{-2}	
Soil layer (cm)		1-6	11-16
Chenopodium album agg.	T	78 ± 24	76 ± 41
	C	43 ± 30	120 ± 38
Veronica verna	T	13 ± 6	0
	C	2 ± 4	0

b)			Chenopodium album agg.		Veronica verna	
	Nd.f.	Dd.f.	F value	p	F value	p
Sheep trail	1	12	0.66	0.4331	6.45	**0.0260**
Soil depth	1	12	4.42	0.0573	15.22	**0.0021**
Sheep trail x soil depth	1	12	6.77	**0.0231**	6.45	**0.0260**

5 Discussion

5.1 Spatial structure and extent of sheep trails

The area occupied by sheep-trail systems on sand grassland paddocks is remarkably large. There is a trend towards decrease in the proportion of sheep trails with respect to the total paddock area with increasing productivity. The functional trail system per paddock might be independent of productivity: the nature of the ground or vegetation may prevent trails from being floristically and structurally visible at all places within a paddock (especially less-used trails in consolidated patches; see also LANGE 1969). In our study system, sheep obviously feed at sites not necessarily linked to trails. The main function of the studied trails is to connect resources (standing phytomass, water, salt) and requisites (shade-producing structures) essential for sheep. This is in line with existing knowledge (PORZIG & SAMBRAUS 1991). Several times we observed sheep walking one behind the other on trails. For instance, they directly walk from a shady place to the water point, then return to shade or start grazing at a non-trail area. In rough terrain, ruminants develop "least-effort pathways" (GANSKOPP et al. 2000); therefore in exposed areas a dense system of slope-parallel trails develops, with the trails functioning as feeding paths. The trails studied here, in a level area, are exclusively "opening-up" structures to provide access to essential resources, and are used exclusively for walking. Several authors stressed the importance of the position of water and salt sources as a management tool to control pasture use by livestock species (GANSKOPP 2001, PUTFARKEN et al. 2008). As was shown by LANGE (1969) in an arid environment (Australia), development of tangential trails is extremely rare in the piosphere; the same was true for two paddocks in our system. According to SQUIRES (1974) the speed of sheep locomotion in approaching a water source is increased seven-fold in comparison to the grazing time (4.3 km h^{-1} versus 0.6 km h^{-1}).

5.2 Vegetation of sheep trails and control plots

We found a regressive successional tendency on sheep trails, especially in mid-successional stages (KA, A; see also SCHWABE et al. 2004). This is in accordance with our hypothesis. Pleurocarpous mosses such as *Hypnum cupressiforme* var. *lacunosum* decreased on trail plots compared to controls; this species is generally an indicator for more consolidated microhabitats and suppresses generative regeneration of vascular plant species (EICHBERG et al. 2007). Amongst cryptogams, *Cladonia* species and *Peltigera rufescens* also decreased in their degree of presence on trail plots. The threat to lichen communities presented by higher trampling pressure was already shown by BIERMANN & DANIËLS (1997). In paddock A three perennial vascular plant species had higher presence values on the trail plots (*Cerastium arvense, Medicago falcata, Plantago lanceolata*) of which *P. lanceolata* and *C. arvense* are known to have good or moderate trampling resistance (DIERSCHKE & BRIEMLE 2002). All seven annual species with significantly higher cover-abundance on trails build up short-term persistent soil seed banks (seeds viable for 1 a to <5 a, according to THOMPSON et al. 1997) in the study system (EICHBERG et al. 2006); in addition, all are endozoochorously dispersed by sheep (EICHBERG et al. 2007) and at least four species are also sheep-epizoochorously dispersed (*A. serpyllifolia* agg., *E. cicutarium*, *M. minima*, *V. myuros*; WESSELS et al.

2008). There is an input of faeces on trails because excretion behaviour is not fixed to particular places in the case of sheep (as in the case of equids), it also occurs while walking (MEYER 1984). In dry open ecosystems on sandy soils evidence was found that sheep trampling can increase seedling emergence by burial of seeds (*Jurinea cyanoides*, EICHBERG et al. 2005). An experiment of ROTUNDO & AGUIAR (2004) has shown that sheep trampling increased seedling emergence of *Bromus pictus* in an arid Patagonian steppe. Factors causing losses of unburied seeds are above-ground predation and desiccation of germinating seeds (EICHBERG et al. 2005).

5.3 Soil seed bank of sheep trails and control plots

Since we did not detect a trail effect on the level of plant community (in contrast to our hypothesis), we conclude that there is a high "robustness" of the studied soil seed banks. Possibly there is also a lag-time in the response of the soil seed bank to the formation of a trail. However, in the case of an extensive grazing regime with moving livestock, as studied here, a seed-bank effect might be rare because paddock boundaries are varied from time to time, for nutritional or conservational reasons. There is also evidence from other open grazing lands, e. g. in arid regions, that soil seed banks can be relatively robust against ungulate impact (KINLOCH & FRIEDEL 2005). However, to our knowledge there are no further studies on the soil seed banks of in particular livestock trails so far. Two annual taxa (*Chenopodium album* agg., *Veronica verna*) showed a significant positive influence of trails on their topsoil seed densities, but since multiple statistical tests were carried out, these results should be interpreted with care. *Chenopodium album* is well known to build up long-term persistent soil seed banks (seeds viable for ≥5 a) with maximal values of >660 a (THOMPSON et al. 1997). According to the data of KROLUPPER & SCHWABE (1998), EICHBERG et al. (2006) and BOES (2006) *Chenopodium album* agg. (comprising *Chenopodium album* and *C. strictum* ssp. *striatiforme*) is one of the most frequent taxa in soil seed banks of inland sand ecosystems in the Darmstadt region. In the KA and A vegetation types of the studied ecosystem, *Chenopodium album* agg. had a higher abundance in the above-ground vegetation on donkey wallows than on control plots (SÜSS & SCHWABE 2007). However, according to our long-term data for permanent vegetation plots (10 years, n. p.), this ruderal plant taxon establishes in disturbed microhabitats if the abiotic conditions (dry periods) are not too extreme.

6 Conclusion

Our results regarding inland sand grasslands show that the linear movement of sheep on trails is driven by the spatial distribution of essential resources and requisites (e. g., water and shade). In our extensive pasture-management system, sheep trails represent a stripe-shaped microhabitat with regressive successional tendencies in the above-ground vegetation. Mostly habitat-typical annual plant species are supported by the presence of trails. Trails are structures that concentrate various ecological processes, such as mechanical disturbance by trampling and activation of the soil seed bank, intermingled with effects of in particular endozoochorous dispersal by sheep (EICHBERG et al. 2007, WESSELS 2007). As soon as they are no longer used they revert to their former structure within a time window of a few years. HASSE & DANIËLS (2006) reported a rapid recapture of gaps by *Corynephorus*-grassland after disturbance (structurally comparable to our K-plots). If there is intensive management, trails of course produce high proportions of bare soil and can cause severe erosion on slopes (WALKER & HEITSCHMIDT 1986). Furthermore, even in the case of extensive management any heavy disturbance of biological soil crusts (comprising Cyanobacteria, Algae, lichens and mosses) should be avoided (HACH et al. 2005, LANGHANS et al. 2009); this is possible by choosing optimal places for water and mineral supply, and in some cases it might be necessary to exclude patches with biological soil crusts from grazing.

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