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Contrasting response of vascular plant and bryophyte species assemblages to a soil-disturbing ecosystem engineer in calcareous grasslands

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ABSTRACT

Species-rich grasslands are highly threatened by land-use change, including fertilization, land-use intensification and abandonment. These changes evoke a loss of structural heterogeneity. Aside from specific management measures to increase structural heterogeneity, small-scale patches of different vegetation within grasslands are promoted naturally by soil-disturbing ecosystem engineers. The aim of this study is to analyse the importance of *Lasius flavus* nest mounds for increasing structural and functional diversity in vascular plant and bryophyte assemblages within Central European calcareous grasslands.

Our study clearly revealed that the mound-building activity of *L. flavus* ants in calcareous grasslands alters soil conditions and vegetation structure. Ant mound soil samples had higher potassium and phosphorus levels than control samples in the matrix vegetation. Ant mounds, in general, and the south-facing sides, in particular, represented highly disturbed microsites with open and low-growing vegetation containing high proportions of bare ground. In contrast, the north-facing sides were characterized by transient vegetation between the dense matrix and the open south-facing sides. However, the effects of soil disturbance by ants were different for vascular plant and bryophyte species assemblages. In vascular plants, differences among the three sample groups were less pronounced; in bryophytes, nearly all parameters differed.

All in all, the occurrence of *L. flavus* increases vegetation heterogeneity within grasslands and, therefore, plays an important role in supporting species richness of both plants and animals in calcareous grasslands. This holds true in particular for fallow sites, where ant mounds often represent the only sites of open vegetation.

1. Introduction

Semi-natural grasslands that originated from traditional land use play an important role for biodiversity conservation throughout Europe (e.g. Dengler et al., 2014; Nilsson et al., 2013; Sutcliffe et al., 2015; Wilson et al., 2012). Due to the long tradition of low-intensive land use they are characterized by structural heterogeneity and high species richness (Diacon-Bolli et al., 2012; Veen et al., 2009). However, species-rich grasslands are highly threatened, most severely by changes in land use, fragmentation and climate change (e.g., Bobbink et al., 2010; Eriksson et al., 2002; Field et al., 2014; Fridley et al., 2016; Gaujour et al., 2012; Krämer et al., 2012b; Sengl et al., 2016). With respect to land use change the most prominent threats to grassland biodiversity include fertilization, an increase in land use intensity and succession as a result of long-term abandonment. These changes evoke a loss of structural heterogeneity, favouring highly competitive plant species that displace rare, endangered species that are less competitive (Enyedi et al., 2008; Jacquemyn et al., 2011; Wesche et al., 2012).

By promoting less-competitive plant species due to a reduced interspecific competition and higher light availability, disturbance and small-scale patches of bare ground are highly relevant for the conservation of both vascular plant and bryophyte diversity within grasslands (Fleischer et al., 2013; Frei et al., 2012; Müller et al., 2014; Preston et al., 2009; Tschöpe and Tielbörger, 2010). Furthermore, small-scale patches of bare ground are key structures for the reproduction of thermophilous arthropod species within

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grasslands, as they offer favourable microclimatic conditions (e.g., Krämer et al., 2012a; Streitberger and Fartmann, 2013; Warren and Büttner, 2008; Wünsch et al., 2012). Due to the large-scale and continent-wide loss of structural heterogeneity the mechanical creation of bare-ground patches is already recommended as a relevant method for grassland restoration and promotion of endangered, less-competitive plant and disturbance-dependent arthropod species (e.g., Ödman et al., 2012; Schnoor and Olsson, 2010; Wagner et al., 2016).

Aside from various management techniques, structural heterogeneity within grasslands is generated naturally by the soil-disturbing activities of ecosystem engineers such as rodents, wild boars or ants and moles, which occur frequently within Central European grasslands (Milton et al., 1997; Seifan et al., 2010; Streitberger and Fartmann, 2013; Streitberger et al., 2014). Due to the strong impact on vegetation structure, knowledge on the influence of soil-disturbing ecosystem engineers on species assemblages is relevant for understanding interspecific relationships and drivers of biodiversity (e.g., Augustine and Baker, 2013; Questad and Foster, 2007; Sasaki and Yoshihara, 2013). In Central European semi-natural grasslands, the yellow meadow ant (*Lasius flavus*) is a common ant species (Seifert, 1993, 2007), which acts as an ecosystem engineer through its mound-building activity. The mounds created by this species take over a relevant role for biodiversity conservation. For example, they function as important microhabitats for the reproduction of thermophilous lepidopteran species (Streitberger and Fartmann, 2015, 2016). Concerning vegetation composition on *L. flavus* mounds within grasslands several studies showed that vegetation on ant mounds represents sub-samples of the matrix vegetation with a dominance of plant species adapted to this kind of disturbance (Dean et al., 1997; Dauber et al., 2006; King, 1977a,b,c; Lenoir, 2009). Especially growth form and reproduction characteristics of vascular plants determine species assemblages on ant mounds (Dauber et al., 2006; King, 1977c; Kovář et al., 2001; Lenoir, 2009). Furthermore, analyses revealed that soil seed banks within the mounds differ from the matrix vegetation (Dauber et al., 2006; Dostál, 2005; King, 2007; OíGrady et al., 2013). However, studies with a high sample size, addressing the differences in the driving forces in vegetation composition and functional traits of both vascular plant and bryophyte assemblages on north- and south-facing sides of ant mounds within semi-natural Central European grasslands are lacking so far.

The aim of this study is to analyse the importance of *L. flavus* nest mounds for increasing structural and functional diversity in vascular plant and bryophyte assemblages within Central European calcareous grasslands by distinguishing between the north- and south-facing sides of the mounds. We expected that small-scale differences in vegetation composition exist between the two sides due to differences in microclimate and ant activity. In contrast to vascular plants, we expected bryophytes to show more distinct species assemblages according to the different sides of the ant mound and matrix vegetation, due to small-scale differences in vegetation structure, light availability, and microclimate. All in all, the following questions are addressed in this study:

- How do soil conditions and vegetation structure differ between the north- and south-facing sides of ant mounds and the surrounding matrix vegetation?
- How does species composition differ among the three sample types with respect to vascular plants and bryophyte species?
- Which functional traits are favoured by this type of small-scale disturbance?
- Which nature conservation aspects can be derived from the results of this study?

2. Study area

The study area, the Diemel Valley, is located in Central Germany at the border of North Rhine-Westphalia and Hesse (51°22′N/8°38′E and 51°38′N/9°25′E). The area is characterized by a suboceanic climate (Müller-Wille, 1981). According to elevation, mean annual values of temperature range from 6.5 to 9 °C and of precipitation from 600 to 1000 mm (Fartmann, 2004). Large parts of the hillsides along the Diemel consist of limestone. Because of a long tradition of sheep grazing, calcareous grasslands are still frequent within the study area. Nowadays, about 55% of these grasslands are still actively managed, mainly by traditional rough sheep grazing (Fartmann, 2004). *Lasius flavus* occurs frequently within calcareous grasslands of the study area, especially within fallow patches.

3. Methods

3.1. Vegetation and soil sampling

For sampling of vegetation we randomly selected in each of the 12 studied calcareous grassland patches a 20 m × 20 m sized site with occurrence of *L. flavus* on southwest- and south-facing slopes (mean aspect ± SD: 166° ± 34°). Sampling was carried out at the beginning of June 2014. Within every site 10 ant mounds of *L. flavus* with a minimum height of 20 cm were randomly selected for recording vascular plants. The minimum distance between selected ant mounds was 2 m. For every selected ant mound three vegetation relevés were analysed on 30 cm × 30 cm plots. Two plots were placed on the ant mound, one within the centre of the south-facing side and one within the centre of the north-facing side of the mound (hereafter referred to as ANTS and ANTN, respectively). Additionally, one plot was recorded within the matrix vegetation one metre north of the ant mound (hereafter referred to as CONTROL). All in all, 30 samples of vascular plants were collected per site and patch, accounting for a total of 360 samples. Every second triple of samples ($N = 180$) was selected for additional recording of bryophyte species. However, bryophytes were only present in 84 ($N_{ANTS} = 32$, $N_{ANTN} = 52$) of the 120 ant mound samples. In contrast, all 60 control samples were occupied by bryophyte species. For further analyses, we distinguished between presence ($N = 32$) and absence ($N = 28$) ant mound south samples. For every plot, the cover of every species was estimated using levels of 5%. Coverage degrees below 5% were differentiated by levels of 3% (species with coverage between 1 and 5%) and 1% (species with coverages $\leq$1%). In addition to species sampling, the following vegetation structure characteristics were recorded: cover of herbs, grasses, bryophytes, litter and bare ground, and vegetation height. Furthermore, ant mound height and width (=longest diameter) were recorded for the 60 ant mound samples which were selected for bryophyte analysis.

Additionally, soil samples were collected within every fifth triple of samples, accounting for a total of 72 samples (24 samples per group). Samples were taken with a soil corer at a soil depth of ten centimetres. Within every plot, three samples were taken and mixed for further analyses. Prior to analyses, samples were air-dried and sieved (2 mm mesh size) and ants, eggs and pupae of ants were removed by hand. The samples were analysed for soil reaction ($CaCl_2$), soluble phosphorus (P) (spectrophotometer, Cadas 200, Düsseldorf, DE), and potassium (K) (flame photometer, Jenway PFP7, Burlington, US). After milling, the soil samples were analysed for percentage total nitrogen (N) and carbon (C) using an elemental auto-analyser (NA 1500, Carlo Erba, Milan, IT).

3.2. Data analysis

To evaluate vascular plants, the following parameters were analysed according to the Biolflor database (Klotz et al., 2002):

proportion of annual species, proportion of rosette species and reproduction type. For analysing reproduction type the categories were indexed by using 0.25 levels (0: vegetative reproduction; 0.25: predominantly vegetative reproduction, rarely by seeds; 0.5: vegetative and sexual reproduction; 0.75: reproduction predominantly by seeds, rarely, vegetatively; 1: reproduction by seeds). Furthermore, the following trait data were extracted from the LEDA database (Kleyer et al., 2008): seed longevity index according to Thompson et al. (1998) and dispersule weight. For every sample, mean trait values were calculated by weighting the species values by species cover. For bryophyte data we analysed life strategy according to During (1992) from Dierßen (2001). We thus distinguished among annual shuttle species, colonists and perennials, which represented 99% of the species scores. For statistical analysis, life strategy was indexed (0: annual shuttle species; 0.5: colonists, 1: perennials) and mean values were calculated for each sample by weighting by species cover. Furthermore, we analysed mean thallus length for every sample according to the BRYOATT database (Hill et al., 2007), also weighted by species cover. In cases of missing values, we used data from Frahm and Frey (2004) or Smith (2004) by considering maximum length values. In addition to that, we analysed growth form by calculating the proportion of acrocarpous species according to Frahm and Frey (2004). Additionally, mean weighted indicator values for light, soil reaction, and moisture were calculated according to Ellenberg and Leuschner (2010) for vascular plants and bryophytes, separately. For vascular plants we also calculated mean weighted indicator value for nitrogen.

Significant differences between the mean values of the sampling groups were detected by applying generalised linear mixed-effects models (GLMM). For comparisons among ant mound north and south samples as well as control samples, ant mound within patch was used as the random effect. For proportional data proportional binomial GLMM were applied. In the case of overdispersion, random individual-level effects were integrated within the random factor. For other data, we used Poisson models and negative binomial models in the case of overdispersion. Bonferroni corrections were considered in cases of multiple testing.

To analyse which parameters determine the occurrence of bryophytes on the southern sides of ant mounds, a GLMM was performed. A binomial model was calculated for comparing presence and absence samples. Vegetation structure and ant mound structure (width/height) parameters were included as explanatory variables within the model. Furthermore, we included land use (grazed/unused) as a nominal variable. Patch served as the random factor. Site selection was balanced with the same amount of sites and ant mounds, respectively, per category. Only non-intercorrelated variables (Spearman correlation coefficient $|r| < 0.6$) were included within the model. The selection of the final model depended on backward selection using likelihood ratio tests with a significance level of $\alpha = 0.05$.

Table 1
Mean values ± SD of soil analyses for ant mound south (ANTS), ant mound north samples (ANTN), and control samples (CONTROL) ($N = 24$ per group). Comparison between groups by GLMM, cf. method section for details. n.s. not significant. Significant differences are based on $P < 0.05$.

Parameter	ANTS	ANTN	CONTROL	*P*
pH	7.2 ± 0.4	7.2 ± 0.4	6.9 ± 0.9	n.s.
C (%)	6.8 ± 2.1	6.7 ± 2.1	7.9 ± 2.2	n.s.
N (%)	0.5 ± 0.1	0.5 ± 0.1	0.5 ± 0.1	n.s.
P (mg/100 g)	0.8 ± 0.3	0.6 ± 0.5	0.5 ± 0.3	S > C
K (mg/100 g)	28.4 ± 8.5	26.9 ± 9.0	8.8 ± 7.5	S, N > C

Table 2
Mean values ± SD of all numerical vegetation structure parameters of (a) vascular plant and (b) bryophyte species relevés for ant mound south (ANTS) and north (ANTN) samples as well as control samples (CONTROL). (a) $N = 120$ per group; (b) ant mound south samples ($N = 32$), ant mound north samples ($N = 52$) and control samples ($N = 60$). Comparison between groups by GLMM, cf. method section for details. Significant differences are based on $P < 0.05$.

Parameter	ANTS	ANTN	CONTROL	*P*
(a) Vascular plant relevés				
Cover (%)				
Herbs	54.8 ± 20.2	45.5 ± 18.6	54.3 ± 14.7	N < S, C
Grasses	30.1 ± 15.0	37.6 ± 13.7	39.0 ± 12.9	S < N, C
Bryophytes	2.4 ± 4.4	14.1 ± 17.4	16.4 ± 13.1	S < N < C
Litter	17.8 ± 10.6	28.0 ± 13.2	43.3 ± 16.1	S < N < C
Bare ground	19.5 ± 13.2	12.3 ± 11.3	0.7 ± 1.6	S > N > C
Vegetation height (cm)	8.3 ± 2.8	10.0 ± 3.3	11.8 ± 4.3	S < N < C
(b) Bryophyte relevés				
Cover (%)				
Herbs	48.9 ± 20.9	42.0 ± 18.9	54.8 ± 13.9	N < C
Grasses	30.7 ± 14.8	39.1 ± 14.5	37.7 ± 12.9	S < N, C
Bryophytes	5.4 ± 5.6	19.8 ± 18.2	16.0 ± 11.9	S < N, C
Litter	19.4 ± 11.5	29.9 ± 13.2	42.6 ± 16.6	S < N < C
Bare ground	19.5 ± 13.7	9.8 ± 10.5	0.5 ± 1.1	S > N > C
Vegetation height (cm)	8.1 ± 1.9	10.1 ± 3.7	11.5 ± 4.3	S < N, C

Furthermore, indicator species analyses (ISA) were carried out for vascular plant and bryophyte samples in order to identify the indicator species for each sampling group (Dufrêne and Legendre, 1997). Vegetation composition was analysed by applying non-metrical multidimensional scaling (NMDS) with the Bray-Curtis distance as a distance measure and a maximum number of 100 random starts in the search for a stable solution. For vascular plant samples, only species that appeared in a minimum of five plots were included in the analyses. For bryophyte samples only species occurring at least three times within the data set were used for NMDS. Vegetation structure and trait parameters were subsequently fitted onto the ordination. Only variables with significant differences between the groups were considered for ordination. In cases of high intercorrelation (Spearman correlation coefficient $|r| > 0.6$) among variables, one of them was excluded from the analysis (Fielding and Haworth, 1995). For vascular plant ordination species number, grass cover and the indicator values for nitrogen and moisture were excluded from the analysis, as these variables were strongly intercorrelated with several others (cf. Appendix A). For bryophyte species the cover of herbs, vegetation height, length and the proportion of acrocarpous species were excluded from the analysis as these were strongly intercorrelated with other variables (cf. Appendix A).

GLMM and NMDS were performed using R 3.2.3 (R Development Core Team, 2016). For Poisson and binomial GLMM we used the lme4-package (Bates et al., 2015) and for negative binomial GLMM the glmmADMB-package (Fournier et al., 2012). NMDS ordinations were performed with the packages MASS (Ripley et al., 2015) and vegan (Oksanen et al., 2016). ISA was carried out by using PC-ORD 5.0 (MjM Software Design, Gleneden Beach, OR, US). The species names of vascular plants and bryophytes are according to Wisskirchen and Haeupler (1998) and Koperski et al. (2000), respectively.

4. Results

4.1. Soil conditions and vegetation structure

Ant mound soil samples had a significantly higher potassium content compared to CONTROL samples (Table 1). Furthermore, phosphorous content was significantly higher for ANTS compared to CONTROL samples. In contrast, no differences were detected for soil reaction or the proportion of carbon and nitrogen.

Vegetation height and cover were significantly lower for ant mounds as compared to CONTROL samples (Table 2a). From CONTROL to ANTN to ANTS vegetation height as well as the cover of bryophytes and litter decreased significantly, while the cover of

Table 3
Statistics of GLMM: binomial, relationship between the occurrence of bryophytes on ant mound south samples and vegetation and plot characteristics. Presence ($N=32$) and absence samples were included ($N=28$). The following variables entered into the analysis were not significant: land use, ant mound height, ant mound width. Non-significant predictors were excluded from the model by stepwise backward-selection ($P>0.05$). Pseudo R^2 (Nagelkerke) = 0.14.

Parameter	Estimate	SE	Z	*P*
Cover of herbs	−0. 0396	0. 01956	−2.024	*
Vegetation height	−0. 3372	0. 15972	−2.111	*

[*] $P<0.05$.

Table 4
Mean values ± SD of all functional traits and indicator values of (a) vascular plant and (b) bryophyte species relevés for ant mound south (ANTS) and north (ANTN) samples as well as control samples (CONTROL). (a) $N=120$ per group; (b) ant mound south samples ($N=32$), ant mound north samples ($N=52$) and control samples ($N=60$). Comparison between groups by GLMM, cf. method section for details. n.s. not significant. Significant differences are based on $P<0.05$.

Parameter	ANTS	ANTN	CONTROL	*P*
(a) Vascular plant relevés				
Number of species	6.5 ± 2.2	8.5 ± 3.0	16.0 ± 3.8	S < N < C
Functional traits				
Rosette species (%)	3.0 ± 6.1	4.7 ± 7.7	15.0 ± 7.0	S, N < C
Cover of annual species (%)	3.4 ± 7.5	3.1 ± 5.7	1.8 ± 4.8	n.s.
Dispersule weight (mg)	1.3 ± 0.7	1.6 ± 0.9	2.4 ± 3.2	S < N < C
Reproduction type[a]	0.6 ± 0.1	0.6 ± 0.1	0.6 ± 0.1	n.s.
Seed longevity index	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.0	n.s.
Indicator values				
Light	7.4 ± 0.3	7.2 ± 0.4	7.2 ± 0.3	n.s.
Moisture	3.7 ± 0.3	3.8 ± 0.2	3.9 ± 0.2	S < C
Soil reaction	7.4 ± 0.5	7.3 ± 0.4	7.4 ± 0.4	n.s.
Nitrogen	2.2 ± 0.6	2.5 ± 0.6	2.9 ± 0.5	S < N < C
(b) Bryophyte relevés				
Number of species	2.9 ± 1.7	2.5 ± 1.9	2.9 ± 1.6	n.s.
Functional traits				
Acrocarpous species (%)	68.5 ± 41.5	18.0 ± 30.7	9.2 ± 17.7	S > N, C
Life strategy[b]	0.7 ± 0.2	0.9 ± 0.2	1.0 ± 0.0	S < N, C
Length (mm)	52.9 ± 46.2	108.7 ± 38.1	111.5 ± 34.7	S < N, C
Indicator values				
Light	7.4 ± 0.8	6.5 ± 1.1	6.6 ± 1.2	S > N, C
Moisture	3.8 ± 1.4	4.1 ± 0.9	3.9 ± 1.0	n.s.
Soil reaction	6.8 ± 0.8	6.0 ± 1.1	6.2 ± 1.3	S > N, C

[a] Scaled from 0 (vegetative reproduction) to 1 (reproduction by seeds).
[b] Scaled from 0 (annual species) to 1 (perennial species).

bare ground increased significantly (Table 2a). Herb cover was significantly lower for ANTN; grass cover was significantly lower for ANTS.

Structural differences in the bryophyte relevés resembled those described above (Table 2b). The cover of bare ground increased, and the cover of litter decreased significantly from CONTROL to ANTN and ANTS. Vegetation height and the cover of grasses and bryophytes were significantly lowest on ANTS compared to the two other sample groups. Herb cover was significantly lower on ANTN than on CONTROL. GLMM revealed that the probability of the occurrence of mosses on the southern side of ant mounds increased significantly by a low growing herb layer and a lower cover of herbs (Table 3).

4.2. Trait analysis and species composition

The species richness of vascular plants decreased significantly from CONTROL to ANTN to ANTS (Table 4a). Significant differences of functional traits and indicator values between the three sample groups were only found for a few parameters in the vascular plant relevés (Table 4a). The dispersule weight and the nitrogen indicator value decreased from CONTROL to ANTN and ANTS. In contrast, annual species cover increased, but not significantly. CONTROL had the highest values for the proportion of rosette species and moisture indicators compared to ant mound samples and ANTS, respectively.

In contrast to vascular plant species numbers, bryophyte species numbers did not differ among the three sample types (Table 4b). Moreover, in the bryophyte relevés, significant effects among the sample groups were observed for nearly all analysed parameters (Table 4b). In most cases, ANTS differed from the other two sample groups. ANTS were characterized by a greater proportion of shortly growing, acrocarpous and ephemeral species, and had higher light and soil reaction indicator values.

ISA identified significant vascular plant indicator species for all three sampling groups (Table 5a). Control samples had many indicator species, among them several calcareous grassland species such as *Carex caryophyllea*, *Centaurea scabiosa*, *Cirsium acaule*, *Leontodon hispidus*, *Potentilla tabernaemontani*, *Prunella grandiflora*, *Ranunculus bulbosus*, *Sanuguisorba minor* or *Scabiosa columbaria*. In contrast, ant mounds were characterized by few indicator species. *Arenaria serpyllifolia* and *Thymus praecox* were the only indicator species for ANTS, *Brachypodium pinnatum*, *Medicago lupulina*, *Pimpinella saxifraga* and *Thymus pulegioides* were indicator species for ANTN. Widespread species occurring frequently within more than one sampling group were, amongst others, *Galium verum*, *Hippocrepis comosa* or *Koeleria pyramidata* (Appendix B).

In contrast, ant mounds were rich in bryophyte indicator species (Table 5b). This was especially the case for ANTS. Aside from *Barbula* and *Bryum* species, *Pottia lanceolata* and *Weissia* species were identified as indicator species. The indicator species for ANTN were *Plagiomnium affine* and *Scleropodium purum*. CONTROL was characterized by *Ctenidium molluscum* and *Hypnum cupressiforme*. *Calliergonella cuspidata* and *Homalothecium lutescens* were the most widespread species occurring frequently within more than one sampling group (Appendix B).

The NMDS ordination of vascular plant relevés showed a clear separation of ant mound samples on the one hand and CONTROL on the other hand along the first axis (Fig. 1a) with several environmental variables showing significant correlations, especially with the first axis (Table 6a). Ant mound and control samples were separated by a vegetation structure gradient and clear differences in functional traits. Ant mounds were characterized by a higher proportion of bare ground, while CONTROL samples exhibited denser, higher and litter-rich vegetation, a higher proportion of rosette species, and species with greater dispersule weight.

With respect to bryophyte relevés, NMDS ordination showed a clear separation of species composition of ANTS on the one hand and ANTN and CONTROL on the other hand (Fig. 1b). This separation was attributed to a gradient in vegetation structure and differences in life strategies along the first axis (Fig. 1b, Table 6b). ANTS were associated with a high proportion of bare ground. CONTROL was characterized by a denser vegetation and more perennial species. ANTN had an intermediate position.

5. Discussion

Our study clearly revealed that the mound-building activity of *Lasius flavus* ants in calcareous grasslands alters soil conditions and vegetation structure. Ant mound soil samples had a higher potassium and phosphorus content compared to control samples in the matrix vegetation. Ant mounds, in general, and the south-facing sides, in particular, represented highly disturbed microsites with open and low-growing vegetation, containing high proportions of bare ground. In contrast, the north-facing sides were characterized by a transient vegetation between the dense matrix and the open south-facing sides.

Table 5
Indicator species of (a) vascular plants and (b) bryophytes of ant mound south (ANTS), ant mound north (ANTN) and control (CONTROL) samples (results of ISA, Dufrêne and Legendre, 1997). Species are sorted by "IV" for the considered sample type. (a) for ANTS and ANTN all species with significant indicator values are shown. For CONTROL only species with significant indicator values above the average indicator value (=10.9) are shown. (b) only species with a minimum occurrence of three in the data set are shown. IV = indicator value, ra = relative abundance, rf = relative frequency. Grey shaded values: Species are indicator species for this sample type. (a) $N = 120$ per group; (b) ant mound south samples ($N = 32$), ant mound north samples ($N = 52$) and control samples ($N = 60$). $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

Species		ANTS			ANTN			CONTROL		
	P	IV	ra	rf	IV	ra	rf	IV	ra	rf
(a) Vascular plant relevés										
Arenaria serpyllifolia	**	**11**	75	14	.	24	15	.	1	2
Thymus praecox	***	**34**	62	54	.	29	51	.	9	38
Brachypodium pinnatum	***	.	34	98	**40**	41	98	.	25	90
Medicago lupulina	**	.	35	16	**15**	51	29	.	14	12
Pimpinella saxifraga	*	.	14	28	**25**	45	55	.	41	60
Thymus pulegioides	*	.	48	39	**20**	44	45	.	8	27
Achillea millefolium	***	.	2	3	.	28	8	**13**	69	19
Briza media	***	.	1	2	.	8	8	**39**	91	43
Carex caryophyllea	***	.	5	6	.	10	9	**59**	85	69
Carex flacca	***	.	3	8	.	1	6	**72**	91	76
Centaurea jacea	***	.	0	0	.	10	7	**16**	90	22
Centaurea scabiosa	***	.	0	0	.	3	3	**20**	97	17
Cirsium acaule	***	.	0	0	.	0	0	**32**	100	32
Danthonia decumbens	***	.	0	0	.	1	1	**14**	99	14
Galium pumilum	*	.	28	16	.	27	16	**14**	45	30
Helictotrichon pratense	*	.	21	25	.	37	30	**20**	42	47
Hieracium pilosella	***	.	5	10	.	9	13	**40**	86	47
Leontodon hispidus	***	.	1	1	.	9	7	**31**	90	34
Leucanthemum vulgare	***	.	1	1	.	18	6	**13**	82	16
Linum catharticum	***	.	0	0	.	25	4	**13**	75	18
Lotus corniculatus	***	.	15	8	.	29	16	**21**	56	37
Plantago lanceolata	***	.	4	3	.	32	8	**22**	64	35
Plantago media	***	.	0	0	.	12	2	**16**	88	18
Potentilla tabernaemontani	***	.	23	17	.	22	17	**26**	55	48
Prunella grandiflora	***	.	0	1	.	12	7	**18**	88	20
Ranunculus bulbosus	***	.	1	1	.	11	9	**35**	88	40
Sanguisorba minor	***	.	2	7	.	5	18	**66**	93	71
Scabiosa columbaria	***	.	3	4	.	21	23	**35**	77	46
Trifolium pratense	***	.	0	0	.	17	2	**12**	83	14
Viola hirta	***	.	1	1	.	5	5	**28**	94	29
(b) Bryophyte relevés										
Barbula convoluta	**	**14**	90	16	.	10	4	.	0	0
Barbula unguiculata	***	**27**	73	38	.	27	13	.	0	0
Bryum argenteum	*	**9**	100	9	.	0	0	.	0	0
Bryum rubens	**	**14**	89	16	.	8	4	.	3	2
Bryum ruderale	**	**19**	85	22	.	15	4	.	0	0
Pottia lanceolata	**	**9**	100	9	.	0	0	.	0	0
Weissia spec.	**	**19**	75	25	.	17	4	.	8	2
Plagiomnium affine	*	.	0	0	**19**	63	32	.	37	22
Scleropodium purum	**	.	5	22	**40**	67	60	.	28	68
Ctenidium molluscum	**	.	0	0		28	8	**18**	72	25
Hypnum cupressiforme	**	.	1	3		6	6	**23**	93	25

Lasius flavus ants keep root aphids and feed on their honeydew (Woodell and King, 1991). This can lead to an enrichment of plant nutrients in the ant mounds, e.g., by frass and the accumulation of organic compounds (cf. Boots and Clipson, 2013; Dauber et al., 2001; Dean et al., 1997; Dostál et al., 2005). As also shown by our study, potassium levels are higher in ant mounds because root aphids feed on the phloem sap, which is very rich in potassium (Woodell and King, 1991). Schreiber (1969) and Woodell and King (1991) demonstrated, that ant activity is highest within the south-facing sides of the mounds due to more favourable microclimatic conditions (cf. Dlussky, 1981; Streitberger and Fartmann, 2015). Consequently, the higher phosphorous content measured at the south-facing sides might be the result of higher ant density and activity compared to that which occurs on north-facing sides

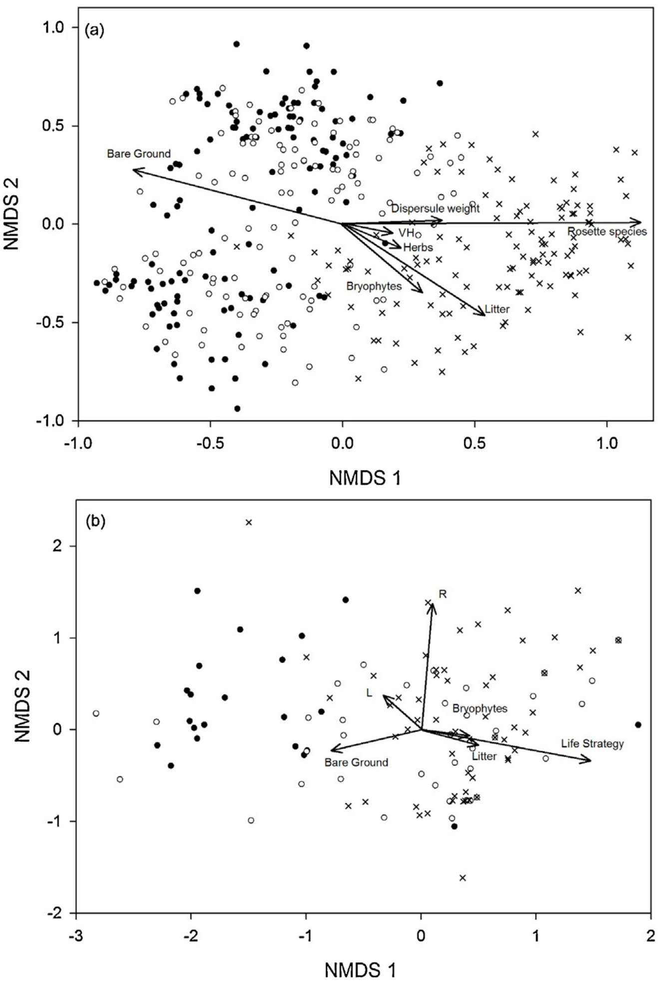

Fig. 1. Results of NMDS ordination for (a) vascular plant species samples (stress = 14.9, 4 dimensions, $N = 360$) and (b) bryophyte species samples (stress = 7.1, 4 dimensions, $N = 144$) and trait and vegetation structure parameters for overlay. Black dots represent ant mound south samples; white dots represent ant mound north samples; crosses represent control samples. Only significant environmental parameters are shown (at $P < 0.05$, based on 1000 permutations). (a) VH = vegetation height, (b) L = light indicator value, R = soil reaction indicator value.

Table 6

Summary of NMDS: Correlation of trait and vegetation structure parameters with ordination for (a) vascular plants and (b) bryophytes. P values are based on 1000 permutations (only significant variables are shown).

Parameter	NMDS 1	NMDS 2	R^2	P
(a) Vascular plant relevés				
Cover				
Herbs	0.86	−0.51	0.02	*
Bryophytes	0.67	−0.75	0.08	***
Litter	0.75	−0.66	0.17	***
Bare ground	−0.94	0.33	0.26	***
Vegetation height	0.99	−0.15	0.02	*
Proportion rosette species	1.00	0.01	0.49	***
Dispersule weight	1.00	0.03	0.05	***
(b) Bryophyte relevés				
Cover				
Byropyhtes	0.95	−0.3	0.08	**
Litter	0.99	−0.17	0.05	*
Bare ground	−0.96	−0.29	0.16	***
Life strategy	0.97	−0.24	0.65	***
Light indicator value	−0.69	0.73	0.07	**
Soil reaction indicator value	0.07	1.00	0.48	***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

of the mounds. Due to the higher ant digging activity it is likely that phosphorous-rich soil compounds are transported from the subsoil to the ground level. While we found no differences in carbon and nitrogen content, other studies produced opposing results with higher or lower values for ant mounds (Boots and Clipson, 2013; Dean et al., 1997; Dostál et al., 2005). Several studies have also reported that pH values are higher at ant mounds (Blomqvist et al., 2000; Boots and Clipson, 2013; Dean et al., 1997; Dostál et al., 2005). However, soil reaction within ant mounds is strongly dependent on soil type (cf. Boots and Clipson, 2013). In contrast, in our study soil reaction did not differ among the sample types, most likely due to the strong buffering effect of the calcareous soil. However, south-facing ant mounds occupied by bryophytes had higher soil reaction indicator values compared to ANTN and CONTROL (see below).

As mound-building activity is highest at the south-facing sides of ant mounds, structural differences between ant mounds and the matrix vegetation should be most pronounced on these sections of the ant mounds (cf. King, 1977b). Indeed, ANTS were characterized by an open and short turf with high amounts of bare ground having clear effects on species richness and plant functional traits. However, the effects of soil disturbance by ants were different for vascular plant and bryophyte species assemblages. In vascular plants, differences in functional traits and indicator values among the three sample groups were less pronounced; in bryophytes, nearly all parameters differed.

In vascular plants with increasing digging activity from CONTROL to ANTN and ANTS species richness, the number of indicator species, proportion of rosette species and dispersule mass of the species decreased. In contrast, the cover of annual species increased, but not significantly. The high disturbance intensity on ant mounds, especially on south-facing ones, leads to the suppression of more competitive species or rosette species with their ground-near leaves and favours the establishment of annual species (King, 1977a,c). However, seedlings are usually sensitive to intensive digging activities of the ants; therefore, their abundance is often limited (King, 1977c). Generally, species with lower seed weights occur to a higher proportion on ant mounds as large seeds hamper the dispersal to ant mounds (Dauber et al., 2006).

Although soil nitrogen content did not differ among the three sample groups, ant mounds (especially ANTS) were characterized by a higher abundance of species with low nitrogen indicator values. Bulk density is generally lower on ant mounds than in the matrix vegetation (King, 1977a). Moreover, evapotranspiration should be higher, due to the warm microclimatic conditions on ant mounds (Streitberger and Fartmann, 2015), especially on south-facing sides. Both the low bulk density and the high evapotranspiration rate lead to drier soils (Blomqvist et al., 2000; Dean et al., 1997; King, 1977a), as evidenced by the lower moisture indicator values observed for ANTS compared to CONTROL.

The most frequent vascular plant species found on the mounds were *Brachypodium pinnatum* and *Thymus* species. The dominance of *B. pinnatum* at the north-facing sides is probably explained by the high invasibility of this species due to its vegetative dispersal (Schläpfer and Fischer, 1998; CLO-PLA trait base, cf. Klimešová and de Bello, 2009). At the south-facing sides, *B. pinnatum* occurred with low cover; *T. praecox* and *Areneria serpyllifolia* were most frequent (cf. Streitberger and Fartmann, 2015). Here, it is very likely that the competitiveness of *B. pinnatum* is reduced due to the higher soil disturbance and more extreme microclimatic conditions. According to King (1977c), *Thymus* species are especially well adapted to the soil-disturbing activity of *L. flavus* due to their ability to grow up through heaped soil by increased branching, whereas *A. serpyllifolia* is typical for mounds where soil disturbance by ants is low (King, 1977b).

Although overall richness of vascular plant species is reduced on ant mounds, the promotion of certain plants species like the indicator species *Thymus praecox* and *T. pulegioides* by the digging activities of the ants can be beneficial for rare herbivorous insects. Streitberger and Fartmann (2015) showed that the monophagous and declining burnet moth *Zygaena purpuralis* preferred ant mounds with a high cover of *Thymus* host plants as larval habitats in calcareous grasslands, as they provide sufficient food for the larvae and a favourable microclimate.

The effects of ant mounds on bryophyte assemblages were clearly different from those on vascular plant assemblages. There were even more similarities between ANTN and CONTROL than between the two ant mound types concerning species assemblage, functional traits and indicator values. Moreover, bryophytes only occurred on one half of the south-facing ant mounds. Here only those characterized by sparse vegetation with a short turf were occupied. Trait analyses revealed that light-dependent, basiphilous colonists dominated at the south-facing sides. Many of these were identified as indicator species. Annual bryophyte species were also more regularly found on these mounds. In contrast to their ephemeral character, some colonist species form long-lasting diaspore banks composed of vegetative diaspores (During and ter Horst, 1983). Different to the southern sides of the mounds, pleurocarpous species were more frequent within the matrix vegetation and the north-facing sides of the mounds. Here, some perennial species such as *Scleropodium purum* were highly competitive and appeared in great abundance, most likely due to the lower cover of vascular plants and a more favourable microclimate. According to King (2003), *S. purum* is more dominant at the north-facing sides of ant mounds compared to the south-facing ones due to more favourable conditions for establishment. *Scleropodium purum* reproduces mainly asexually, through fragments that are dispersed by grazing animals (Pauliuk et al., 2011). At the south-facing sides the very warm and dry microclimatic conditions lead to desiccation of the stems. In contrast, the open vegetation structure favours less-competitive species that mainly reproduce sexually or by small, specialised vegetative diaspores (cf. During and ter Horst, 1983). The identified indicator species of the genus *Barbula*, *Bryum* or *Weissia* are typical for such microsites (Marstaller, 2005, 2007; Preston et al., 2009; Werner, 1992).

However, more detailed analyses are necessary for a better understanding of the role of ant mounds in bryophyte diversity within calcareous grasslands. It is very likely, that bryophyte occurrence is strongly dependent on burial activity by ants which was not measured within our analyses. Ant mounds with very intense soil disturbing activity by *L. flavus* are unlikely to be suitable microsites for less-competitive bryophytes. Most bryophytes were found on mature ant mounds where soil disturbing by ants is low and the soil is consolidated (own observation). Although we found no influence of land use on the occurrence of bryophytes on ant mounds, we recommend further analyses with respect to the interacting effects of different land-use types and vegetation composition on ant mounds. There is evidence that vegetation composition on ant mounds is strongly influenced by the interacting effects of different grazers (Veen et al., 2012).

6. Conclusion

Our study clearly showed that *L. flavus* promotes structural heterogeneity within semi-natural grasslands. The influence of ant mounds on vascular plant species diversity on the patch level is low. However, by favouring certain plant species adapted to disturbance vegetation, vegetation heterogeneity is increased. Such microsites can have an impact on overall biodiversity within grasslands, for example by favouring thermophilous, disturbance-dependent insect species (Streitberger and Fartmann, 2015).

In contrast to vascular plants, ant mounds, in general, and south-facing sides, in particular, increase bryophyte diversity by favouring less-competitive bryophyte species dependent on open vegetation with bare ground. The study underlines the importance of disturbance and small-scale vegetation heterogeneity for promoting bryophyte species richness in calcareous grasslands (cf. Preston et al., 2009).

All in all, the occurrence of *L. flavus* increases vegetation heterogeneity within grasslands and, therefore, plays an important role in supporting the species richness of both plants and animals in calcareous grasslands. This especially holds true for fallow sites where ant mounds often represent the only sites of open vegetation which favour certain disturbance-dependent species (cf. Streitberger and Fartmann, 2015, 2016). Within the study site, *L. flavus* is especially abundant within unmanaged sites (Streitberger and Fartmann, 2016). Here, successional speed is low and the low-growing vegetation structure combined with a low disturbance regime promote *L. flavus*. However, there is a risk of nest abandonment when vegetation development succeeds and thus microclimatic conditions become unsuitable for this species due to tall growing vegetation and grass encroachment on the mounds (cf. King, 1977b). Therefore, for maintaining *L. flavus* populations in the long run, we propose the application of low-intensive land use in the form of traditional rough grazing in order to maintain a suitable vegetation structure for this species. Mowing with heavy machinery on sites with *L. flavus* nest mounds should be banned as the mounds are destroyed by this activity (own observation).

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Appendix A.

Overview of intercorrelations (Spearman correlation coefficient $|r_s| > 0.6$) between variables with significant differences between the sampling groups for (a) vascular plant relevés and (b) bryophyte relevés. ***$P < 0.001$.

Excluded variables	Intercorrelated variables	r_s	P
(a) Vasular plant relevés			
Number of plant species	Proportion of rosette species	0.67	***
Nitrogen indicator value	Cover of grasses	0.61	***
	Dispersule weight	0.74	***
Moisture indicator value	Dispersule weight	0.71	***
Cover of grasses	Dispersule weight	0.61	***
(b) Bryophyte relevés			
Cover of herbs	Cover of grasses	−0.61	***
Vegetation height	Cover of litter	0.63	***
Length	Proportion of acrocarpous species	−0.66	***
	Life strategy	0.64	***
	Soil reaction indicator value	−0.70	***
Proportion of acrocarpous species	Life strategy	−0.88	***

Appendix B.

Relative frequencies of widespread vascular plant and bryophyte species (species occurring with a minimum frequency of 10% within at least two of the sampling groups) for ANTS (ant mound south), ANTN (ant mound north) and CONTROL samples.

Species	ANTS	ANTN	CONTROL
Calliergonella cuspidata	6	12	12
Campanula rotundifolia	18	21	35
Festuca ovina agg.	18	22	18
Festuca rubra agg.	50	62	69
Galium verum	39	33	37
Genista tinctoria	6	12	20
Helianthemum nummularium ssp. *obscurum*	33	35	35
Hippocrepis comosa	11	13	23
Homalothecium lutescens	6	17	22
Koeleria pyramidata	48	53	55
Poa angustifolia	18	9	18

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