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

Merle Streitberger[a,b,*], Carsten Schmidt[c], Thomas Fartmann[a,b]

[a] *Department of Biodiversity and Landscape Ecology, University of Osnabrück, Barbarastraße 13, 49076 Osnabrück, Germany*
[b] *Institute of Biodiversity and Landscape Ecology (IBL), Hafenweg 31, 48155 Münster, Germany*
[c] *Sudmühlenstraße 88, 48157 Münster, Germany*

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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

* Corresponding author at: Department of Biodiversity and Landscape Ecology, University of Osnabrück, Barbarastraße 13, 49076 Osnabrück, Germany.
E-mail address: merle.streitberger@uos.de (M. Streitberger).

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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 ≤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):