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Vegetation and climate determine ant-mound occupancy by a declining herbivorous insect in grasslands

Merle Streitberger ^{a,*}, Thomas Fartmann ^{a,b}^a Department of Community Ecology, Institute of Landscape Ecology, University of Münster, Heisenbergstraße 2, 48149 Münster, Germany^b Ecology, Department of Biology/Chemistry, University of Osnabrück, Barbarastraße 13, 49076 Osnabrück, Germany

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ABSTRACT

There is considerable research on the effects of soil-disturbing ecosystem engineers in semi-natural Central European grasslands in terms of plant species diversity, soil properties and soil microorganisms. However, knowledge on the importance of such ecosystem engineers for animal diversity is still relatively rare. In this study we analyse the role of *Lasius flavus* nest mounds as habitats for larvae of the declining burnet moth species *Zygaena purpuralis* in calcareous grasslands. We assumed that anthills act as preferred larval habitats in dependence on climate or vegetation structure. The analysis considers a macroclimatic gradient by comparing sites with differing elevation and, hence, local climates. Additionally, we analysed the importance of anthills for *Z. purpuralis* along a microclimatic gradient by comparing sites with different vegetation structures. The study clearly shows that anthills are important larval habitats when general microclimatic conditions in the grasslands are unfavourable due to a cool climate at higher elevation or dense vegetation. The likelihood of detecting larvae of the burnet moth species on sites where anthills were occupied was higher on the mounds than within the surrounding vegetation. Anthills were preferred as larval habitats by *Z. purpuralis* as they combine two essential elements for successful larval development: (i) a favourable microclimate thanks to an open vegetation structure and (ii) a sufficient amount of food. The study underlines the importance of *L. flavus* as an ecosystem engineer for maintaining habitat heterogeneity and biodiversity within semi-natural grasslands.

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1. Introduction

Research on species relationships is of special scientific concern for the understanding of ecosystem functioning (Laska and Wootton, 1998). Therefore, a great number of theories describe functional relationships between species such as the concept of keystone species or ecosystem engineers (Bond, 1993; Jones et al., 1994). Ecosystem engineers are organisms that alter the availability of resources by modifying the physical state of biotic or abiotic materials and therefore create habitats (Jones et al., 1994). Autogenic ecosystem engineers provide resources and habitats by means of their own physical structures. A typical example are mussel beds of *Mytilus edulis* which function as habitats for a wide variety of marine invertebrate species (e.g. Arribas et al., 2014).

Allogenic ecosystem engineers transform other living or non-living materials and thus create habitats indirectly (Jones et al., 1994). Concerning allogenic ecosystem engineers the ecological influence of fossorial or hypogeic species which cause soil disturbance and create microhabitats because of their burrowing or mound-building activities is of special scientific interest (Folgarait, 1998; Davidson et al., 2012). Classic and well-studied examples comprise subterranean herbivores such as pocket gophers or marmots within grasslands (van Staalduinen and Werger, 2006; Reichman, 2007; Yoshihara et al., 2009). Several studies demonstrated that microsites created by these species serve as important habitats for certain taxonomic groups, such as plants or insects (e.g. Davidson and Lightfoot, 2007; Yoshihara et al., 2010).

Within Europe, typical soil-disturbing ecosystem engineers include different species of ants (e.g. the yellow meadow ant, *Lasius flavus*) or rodents (e.g. the European rabbit, *Oryctolagus cuniculus*) and the European mole (*Talpa europaea*) (Dostál, 2005; Seifan et al., 2010; Ferreira, 2012). These ecosystem engineers frequently reside

* Corresponding author.

E-mail addresses: m_stre05@uni-muenster.de (M. Streitberger), Thomas.Fartmann@Biologie.Uni-Osnabrueck.de (T. Fartmann).

within open habitats, especially semi-natural grasslands. In Europe, semi-natural grasslands maintained by traditional, low-intensive land use practices are among the most species-rich habitats (Veen et al., 2009). Within these grasslands the effects of soil-disturbing ecosystem engineers have been extensively studied in terms of plant species diversity, soil properties and soil microorganisms (e.g. Dean et al., 1997; Blomqvist et al., 2000; Lenoir, 2009; Schiffers et al., 2010; Seifan et al., 2010; Boots and Clipson, 2013). Mounds created by ants or moles harbour a reduced plant biomass and favour certain plant species such as annual plants (King, 1977, a, b, c; Dean et al., 1997; Dauber et al., 2006; Lenoir, 2009; Streitberger et al., 2014). Therefore, these mounds increase vegetation heterogeneity in grasslands (Dauber et al., 2006).

However, with regards to Central European grassland ecosystems knowledge on the importance of these microsites for animal diversity is still relatively sparse. Yet, there is evidence that mounds created by soil-disturbing ecosystem engineers play an important role as habitats for insect species dependent on a warm microclimate. For example, the ant species *Formica exsecta* prefers molehills as nesting grounds as these sites are subject to high solar insolation (Bliss et al., 2006; Katzerke et al., 2010). Furthermore, molehills are the preferred perching sites of the butterfly species *Inachis io* and other territorial Nymphalid species thanks to favourable microclimatic conditions (Dennis, 2004; Dennis and Sparks, 2005). In addition to that, the two butterfly species *Pyrgus malvae* and *Lycaena phlaeas* prefer molehills for oviposition as these sites offer suitable microclimatic conditions for larval development (Streitberger and Fartmann, 2013; Streitberger et al., 2014).

In general, a favourable microclimate which is interlinked with vegetation structure (Stoutjesdijk and Barkman, 1992) plays an important role in the larval development of Lepidoptera (García-Barros and Fartmann, 2009). For example, in Central Europe a warm microclimate owed to an open vegetation structure is essential for the development of the immature stages of many thermophilous butterfly species (e.g. Salz and Fartmann, 2009; Krämer et al., 2012; Helbing et al., 2015). However, the microclimatic requirements of Lepidoptera species depend on the macroclimatic conditions. In fact, geographically shifting microhabitats along macroclimatic gradients are evident among a wide variety of Lepidoptera species (Thomas et al., 1998; García-Barros and Fartmann, 2009; Henry and Schultz, 2013).

Because of the open vegetation structure, in contrast to the surrounding matrix vegetation, it is likely that anthills serve as important larval habitats for thermophilous Lepidoptera species within Central European grasslands. However, knowledge on the role of ant mounds in the reproduction of Lepidoptera is still lacking.

In this study we analyse the role of *Lasius flavus* ant nest mounds as habitats for larvae of the declining burnet moth species *Zygaena purpuralis* in calcareous grasslands in Central Germany. As larvae of this species depend on a warm microclimate (Fartmann, 2004) we assume that anthills act as preferred larval habitats. Nonetheless, it is conceivable that the importance of anthills as a larval habitat for this species differs according to climate or vegetation structure. We suppose that anthills play an important role as larval habitats for this species within abandoned grasslands with a dense vegetation structure and cool microclimate and within grasslands located in regions with a cooler local climate. Therefore, the analysis takes place along a macroclimatic gradient and compares sites with differing elevation and, hence, local climates. Additionally, we analyse the importance of anthills for *Z. purpuralis* along a microclimatic gradient by comparing sites with different vegetation structures. In the light of the results we derive management strategies for the conservation of the burnet moth species.

2. Materials and methods

2.1. Study species

2.1.1. *Lasius flavus*

Lasius flavus (Fabricius 1782) (Hymenoptera: Formicidae) has a Palearctic distribution and is one of the most dominant *Lasius* species found within agricultural and urban habitats throughout Europe (Seifert, 2007). In Central Europe, this oligothermic ant species occurs frequently within moist to wet grasslands maintained by low-intensity land use (Seifert, 1993, 2007). *L. flavus* is a hypogeic species which builds above-ground nest mounds in order to create suitable microclimatic conditions for its offspring (Dlussky, 1981). The main food sources of this species are root aphids and their honeydew (Pontin, 1978). Even though *L. flavus* still occurs frequently within grasslands in Central Europe, it is sensitive to eutrophication (Seifert, 1993).

2.1.2. *Zygaena purpuralis*

The distribution of the transparent burnet *Zygaena purpuralis* (Brünnich 1763) (Lepidoptera: Zygaenidae) ranges from the British Isles to North-Western China (Ebert, 1994). Within our study area, the Diemel Valley, *Z. purpuralis* is on the wing from mid-June until the end of July (Fartmann, 2004). It is a univoltine species and hibernates in the larval stage. The larvae feed monophagously on *Thymus* species (Ebert, 1994; Fartmann, 2004). In Central Europe, the species prefers warm south- or west-facing open habitats, especially thyme-rich, semi-dry or dry grasslands with a high proportion of bare ground (Ebert, 1994; Fartmann, 2004; Wagner, 2006). In Germany *Z. purpuralis* is listed as near-threatened (Reinhardt and Bolz, 2011).

2.2. 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). Overall, the area is characterized by a suboceanic climate (Müller-Wille, 1981). However, because of a strong elevational gradient climatic conditions differ strongly across the study area (Fartmann, 2004). The Upper Diemel Valley (300–500 m a.s.l.), located around the city of Marsberg, represents the coldest (mean annual temperature 6.5–8 °C) and wettest part (mean annual precipitation of 700–1000 mm). Further east, the middle and lower parts of the Diemel Valley (100–300 m a.s.l.) exhibit milder and drier climatic conditions (mean annual temperatures between 7.5 and 9 °C, mean annual precipitation 600–850 mm). Large parts of the hillsides along the Diemel Valley consist of limestone and have been grazed for centuries. Because of a long tradition of shepherd grazing calcareous grasslands are still frequent within the region. Nowadays, about 55% of these grasslands are still actively managed, mainly by traditional rough sheep grazing (Fartmann, 2004). In the northern half of Germany the Diemel Valley represents the region with the greatest area of calcareous grasslands (Fartmann, 2004).

2.3. Sampling design

Sampling of *Z. purpuralis* larvae took place in the second half of May 2013. Within 22 calcareous grassland patches across the study area with known occurrence of the burnet moth species (own unpublished data) altogether 40 sites measuring 10 × 10 m and a high abundance of *L. flavus* anthills were randomly selected. Within these sites all anthills with a minimum height of 5 cm and the presence of at least one of the host plants (*Thymus praecox* ssp. *praecox* and *T. pulegioides* ssp. *pulegioides*, respectively) underwent further analyses. At each selected anthill we set up a plot measuring

30 × 30 cm at the spot with the highest abundance of host plants which we searched for *Z. purpuralis* larvae. If larvae were present (hereafter called occupied anthills) we analysed the following microclimatic, vegetation and anthill characteristics for the whole plot: aspect (converted into 'northness' and 'eastness' by cosine and sine transformation [northness: 360° = 1; 180° = -1; eastness: 90° = 1; 270° = -1]), slope, daily potential sunshine duration for May using a horizontoscope (cf. Tonne, 1954), cover of host plants, herbs, cryptogams, litter and bare ground, turf height, height and diameter of the anthill. Furthermore, we estimated the vegetation density by using a horizontal frame of 20 cm depth and 40 cm width at 5 cm above ground.

In order to document the complete range of available microhabitats, we analysed microclimatic and vegetation characteristics at control samples ($N = 51$) of the same size within the matrix vegetation. Control samples occurred at the nearest host plant at a minimum distance of 1 m north of every occupied anthill. Furthermore, we selected unoccupied anthills where at least one of the host plants of the study species was present but where larvae of *Z. purpuralis* were missing to analyse which parameters explain the usage of a certain anthill by *Z. purpuralis* as a larval habitat. We chose a number of samples at a ratio of 1:2 in comparison with the occupied anthills. We selected the unoccupied anthills randomly from the five patches with the highest abundance of *Z. purpuralis* larvae. We chose these patches for analysis in order to maximize the likelihood that the non-occupancy of the anthills was a result of unsuitable environmental conditions and independent of population size. Here, we analysed the same parameters as mentioned above at plots measuring 30 × 30 cm on the anthill where the host plants occurred in greatest abundance.

Additionally, we analysed the following parameters on the whole site of 10 × 10 m: geographical coordinates, elevation, aspect, slope, daily potential sunshine duration for May, covers of herbs, cryptogams, litter and bare ground and turf height. For further analyses we derived the local climate of each patch (mean temperature and mean precipitation in the month of May) from 1 km² grid datasets of Germany's National Meteorological Service (DWD), which contained 30-year (1961–90) mean values.

In total, we found larvae of *Z. purpuralis* on anthills within half of the analysed sites ($N = 20$). These sites are referred to as occupied sites. Sites where we found no larvae on anthills are labelled as unoccupied sites.

Moreover, we took temperature measurements on a sunny day in July (19-Jul-2014) to reveal different microclimatic conditions near the ground between anthills and the matrix vegetation. For this purpose, we placed 20 iButton data loggers (Thermochroni-Buttons DS1922L; Maxim Integrated Products, Sunnyvale, CA, USA) within 10 sites which enjoyed a high amount of daily sunshine (about 12 h in July) and where the study species occurred in abundance. We placed one iButton per site at a randomly selected and occupied anthill and a further logger within the matrix vegetation 1 m north of the anthill. We fixed the iButtons onto a 1 cm³ sized piece of styrofoam glued on a nail and inserted it into the ground. Measurements took place 2 cm above ground and were recorded every 10 min.

2.4. Statistical analyses

For the comparison of sites where larvae of *Z. purpuralis* were present on anthills (occupied sites, $N = 20$) and absent from anthills (unoccupied sites, $N = 20$) we detected differences between numerical variables using the t test in the cases of normal distribution of the variables and homogeneous variances. When these requirements were unfulfilled the Mann–Whitney U test served as an alternative method. We used Wilcoxon signed-rank tests for

comparing significant differences between occupied anthills and control samples as the analysed parameters did not fulfil the requirements for parametric analyses. For comparing occupied and unoccupied anthills we used the Mann–Whitney U test since the variables were not normally distributed or characterized by homogeneity of variances. In cases of multiple comparisons we applied Bonferroni corrections of the significance levels. In order to compare differences in temperatures between anthills and the matrix vegetation, we divided the dataset into daytime and nighttime according to local time of sunrise and sunset during the measurement period. The daytime period included all hours with full solar radiation (from 6.0 a.m. to 9.0 p.m.) and the nighttime period the rest of the day. We tested temperature differences between anthills and the matrix vegetation on the basis of hourly data using Wilcoxon signed-rank test.

We applied binomial generalized mixed-effects models (GLMM) to compare occupied and unoccupied samples. On the site level (occupied vs. unoccupied sites), we used two models in order to prevent overfitting. The first model contained climatic data as explanatory variables (mean temperature and precipitation in May, heat load index calculated using aspect and slope after McCune and Keon [2002]) and the daily potential sunshine duration in May). The second model included the vegetation structure data. Patch served as the random factor within the two models. Furthermore, we performed a binomial GLMM to ascertain which parameters had the highest explanatory power in relation to the occurrence of *Z. purpuralis* larvae on anthills in general (occupied anthills vs. control samples). Additionally, we calculated a binomial GLMM to ascertain which environmental parameters explained the occurrence of *Z. purpuralis* larvae on a certain anthill (occupied vs. unoccupied anthills). In both models site within patch served as the random factor. We used only non-intercorrelated variables (Spearman correlations with $|r_s|$ values < 0.7) as explanatory variables to avoid intercorrelations in all models. The selection of the final models depended on backward selection using likelihood ratio tests with a significance level of $\alpha = 0.05$.

We ascertained significant differences between analysed variables using SPSS 22. For the calculation of the GLMMs we used the lme4-package in R 3.0.3 (R Development Core Team, 2014).

3. Results

Within 20 of the selected sites (50% of all sites) we found larvae of *Z. purpuralis* on anthills. On these 20 sites, 51 anthills with the presence of a host plant were occupied (25% of all anthills with host-plant occurrence) by a total of 78 larvae of *Z. purpuralis*. In contrast, only at 10% of all control samples larvae of *Z. purpuralis* occurred with only five larvae in total. Occupation rates of anthills with host plants per site (mean ± SD = 24.6 ± 12.5%) and control samples per site (mean ± SD = 5.5 ± 14.0%) differed significantly (Wilcoxon signed-rank test: $Z = -3.381$, $P = 0.001$).

The sites where larvae of *Z. purpuralis* occurred on anthills (occupied sites) differed significantly from sites where larvae were absent from anthills (unoccupied sites) with respect to climatic as well as vegetation structure characteristics (Table 1). Occupied sites had a higher elevation and more southerly aspects. Moreover, these sites enjoyed lower mean temperature in May.

With respect to vegetation structure, occupied sites had a higher turf layer and cover of litter as well as a lower cover of cryptogams. A similar pattern appeared in the GLMMs (Table 2). The likelihood of finding larvae of *Z. purpuralis* on anthills was increased on sites with a higher heat load and a lower temperature in May (Table 2a). Furthermore, a high cover of litter as well as a low cover of bare ground and cryptogams within the sites increased the likelihood of finding larvae of *Z. purpuralis* on anthills (Table 2b). The pseudo R^2 -

Table 1

Mean values \pm SD of all numerical parameters at sites where larvae of *Zygaena purpuralis* were present on anthills (occupied sites, $N = 20$) and absent from anthills (unoccupied sites, $N = 20$). Comparison between groups by t test (t) and Mann–Whitney U test (U), respectively. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. not significant.

Variable	Occupied sites	Unoccupied sites	P
<i>Climate</i>			
Elevation (m a.s.l.)	312.3 \pm 72.7	250.3 \pm 68.5	**U
Mean temperature (May)	11.4 \pm 0.4	11.8 \pm 0.5	**U
Mean precipitation (May)	71 \pm 5.9	70.1 \pm 4.5	n.s. ^U
Northness ^a	-0.6 \pm 0.4	-0.2 \pm 0.7	*U
Eastness ^a	-0.3 \pm 0.6	-0.2 \pm 0.7	n.s. ^U
Slope ($^{\circ}$) ^a	24.5 \pm 9.6	22.9 \pm 14.6	n.s. ^U
Heat load index	0.9 \pm 0.1	0.8 \pm 0.2	n.s. ^U
Daily sunshine duration (h)			
May	11.2 \pm 1.8	11.1 \pm 2.0	n.s. ^t
<i>Vegetation structure</i>			
Cover (%)			
Herb layer	72.3 \pm 7.9	68.3 \pm 8.3	n.s. ^U
Litter	62.5 \pm 13.2	34.0 \pm 16.3	***U
Cryptogams	27.8 \pm 13.3	40.0 \pm 2.7	**U
Bare ground	6.1 \pm 7.3	5.2 \pm 2.9	n.s. ^U
Turf height (cm)	14.6 \pm 4.1	11.1 \pm 2.6	*U

^a Aspect and slope were converted into the 'heat load index' after McCune and Keon (2002), which we used for GLMM.

Table 2

Statistics of GLMM: binomial, relationships between the occurrence of larvae of *Zygaena purpuralis* on anthills within the study sites ($N = 20$ sites where larvae of *Z. purpuralis* occurred on anthills and $N = 20$ sites where larvae of *Z. purpuralis* were absent from anthills) and climatic data (a) and vegetation structure parameters (b). The following variables entered into the analyses were not significant: (a) daily sunshine duration May, mean precipitation May, (b) vegetation height, cover of herb layer. Non-significant predictors were excluded from the models by stepwise backward-selection ($P > 0.05$). Pseudo $R^2 =$ Pseudo R^2 [Nagelkerke]; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Variable	Estimate	SE	Z	P
(a) Climate (Pseudo $R^2 = 0.49$)				
Heat load index	41.67	254.3	0.164	**
Mean temperature (May) ^a	-59.6	72.78	-0.819	***
(b) Vegetation structure (Pseudo $R^2 = 0.71$)				
Cover of bare ground	-4.196	27.821	-0.151	*
Cover of litter	3.368	20.511	0.164	***
Cover of cryptogams	-1.683	40.976	-0.041	**

^a Elevation (m a.s.l.) was intercorrelated with mean temperature (May) ($r_s = -0.87^{**}$) and not entered into the analysis.

values of both models were high (model a: 0.49; model b: 0.71, Table 2).

Occupied anthills differed significantly in some climatic and many vegetation characteristics from control samples (Table 3). Plots on anthills occupied by *Z. purpuralis* larvae were less south-facing and had a lower heat load. Here, vegetation structure typically had a higher cover of host plants and bare ground. The values for the cover of litter, cryptogams and in 5 cm height as well as the turf height were significantly lower.

In contrast, significant differences between occupied and unoccupied anthills were fewer (Table 3). Occupied anthills had a significantly lower potential duration of daily sunshine in May and a significantly smaller diameter.

According to the results of the GLMM the likelihood of finding larvae of *Z. purpuralis* on anthills in comparison with the control samples increased thanks to a higher cover of host plants and bare ground (Table 4a). The model selection resulted in a high pseudo R^2 -value of 0.62. The likelihood of a certain anthill's acceptability as a larval habitat depended on the size of the anthill and the cover of host plants (Table 4b). Larvae of *Z. purpuralis* preferred anthills with a smaller diameter and a higher cover of host plants (Table 4b).

Temperatures significantly differed between anthills and matrix vegetation (Fig. 1). During the daytime temperatures were higher on anthills, whereas during the nighttime temperatures were lower.

4. Discussion

This study clearly showed that *L. flavus* nest mounds can be important microhabitats for immature stages of *Z. purpuralis* in calcareous grasslands. The drivers of ant-mound occupancy were (i) climate, (ii) vegetation structure and (iii) host-plant availability. Ant mounds were used as preferred larval habitats if grasslands occurred at higher elevations with a cooler climate, had a higher heat load and typically had more litter as well as a lower cover of cryptogams and bare ground. The likelihood of detecting larvae of the burnet moth species on sites where anthills were occupied was higher on the mounds than within the surrounding vegetation. *Z. purpuralis* preferred anthills as larval habitats because of specific vegetation and microclimatic conditions differing from the matrix vegetation. Anthills occupied by larvae had a greater abundance of host plants and a higher proportion of bare ground. Moreover, occupied anthills typically enjoyed higher temperatures during the daytime and lower temperatures during the nighttime compared to control samples within the matrix vegetation.

Lasius flavus ants build nest mounds to ensure conditions warm enough for successful development of their brood (Dlussky, 1981). The selection of anthills by females of *Z. purpuralis* as habitats for their pre-adult stages is probably also dependent on favourable microclimatic conditions. Anthills in our study were covered by sparser and low-growing vegetation with more bare ground and higher day temperatures than the surrounding vegetation. A suitable microclimate is essential for larval development of Lepidoptera (Weiss et al., 1988; Roy and Thomas, 2003; Pradel and Fischer, 2011; O'Connor et al., 2014). For similar reasons molehills in grasslands function as important oviposition microhabitats for the butterfly species *L. phlaeas* (Streitberger and Fartmann, 2013) and *P. malvae* (Streitberger et al., 2014).

However, not every anthill offered suitable conditions for the immature stages. *Z. purpuralis* avoided large anthills and the likelihood of finding larvae was increased by anthills with a higher cover of host plants. Furthermore, occupied anthills were characterized by a significantly lower sunshine duration in May compared to unoccupied anthills, indicating that the suitability of anthills as larval habitats is limited when microclimatic conditions become too extreme. In line with this assumption, Bourn (1995) showed for Scotland that larvae of *Z. purpuralis* avoided microhabitats with a very high amount of bare ground although the host plants were present. As Dlussky (1981) demonstrated, temperatures within *L. flavus* nest mounds increase with the size of the mounds and surface temperatures can reach values of over 50 °C when there is no shade (this study).

In addition to a suitable microclimate, a sufficient number of host plants is important for successful larval development (García-Barros and Fartmann, 2009). This is especially true for egg-clustering species such as *Z. purpuralis* (Ebert, 1994). To avoid food shortage such species require either large host plants or dense patches of hosts (Courtney, 1984; Davies and Gilbert, 1985; Eichel and Fartmann, 2008). In line with this, the cover of *Thymus* host plants at occupied anthills was five times higher in comparison with control samples.

The digging activity of *L. flavus* drastically affects the occurrence of plants. Generally, low-competitive plant species, such as annual or low-growing species, occur more frequently on anthills because of suitable establishment conditions (King, 1977a; Woodell and King, 1991; Dean et al., 1997; Dauber et al., 2006; Lenoir, 2009).

Table 3

Mean values \pm SD of all numerical parameters at occupied anthill ($N = 51$), control ($N = 51$) and unoccupied anthill ($N = 25$) samples of *Zygaena purpuralis*. Comparisons between groups by Wilcoxon signed-rank tests (W) and Mann–Whitney U tests (U), respectively. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. not significant.

Variable	Occupied anthills	Control samples	P	Unoccupied anthills	P ^a
<i>Climate</i>					
Northness ^b	-0.5 ± 0.5	-0.8 ± 0.3	*W	-0.6 ± 0.5	n.s. ^U
Eastness ^b	0.0 ± 0.7	-0.2 ± 0.5	n.s. ^W	0.0 ± 0.7	n.s. ^U
Slope ($^{\circ}$) ^b	20.0 ± 16.3	25.4 ± 11.3	n.s. ^W	23.0 ± 11.8	n.s. ^U
Heat load index	0.8 ± 0.1	0.9 ± 0.1	***W	0.8 ± 0.1	n.s. ^U
Daily sunshine duration (h)					
May	11.1 ± 1.5	11.0 ± 1.6	n.s. ^W	12.0 ± 0.8	*U
<i>Vegetation structure</i>					
Vegetation cover (%)					
Host plants	37.7 ± 20.9	6.7 ± 9.5	***W	27.5 ± 21.8	n.s. ^U
Herb layer	65.8 ± 14.7	63.8 ± 12.4	n.s. ^W	67.0 ± 14.9	n.s. ^U
Litter	23.3 ± 15.9	53.5 ± 22.7	***W	23.5 ± 15.1	n.s. ^U
Cryptogams	4.6 ± 12.6	19.1 ± 24.1	***W	1.7 ± 4.2	n.s. ^U
Bare ground	15.6 ± 12.5	1.3 ± 4.1	***W	17.8 ± 7.8	n.s. ^U
Vegetation density (%)					
5 cm above ground	56.2 ± 16.6	68.1 ± 17.8	**W	54.6 ± 20.9	n.s. ^U
Turf height (cm)					
Herb layer	5.5 ± 1.6	9.9 ± 3.2	***W	6.2 ± 2.2	n.s. ^U
<i>Anthill structure (cm)</i>					
Height	24.6 ± 8.7	–	–	27.6 ± 11.4	n.s. ^U
Diameter	56.7 ± 13.8	–	–	66.7 ± 16.0	**U

^a Occupied and unoccupied anthills were tested against each other.

^b Aspect and slope were converted into the 'heat load index' after McCune and Keon (2002), which was used for GLMM.

Table 4

Statistics of GLMM: (a) binomial, prediction of the use of anthills as larval habitats by *Z. purpuralis* ($N = 51$ occupied anthills) in comparison to the control samples ($N = 51$). (b) binomial, prediction of the use of a certain anthill as a larval habitat ($N = 51$ occupied anthills) in comparison with unoccupied anthills ($N = 25$). The following variables entered into the analysis were not significant: (a) heat load index, daily sunshine duration May, cover of herbs and cryptogams, vegetation density 5 cm above ground, (b) heat load index, daily sunshine duration May, covers of herbs, cryptogams and bare ground, vegetation density 5 cm above ground, height of anthill. Non-significant predictors were excluded from the models by stepwise backward-selection ($P > 0.05$). Pseudo $R^2 =$ Pseudo R^2 [Nagelkerke]; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Variable	Estimate	SE	Z	P
(a) Anthills vs. control samples (Pseudo $R^2 = 0.62$)				
Cover of host plants ^a	0.09947	0.02686	3.704	***
Cover of bare ground ^b	0.20974	0.07624	2.751	**
(b) Occupied vs. unoccupied anthills (Pseudo $R^2 = 0.14$)				
Cover of host plants	0.0376	0.0184	2.044	*
Diameter of anthill	-0.07032	0.02732	-2.574	**

^a Height of herb layer ($r_s = -0.72^{**}$) and cover of litter ($r_s = -0.71^{***}$) were intercorrelated with cover of host plants and not entered into the analysis.

^b Height of herb layer was intercorrelated with cover of bare ground ($r_s = -0.73^{***}$) and not entered into the analysis.

Thymus species belong to this group of plants (this study; King, 1977a, b, c; Bonte et al., 2003; Dauber et al., 2006). Within our study area *Thymus* ssp. was especially dominant on the southern slopes of the nest mounds (own observation) where soil-heaping activity by ants is very high because of favourable temperatures (cf. Dlussky, 1981). King (1977c) showed that *Thymus drucei* (= *T. praecox* ssp. *britannicus*) is abundant on anthills thanks to its special ability to grow up through heaped soils. In contrast, myrmecochory is unimportant for the observed plant abundance patterns as *L. flavus* has no role in this type of seed dispersal (Woodell and King, 1991).

However, only on some sites anthills played an important role as larval habitats of *Z. purpuralis*. Larvae were only found on anthills if the sites had a certain (i) climate and (ii) vegetation structure. Anthills were important larval habitats when general microclimatic conditions in the grasslands were unfavourable because of a cool climate of higher elevations or dense vegetation. Under such

conditions occupied sites even had a higher heat load than unoccupied sites because of their more southerly aspect. In contrast, under more favourable local climatic conditions or because of sparser vegetation anthills are less important for larvae of *Z. purpuralis*. Similar observations applied to the eastern Swabian Alb (SW Germany), where larvae of *Z. purpuralis* are strictly dependent on anthills within dense calcareous grasslands harbouring a high litter layer (Wagner, pers. com.). Especially on old fallows, anthills often represent the only microsites where *Thymus* species still occur frequently (cf. Bonte et al., 2003). In our study, the cover of host plants was also strongly negatively correlated with the height of the herb layer and the cover of litter (cf. Table 4) as measures for decreasing land-use intensity. In contrast, within grazed calcareous grasslands of the study area characterized by an open vegetation structure both *Thymus* species are competitive enough to grow abundantly within the matrix vegetation (Fartmann, 2004).

Our results demonstrate that anthills of *L. flavus* facilitate the use of calcareous grasslands with adverse habitat characteristics for reproduction of *Z. purpuralis*. This seems to be especially true for the Upper Diemel Valley. Thanks to the higher precipitation and cooler climate the calcareous grasslands in this area are much more productive than compared to the Middle or Lower Diemel Valley (Fartmann, 2004). Under such conditions open patches with occurrence of *Thymus* species disappear much faster after abandonment.

5. Conclusion

By creating nest mounds *L. flavus* increases habitat heterogeneity and creates small-scale vegetation mosaics within semi-natural grasslands. For the first time we demonstrate that nest mounds of *L. flavus* play an important role in the reproduction of a declining burnet moth species because of an altered vegetation compared with the matrix vegetation.

These microsites represent preferred larval habitats of *Z. purpuralis* as they combine two essential elements for successful larval development: (i) a favourable microclimate because of an open vegetation structure and (ii) a sufficient amount of food. The study underlines the importance of *L. flavus* as an ecosystem engineer for

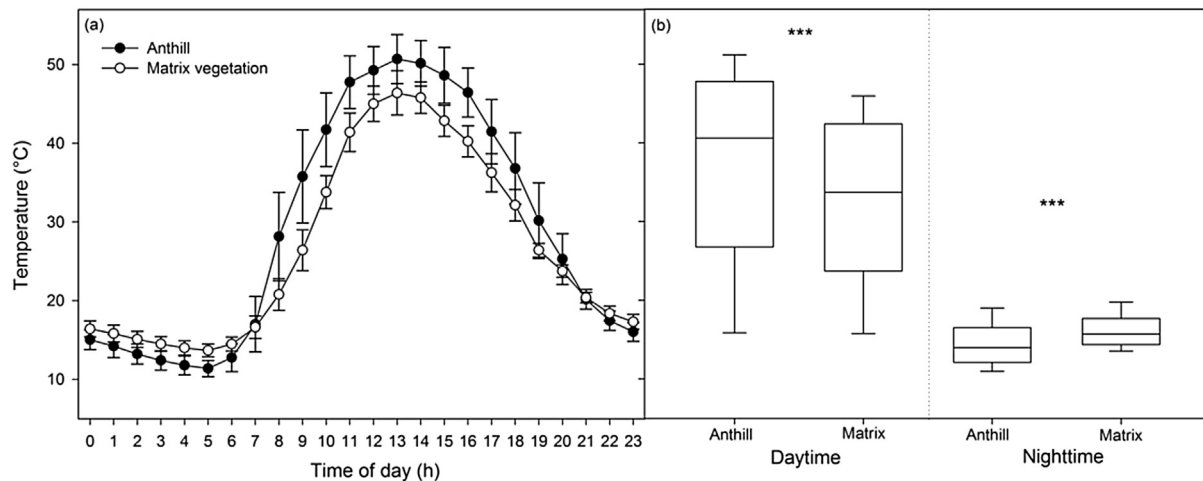


Fig. 1. (a) Hourly mean temperatures on anthills ($N = 10$) and within the matrix vegetation ($N = 10$) during the total measuring period, (b) differences in total hourly mean temperatures during daytime (6 a.m.–9 p.m.) and nighttime (10 p.m.–5 a.m.) between anthills and matrix vegetation. The boxes show the median and the first and third quartile, the whiskers indicate the 10th and 90th percentiles. Comparisons were carried out with Wilcoxon signed-rank tests, *** $P < 0.001$.

maintaining habitat heterogeneity and biodiversity within semi-natural grasslands. Especially within more productive sites and regions with a cooler local climate where small-scale patches with bare ground and low-competitive host plants are rare because of the abandonment of land-use and fast succession, nest mounds of *L. flavus* serve as important refuge sites for *Z. purpuralis*.

It is likely that anthills promote further arthropod species dependent on an open vegetation structure. Therefore, continuing research is necessary to detect the significance of ant nest mounds for rare arthropod species within semi-natural grasslands.

With respect to the conservation of *Z. purpuralis* the results of our study emphasize the importance of soil disturbance for the reproduction of this species. Within sites where anthills are missing conservation measures should focus on maintaining an appropriate vegetation structure offering suitable conditions for reproduction of the burnet moth species. In order to maintain an open vegetation structure with small-scale patches of soil disturbance and a high cover of host plants we recommend traditional rough sheep grazing as a suitable management option for the species (cf. Fartmann, 2006; Löffler et al., 2013). Consequently, trampling by animals creates small-scale gaps of soil disturbance which are beneficial for the establishment of low-competitive plant species (McIntyre et al., 1995; Bullock et al., 2001; Fleischer et al., 2013).

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