SHORT COMMUNICATION

The role of a mound-building ecosystem engineer for a grassland butterfly

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Abstract Both land use intensification and abandonment within grasslands lead to a homogenisation of vegetation structure. Therefore, specially structured microsites such as vegetation gaps with bare ground play an important role for species conservation within grasslands. Vegetation gaps are crucial for the establishment of low-competitive plant species and offer special microclimatic conditions essential for the development of the immature stages of many invertebrate species. The influence of small-scale soil disturbance in the form of mounds created by ecosystem engineers such as ants or moles on biodiversity is therefore of special scientific concern. The effects of mound-building species on plant species diversity have been extensively studied. However, knowledge on the significance of these species for the conservation of other animals is rare. In this study we analyse the importance of mounds created by the European mole (*Talpa europaea*) as an oviposition habitat for the small copper (*Lycaena phlaeas*) within Central European mesotrophic grasslands. Our study showed that host plants occurring at molehills were preferred for oviposition. Oviposition sites were characterised by an open vegetation structure with a high proportion of bare ground (with a mean coverage of about 50 %), a low cover of herbs and low-growing vegetation (mean height: 4.5 cm). Our study clearly illustrates the importance of small-scale soil disturbance for immature stages of *L. phlaeas* and the conservation of this species within mesotrophic grasslands. Mound-building ecosystem engineers, such as *T. europaea*, act as important substitutes for missing dynamics within mesotrophic grasslands by diversifying vegetation structure and creating small patches of bare soil.

Keywords Bare ground · Conservation · Disturbance · Microclimate · Molehill · Oviposition

Introduction

In Europe semi-natural grasslands maintained by traditional, low-intensive land use practices are among the most species-rich terrestrial habitats (Veen et al. 2009). However, semi-natural grasslands are strongly declining throughout the continent (Cousins 2009; Hooftman and Bullock 2012) and are therefore of high conservation value (Veen et al. 2009). On the one hand, species richness of semi-natural grasslands is negatively affected by far-reaching threats such as climate change, atmospheric nitrogen deposition or habitat fragmentation as a consequence of land use changes (Duprè et al. 2010; Krauss et al. 2010; Parmesan 2006; Sala et al. 2000). On the other hand, direct effects of land use change have local impact on species composition within species-rich grasslands. As a consequence of intensive land use practices, fertilisation or abandonment, highly competitive plant species are favoured (Drobnik et al. 2011; Grime et al. 2007; Mariotte et al. 2013). This not only leads to biodiversity loss as a consequence of changes in plant species composition, but

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Fig. 1 **a** Mesotrophic grassland disturbed by *T. europaea*; **b** *Rumex acetosa* used for oviposition growing at the edge of a molehill

also influences species communities due to the homogenisation of the vegetation structure with a loss of specially structured microsites such as vegetation gaps with bare ground (Vickery et al. 2001). However, a heterogeneous vegetation structure plays a significant role for the conservation of high species richness within grasslands. For example, local soil disturbance is crucial for the establishment of low-competitive plant species (Fleischer et al. 2013; Ödman et al. 2012; Tschöpe and Tielbörger 2010). Furthermore, such sites act as important microhabitats for disturbance-dependent invertebrate species (e.g. Gröning et al. 2007; Warren and Büttner 2008; Wünsch et al. 2012). Many butterfly species require a specific vegetation structure as they are dependent on certain microclimatic conditions for larval development (García-Barros and Fartmann 2009). For example, open soil is an important key resource for the successful development of the pre-adult stages of many thermophilous species (e.g. Krämer et al. 2012; Möllenbeck et al. 2009). Furthermore, butterflies are characterised by a high host plant specificity (Munguira et al. 2009) and a metapopulation structure (Anthes et al. 2003; Bergman and Kindvall 2004; Eichel and Fartmann 2008; Thomas et al. 2001). Therefore, the decline of butterfly species exceeds those of many other species groups (Thomas 2005; Thomas and Clarke 2004).

There are several ways in which small-scale soil disturbance is created within grasslands. Trampling by grazers is an important driver of soil disturbance and the establishment of vegetation gaps (Bullock et al. 1994). However, such sites also occur within grasslands due to mound-building activities of certain ecosystem engineering species. Generally, ecosystem engineers are defined as organisms that alter the availability of resources by modifying the physical state of biotic or abiotic materials (Jones et al. 1994). In Central European grasslands classic examples of mound-building ecosystem engineers are yellow meadow ants (*Lasius flavus*) or the European mole, *Talpa europaea* (Fig. 1a). The effects of these ecosystem

engineers have been extensively studied with regard to plant species diversity (King 1977; Lenoir 2009; Schiffers et al. 2010; Seifan et al. 2010). However, knowledge on the importance of mounds created by these species as habitats for other taxa is still rare. For the first time, Streitberger and Fartmann (2013) demonstrated the importance of molehills as a preferred larval habitat for the threatened butterfly species *Pyrgus malvae*. In the current study we focus on the oviposition site selection of *Lycaena phlaeas* (Lepidoptera: Lycaenidae). This butterfly species is a typical grassland species and an open vegetation structure with a certain amount of bare ground is assumed to be essential for the development of the pre-adult stages (Ebert and Rennwald 1991). In general butterfly species are declining throughout large parts of Europe, especially within grassland ecosystems (EEA 2013). Even though *L. phlaeas* is a widespread species, there is clear evidence that in parts of its range it is declining as a consequence of land use intensification (EEA 2013; Léon-Cortés et al. 2000; Wenzel et al. 2006). Knowledge on the larval ecology is therefore essential for future conservation of this species (cf. García-Barros and Fartmann 2009). The hypothesis of this study is that within mesotrophic grasslands where open soil is usually scarce, molehills serve as important larval habitats for *L. phlaeas*. Based on the results of this study conservation recommendations are derived.

Materials and methods

Study area

The study was carried out on the military training site Handorf-Ost, which is located 10 km north-east of the city of Münster (federal state of North Rhine-Westphalia, Germany; 51°59′45″ N, 07°44′00″ E). The area is a plain (about 55 m above sea level) with an extent of about 320 ha. It is characterised by a suboceanic climate with a

mean annual temperature of 9.2 °C and a mean precipitation of 760 mm (Deutscher Wetterdienst, pers. comm.). The area is mainly dominated by silty sands (Fleischer et al. 2010). Due to a high degree of variation in soil humidity and local differences in land use intensity the study site is characterised by a patchwork of different vegetation types (Fleischer et al. 2010). Large parts of the site comprise grasslands managed by mowing or sheep paddock grazing (Standortverwaltung Münster, unpublished). Due to the abandonment of fertilisation since the 1980s, rare grassland communities typical for low-intensive usage such as the *Diantho-Armerietum* (sandy grasslands) or species-rich stands of the *Lolio-Cynosuretum* (mesotrophic grasslands) are still widespread within the site (Fleischer et al. 2010).

Study species

L. phlaeas has a widespread distribution within the Northern Hemisphere (Kudrna et al. 2011). *L. phlaeas* is multivoltine with three to four generations per year and hibernates in the larval stage. Adults are on the wing between April and October (Ebert and Rennwald 1991). In Germany, the species occurs within different kinds of open habitats such as nutrient-poor grasslands or ruderal sites (Ebert and Rennwald 1991). The larvae feed monophagously on *Rumex* species, especially *R. acetosa* and *R. acetosella* (Ebert and Rennwald 1991; Léon-Cortés et al. 2000).

Sampling design

To analyse the oviposition site selection of *L. phlaeas*, potential host plants were searched for eggs. Sampling was carried out from mid-August until the end of September 2008. A total of 23 mesotrophic grassland patches (*Lolio-Cynosuretum*) where molehills were abundant were selected within the study area. Within each patch a 100 m² sized plot was randomly chosen for egg searching.

Next to *L. phlaeas*, *Lycaena tityrus* occurs within the study area. The eggs of both species cannot be clearly distinguished by morphological criteria. Eggs of *L. tityrus* are found within the study area until mid-August (Rose, unpublished). To control for the absence of *L. tityrus* eggs during the study period, we gathered three to four eggs per plot for rearing of eggs to the adult stage. All reared eggs ($N = 82$) which were brought up to the adult stage belonged to *L. phlaeas*. Nevertheless, to avoid confusion with eggs of a possible third generation of *L. tityrus* (cf. Ebert and Rennwald 1991) all further analyses were carried out using two groups: definite *L. phlaeas* samples and undetermined *Lycaena* spec. samples.

Egg search was undertaken by dividing the plot into a grid of 1×1 m (=100 grids per plot). Within each square meter three host plants (*R. acetosa* or *R. acetosella*) were randomly selected and searched for eggs. In each case an egg was found ($N = 888$) the following vegetation structure parameters were analysed within 20×20 cm around the oviposition site: cover of herb and litter layer; cover of bare ground and molehill; the total and single cover of potential host plant species and heights of herb layer, host plant and oviposition. Furthermore, the vegetation density was estimated by using a frame of 20 cm depth and 40 cm width in three layers of 5 cm from 5–15 cm height above ground. In order to document the complete range of available host plants, 11 to 12 control samples were selected within each plot by searching for the nearest host plant to a randomly thrown stick (Anthes et al. 2003). A 20×20 cm sized plot was laid around the host plant and the same parameters as mentioned above were analysed for these control samples ($N = 260$).

Statistical analysis

Significant differences between the parameters were tested using generalised linear mixed-effects models (GLMMs; Bates et al. 2014). Two binomial GLMMs were carried out to reveal which vegetation structure parameters determine the oviposition site choice of *L. phlaeas* and *Lycaena* spec., respectively. Additionally, the same model was applied by using the total data set. In all GLMMs, *plot* served as the random factor. To avoid intercorrelations, only non-intercorrelated parameters (correlations with $|r_s| < 0.7$) were introduced as explanatory variables into the models (intercorrelated parameters in all datasets: cover of bare ground and molehills; cover of bare ground and herb layer; vegetation density and cover of herb layer). The selection of the final models was based on backward selection using likelihood ratio tests with a significance level of $\alpha = 0.05$. All analyses were applied using R 3.0.2 (R Development Core Team 2014).

Results

R. acetosa was the most frequently used host plant (*L. phlaeas*: $N = 64$, 78 %; *Lycaena* spec.: $N = 570$, 71 %; control samples: $N = 230$, 88 %). 58 eggs of *L. phlaeas* and 513 eggs of *Lycaena* spec. were found directly at a molehill (71 and 64 %, respectively).

There were significant differences between *L. phlaeas* and *Lycaena* spec. oviposition sites compared to control samples (Table 1). All oviposition sites had a more open vegetation structure. The cover of the herb layer was lower and oviposition sites had a higher cover of bare ground and molehills. However, the cover of litter was higher at oviposition sites. The vegetation height and vegetation density up to 15 cm above ground were lower in comparison to

Table 1 Mean values ± SD of all the parameters of *L. phlaeas* oviposition sites (N = 82), *Lycaena* spec. oviposition sites (N = 806) and control samples (N = 260)
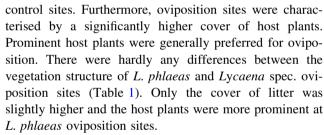
	L. phlaeas (N = 82) MW ± SA	*L.* spec. (N = 806) MW ± SA	Control (N = 260) MW ± SA	L. p. versus C. P	L. s. versus C. P	L. p. versus L. s. P
Vegetation cover (%)						
Herb layer	40.9 ± 17.8	37.8 ± 17.3	90.5 ± 18.9	***	***	n.s.
Litter	10.9 ± 19.3	10.3 ± 18.3	4.1 ± 9.3	***	***	*
Bare ground	48.0 ± 27.2	51.8 ± 24.6	4.9 ± 16.3	***	***	n.s.
Molehills	37.6 ± 28.5	37.9 ± 31.9	2.2 ± 10.8	***	***	n.s.
R. acetosa	11.2 ± 10.6	8.0 ± 8.9	6.4 ± 7.8	***	***	n.s.
R. acetosella	1.3 ± 3.3	2.3 ± 4.9	0.5 ± 1.8	*	***	n.s.
All host plants	12.5 ± 9.7	10.3 ± 8.9	6.9 ± 7.6	***	***	n.s.
Horizontal cover (%)						
5 cm	20.7 ± 13.4	22.1 ± 13.1	77.0 ± 25.2	***	***	n.s.
10 cm	6.4 ± 7.3	6.1 ± 7.9	41.5 ± 26.8	***	***	n.s.
15 cm	1.7 ± 3.8	1.4 ± 3.2	14.4 ± 18.6	***	***	n.s.
Height (cm)						
Herb layer	4.3 ± 1.9	4.5 ± 2.7	8.9 ± 3.0	***	***	n.s.
Prominence[a]	1.4 ± 3.0	0.4 ± 2.9	−1.1 ± 3.6	***	***	**
Oviposition	1.6 ± 1.3	1.4 ± 1.4	–	–	–	n.s.

Comparison between groups was done using GLMMs with plot as a random factor: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, n.s. not significant

L. p. L. phlaeas, C. Control samples, *L. s. Lycaena* spec.

[a] Prominence = Host plant height minus herb layer height

Table 2 Statistics of GLMMs (binomial): relationship between the probability of oviposition by *L. phlaeas* and *Lycaena* spec. and environmental parameters

Variable	Estimate	SE	Z	P
(a)				
Cover of herbs	−0.08124	1.11475	2.191	***
Cover of molehill	0.04521	0.01571	2.878	**
Cover of host plants	0.07043	0.03226	2.183	*
Pseudo R^2 [Nagelkerke] = 0.62				
(b)				
Cover of herbs	−0.1108	0.01079	−10.273	***
Cover of molehill	0.04288	0.01341	3.198	**
Cover of host plants	0.06141	0.02031	3.023	***
Pseudo R^2 [Nagelkerke] = 0.71				
(c)				
Cover of herbs	−0.11001	0.0104	−10.580	***
Cover of molehill	0.04392	0.01331	3.300	***
Cover of host plants	0.06182	0.02019	3.063	**
Pseudo R^2 [Nagelkerke] = 0.71				

(a) $N = 82$ *L. phlaeas* samples and $N = 260$ control samples; (b) $N = 806$ *Lycaena* spec. and $N = 260$ control samples; (c) $N = 888$ *Lycaena* samples and $N = 260$ control samples. The following variables entered into the analyses were not significant (a, b, c): cover of litter and host plant prominence. Non-significant predictors were excluded from the models by stepwise backward-selection ($P > 0.05$): * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

control sites. Furthermore, oviposition sites were characterised by a significantly higher cover of host plants. Prominent host plants were generally preferred for oviposition. There were hardly any differences between the vegetation structure of *L. phlaeas* and *Lycaena* spec. oviposition sites (Table 1). Only the cover of litter was slightly higher and the host plants were more prominent at *L. phlaeas* oviposition sites.

The GLMMs revealed a similar pattern in oviposition site selection (Table 2): a low cover of the herb layer as well as a high cover of molehills and host plants increased the likelihood of a site being accepted for oviposition by *L. phlaeas*, *Lycaena* spec. and the total data set. The explanatory power of all three models was high with Nagelkerke Pseudo R^2 values of 0.61–0.71.

Discussion

As there were hardly any differences in the oviposition site selection of *L. phlaeas* compared to those of *Lycaena* spec. and we had no evidence for a third generation of *L. tityrus* in our study area we believe that it is justified to relate all analysed oviposition sites to *L. phlaeas*. Even though *L. phlaeas* is considered a generalist species inhabiting a wide range of open habitats, a high proportion of eggs were

found on molehills where the vegetation structure clearly differed from the surrounding vegetation (Fig. 1b). Oviposition sites were characterised by a more open vegetation structure with a higher proportion of bare ground, a lower cover of herbs and a less dense and low-growing vegetation.

We assume that molehills were preferred as oviposition sites by *L. phlaeas* as they offer suitable microclimatic conditions for the development of the pre-adult stages. In general, a warm microclimate is known to favour larval development of butterflies (Weiss et al. 1988; Roy and Thomas 2003). Microclimate is strongly influenced by vegetation structure characteristics (Stoutjesdijk and Barkman 1992). Generally, a low-growing and open vegetation structure induces higher temperatures near the ground due to higher solar radiation compared to dense and high swards (cf. Stoutjesdijk and Barkman 1992).

Molehills presumably act as important refuge sites for oviposition by *L. phlaeas* within more productive habitats where succession speed is high and open soil rarely occurs (cf. Ellenberg and Leuschner 2010). The same phenomenon has also been observed for another disturbance-dependent butterfly species, *Pyrgus malvae* (Streitberger and Fartmann 2013). Within calcareous grasslands on deeper soils where patches of bare ground are scarce, host plants located directly at molehills were regularly occupied by immature stages of this species. Besides a favourable microclimate, these sites also offered sufficient food. A sufficient amount of food is a further crucial parameter determining oviposition site selection of butterfly females (Fartmann and Hermann 2006; García-Barros and Fartmann 2009). Several studies demonstrate a preference for high-growing host plants or sites with a high cover of host plants for oviposition (e.g. Porter 1992; Küer and Fartmann 2005; Streitberger et al. 2012). Both are also true for *L. phlaeas*. Sites with a higher cover of host plants and more prominent host plants were preferred for oviposition. The leaves of a *Rumex* plant, especially in *R. acetosella*, provide relatively little biomass. Hence, food shortage might become a limiting factor for the caterpillars of *L. phlaeas*. Prominent plants are more conspicuous and allow a better host plant accessibility for the ovipositing females, possibly explaining the preference for protruding host plants (e.g. Wiklund 1984; García-Barros and Fartmann 2009).

Next to the use of molehills as larval habitats, such microsites also play an important role as a non-consumable resource for butterflies. As demonstrated by Dennis (2004) and Dennis and Sparks (2005), molehills are used as preferred perching sites by *Inachis io* and other territorial Nymphalid species due to favourable microclimatic conditions.

Implications for conservation

Our study clearly illustrates the importance of small-scale soil disturbance for the development of immature stages of *L. phlaeas* and underlines the significance of a heterogeneous vegetation structure for the conservation of biodiversity within mesotrophic grasslands. There are several other studies which highlight the importance of small-scale soil disturbance for the conservation of rare and endangered species (e.g. Fleischer et al. 2013; Gröning et al. 2007; Tschöpe and Tielbörger 2010; Warren and Büttner 2008). Within mesotrophic grasslands where bare ground is usually rare, mound-building ecosystem engineers, such as *T. europaea*, play an important role for *L. phlaeas*. They act as important substitutes for missing soil disturbance by diversifying vegetation structure (Seifan et al. 2010) and creating small patches of bare soil which are used for oviposition. These sites also play an important role for other species groups. For example, within dense vegetation swards molehills are important refuge habitats for low-competitive and small plant species (Watt 1974). For the conservation of *L. phlaeas* within mesotrophic grasslands the creation of microsites with bare ground is the key management option. Grazing in particular causes a significant amount of soil disturbance (Bullock et al. 2001; McIntyre et al. 1995). Within mown sites where gaps of open soil are rare the mechanical creation of local soil disturbance is an alternative method to create a suitable oviposition habitat of *L. phlaeas*. Within grasslands frequented by *T. europaea* mole control measures should be avoided. Additionally, an increase in earthworm abundance by a reduction of land use intensity is beneficial for *T. europaea* (cf. Edwards et al. 1999).

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