CrossMark

ORIGINAL PAPER

Vegetation heterogeneity caused by an ecosystem engineer drives oviposition-site selection of a threatened grassland insect

Merle Streitberger[1,2] · Thomas Fartmann[1,2]

Abstract Soil-disturbing ecosystem engineers play an important role in plant-species diversity in grasslands as they increase vegetation heterogeneity by creating gaps due to burrowing or mound-building activities. However, knowledge of the ecological importance of these microsites for arthropods is still rare. In this study, we analyse the role of ant-nest mounds of the yellow meadow ant (*Lasius flavus*) for oviposition-site selection of the silver-spotted skipper (*Hesperia comma*). Ant mounds were searched for *H. comma* eggs. Microclimatic and vegetation parameters were ascertained at occupied sites and control sites within the matrix vegetation. Furthermore, we analysed the habitat requirements of *L. flavus* by means of nest counting and the sampling of environmental parameters within different sites. *L. flavus* occurred most frequently in abandoned and less steep sites with deeper soils. Mean egg occupancy rates of *H. comma* on ant hills were 32 %, nearly twice as high as at control sites (18 %). In contrast to the surrounding vegetation, nest mounds were characterized by a lower vegetation cover and litter and a higher proportion of bare ground. Furthermore, they had a higher cover of host plants compared with control samples. These microhabitats offered the following essential key factors for the larval development of *H. comma*: (1) a suitable microclimate due to open vegetation and (2) a high amount of host plants.

This study highlights the importance of *L. flavus* as an ecosystem engineer within central European grasslands because this species increases vegetation heterogeneity.

Keywords Calcareous grassland · Disturbance · Egg-laying · *Hesperia comma* · *Lasius flavus* · Microhabitat preference

Handling Editor: Heikki Hokkanen.

✉ Merle Streitberger
merle.streitberger@uni-osnabrueck.de

1 Department of Biodiversity and Landscape Ecology, University of Osnabrück, Barbarastraße 13, 49076 Osnabrück, Germany

2 Institute of Biodiversity and Landscape Ecology (IBL), Hafenweg 31, 48155 Münster, Germany

Introduction

Land-use change is one of the most important drivers of the current global biodiversity crisis (Sala et al. 2000). In Europe, semi-natural grasslands maintained by traditional management such as low-intensive grazing harbour a great proportion of biodiversity. However, due to the intensification or abandonment of land use, semi-natural grasslands have declined dramatically during the past 60 years (cf. Van Dijk 1991; Critchley et al. 2003; Cousins and Eriksson 2008; Cousins 2009; Walker et al. 2009). Among grasslands, calcareous grasslands represent one of the most species-rich types (Veen et al. 2009). Due to their high plant-species diversity and low land-use intensity, these grasslands function as important habitats for butterflies. Within Europe, they harbour approximately 50 % of all native butterfly species (Van Swaay 2002), and they are home to many specialized and rare species (Krämer et al. 2012a; Börschig et al. 2013).

As a consequence of the very specific habitat requirements of many butterfly species, the decline of butterflies exceeds that of many other taxonomic groups (Thomas et al. 2004; Thomas 2005). The immature stages of butterflies are highly dependent on certain conditions for their development (Thomas 1991; García-Barros and Fartmann 2009). For example, the larvae of many species are

🍎 Springer

characterized by high host-plant specificity (Munguira et al. 2009). In addition, a suitable microclimate plays an important role for the successful development of the pre-adult stages (García-Barros and Fartmann 2009). Within Central European grasslands, many thermophilous species prefer open vegetation with a warm microclimate for oviposition and the development of their larvae (e.g. Möllenbeck et al. 2009; Eilers et al. 2013; Löffler et al. 2013). Small-scale patches of bare ground are therefore of special importance for the conservation of these species. However, due to intensive land-use practices with fertilization or abandonment, only a few highly competitive plant species are favoured (Grime et al. 2007; Drobnik et al. 2011; Mariotte et al. 2013), which leads to closed turf and homogenous vegetation (Vickery et al. 2001).

Therefore, soil-disturbing ecosystem engineers play an important role in maintaining the species diversity within central European semi-natural grasslands. They create small-scale patches of open vegetation due to burrowing or mound-building activities and increase vegetation heterogeneity (cf. King 1977; Dean et al. 1997; Seifan et al. 2010; Streitberger and Fartmann 2013). In general, 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). Social burrowing rodents such as prairie dogs represent an intensively studied example of soil-disturbing ecosystem engineers in terms of biodiversity research (e.g. Davidson and Lightfood 2008; Augustine and Baker 2013). Within central European calcareous grasslands, typical examples of soil-disturbing ecosystem engineers are represented by mound-building ant species such as the yellow meadow ant (*Lasius flavus*, Fabricius 1782) or the European mole (*Talpa europaea*, Linnaeus 1758), a fossorial insectivorous mammal. The importance of these ecosystem engineers has been well studied in terms of plant species diversity. Mounds created by ants or moles favour annuals or low-competitive plant species (King 1977; Dean et al. 1997; Dauber et al. 2006; Lenoir 2009; Streitberger et al. 2014). However, there is also evidence that these microsites function as preferred habitats for the pre-adult stages of certain butterfly species. For example, host plants growing at the edge of molehills are preferred for oviposition by the grizzled skipper (*Pyrgus malvae*, Linnaeus 1758) and the small copper (*Lycaena phlaeas*, Linnaeus 1761) as these sites offer optimal microclimatic conditions for the development of their offspring (Streitberger and Fartmann 2013; Streitberger et al. 2014). In addition, the nest mounds of *L. flavus* function as important habitats for the larvae of the endangered transparent burnet moth (*Zygaena purpuralis*, Brünnich 1763) as the mounds harbour high host-plant abundance and offer optimal microclimatic conditions for the development of the pre-adult stages (Streitberger and Fartmann 2015).

In this study, we analyse whether the nest mounds of *L. flavus* function as important microhabitats for the oviposition of the silver-spotted skipper (*Hesperia comma*, Linnaeus 1758). In central Europe, *H. comma* is a thermophilous species that strongly depends on open vegetation with a warm microclimate for the development of the immature stages (Thomas et al. 1986; Fartmann 2004). We therefore assume that the ant hills of *L. flavus* are the preferred oviposition sites within semi-natural grasslands. We suppose that these sites offer suitable conditions for larval development due to the open vegetation and high host-plant abundance. Additionally, we analyse the habitat requirements of *L. flavus* by means of nest counts. According to these results, we have derived management strategies for the conservation of the species.

Materials and methods

Study species

Lasius flavus

Lasius flavus (Hymenoptera: Formicidae) has a Palearctic distribution (Seifert 2007). The ant species occurs frequently within agricultural and urban habitats (Seifert 2007). In central Europe, *L. flavus* prefers fresh to wet grasslands maintained by low-intensity land use (Seifert 1993, 2007). Even though *L. flavus* is widespread within central Europe, it is declining due to its sensitivity to eutrophication (Seifert 1993). *L. flavus* is a hypogeic species that builds aboveground nest mounds to create warm microclimatic conditions for their offspring (Dlussky 1981). Their main food source is root aphids and their honeydew (Pontin 1978).

Hesperia comma

Hesperia comma (Lepidoptera: Hesperiidae) is widely distributed throughout the Palearctic region. The core of its range is found from Europe to East Asia (Ebert and Rennwald 1991). In Germany, *H. comma* is relatively rare and is listed as endangered (Reinhardt and Bolz 2011). The species is univoltine and hibernates in the egg stage. Within our study area, the Diemel Valley (central Germany), the flight period ranges from the end of July until the beginning of September, and the larvae feed monophagously on *Festuca ovina* agg. (Fartmann and Mattes 2003; Fartmann 2004). In general, the species prefers a wide range of different open habitats, such as dry and nutrient-poor grasslands or woodland glades (Ebert and Rennwald 1991). However, *H. comma* is strongly dependent on open and short turf with a high proportion of bare ground for oviposition (Thomas et al. 1986; Hermann and Steiner 1997; Fartmann and Mattes

2003; Fartmann 2004). Within the Diemel Valley, preferred oviposition sites of *H. comma* are mainly found within steep south- or south-west-facing slopes with a high sunshine duration and a warm microclimate (Fartmann and Mattes 2003; Fartmann 2004).

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 sub-oceanic climate (Müller-Wille 1981) and has elevations between 100 and 500 m a.s.l. Large parts of the hillsides along the Diemel Valley consist of limestone and have been grazed for centuries by traditional shepherd grazing. Currently, approximately 55 % of these grasslands are still being actively managed, mainly by traditional rough sheep grazing (Fartmann 2004). The calcareous grasslands harbour a high species richness and are therefore of great value for conservation. Large parts of the area contribute to the Natura 2000 network (Fartmann 2004) and are considered a Prime Butterfly Area (Van Swaay and Warren 2003). A detailed description of the study area is given by Fartmann (2004).

Habitat preferences of *Lasius flavus*

The habitat preferences of *L. flavus* were analysed at the beginning of June 2013. Forty 10 m × 10 m sized sites were selected within 22 calcareous grassland patches where nest mounds of *L. flavus* were abundant (hereafter referred to as 'occupied sites'). Within every site, all visible nest mounds in which *L. flavus* was present were counted. Additionally, the following climatic and vegetation structure parameters were analysed for the whole patch: elevation, aspect, slope, land use (grazed, abandoned), mean daily potential sunshine duration for the growing season (April to September) using a horizontoscope (cf. Tonne 1954), cover of herbs, cryptogams, litter and stones as well as turf height. For further analyses, aspect was converted into 'northness' and 'eastness' by cosine and sine transformation (northness: 360° = 1; 180° = −1; eastness: 90° = 1; 270° = −1). In addition, the soil depth was measured at five randomly selected plots within the site. The mean of the five values was calculated for statistical analysis. The same parameters were analysed at 11 randomly selected sites within 11 randomly selected patches where *L. flavus* was absent (hereafter referred to as 'unoccupied sites').

Ant hills as oviposition habitats for *Hesperia comma*

To analyse the importance of ant hills as an oviposition habitat of *H. comma* in calcareous grasslands, nest mounds

of *L. flavus* were searched for eggs of *H. comma*. The sampling took place at the beginning of September 2013 shortly after the peak of the flight period (cf. Fartmann and Mattes 2003; Fartmann 2004). Altogether, 31 randomly selected 10 m × 10 m sites were set up at locations with a high abundance of ant hills within 16 patches of calcareous grasslands where the occurrence of the species was known by the authors. Within these sites, all ant hills with a minimum height of 5 cm and the presence of the host plant (*F. ovina* agg.) were selected for further analyses. At each selected ant hill, a 30 cm × 30 cm sized plot was arranged at the spot with the highest abundance of host plants. The whole plot was searched for eggs of *H. comma*. Whenever an egg was found (hereafter called occupied ant hills) the following microclimatic, vegetation and ant hill characteristics (height, diameter) were analysed for the whole plot: aspect (converted into 'northness' and 'eastness', see above), slope, daily potential sunshine duration in August using a horizontoscope, cover of host plants, herbs, cryptogams, litter and bare ground, turf height and height and diameter of the ant hill. Furthermore, the vegetation density was estimated by using a horizontal frame of 20 cm depth and 40 cm width in two layers of 5 cm from 5 to 10 cm height above ground. Within all selected sites, eggs of *H. comma* were found on a total of 90 ant hills.

To document the complete range of available habitats, the same microclimatic and vegetation characteristics as mentioned above were analysed at control samples of the same size within the matrix vegetation. The control samples (N = 90) were arranged whenever an egg was found on an ant hill at the nearest host plant occurring with a minimum distance of one metre north of the analysed ant hill.

In addition, the same parameters as mentioned above were analysed at ant hills where the host plant of the study species was present, but the eggs of *H. comma* were missing (N = 45). Here, the analyses also took place in 30 cm × 30 cm sized plots that were arranged on the ant hill where the host plants occurred most frequently. These samples were selected randomly within the five patches of highest abundance of the pre-adult stages of the species. These patches were used for analysis to maximize the likelihood that the unoccupancy of the ant hills was a result of unsuitable environmental conditions and independent from population size.

Statistical analysis

To compare the sites occupied and unoccupied by *L. flavus* and for comparing ant hills containing eggs of *H. comma* with the control samples and the unoccupied ant hills, binomial generalized linear mixed-effect models (GLMM) were applied with the presence and absence data of the species as the response variable. Models were compared with null models which included solely the random term by

using likelihood ratio tests (χ^2 analysis). In cases of multiple comparisons, Bonferroni corrections of the significance levels were considered. For analysing the effect of sampling (ant hills and control samples) on occupation rates per site (=proportion of occupied samples with host plants) by *H. comma*, proportional binomial GLMM were calculated and compared with null models by likelihood ratio tests.

Furthermore, linear mixed and generalized linear mixed models were applied to identify which environmental parameters possess the highest explanatory power for the occurrence of the study species by inserting all variables with a significant effect on species occurrence within the models. In the case of *L. flavus*, a linear mixed model (LMM) was applied to the number of inhabited nest mounds as the dependent variable (unoccupied sites included in model). Patch served as the random factor.

A binomial GLMM was performed to ascertain which parameters had the highest explanatory power for the occurrence of eggs of *H. comma* on ant hills in general (occupied ant hill and control samples were introduced in the models). Additionally, a binomial GLMM was calculated to ascertain which environmental parameters explain the use of a certain ant hill as an oviposition habitat by *H. comma* (occupied ant hill and unoccupied ant hill samples were inserted in the models). Sites within patches served as the random factor within the two models.

Only variables with a significant effect on species occurrence were inserted into the models as explanatory variables to avoid overfitting. The vegetation density, measured 5 and 10 cm above ground, was strongly inter-correlated (Spearman rank correlation [r_s] value >0.7) and was therefore merged into one synthetic variable ('vegetation density') by using a principal component analysis (PCA). Vegetation density was used as an explanatory variable in the GLMM for comparing occupied and unoccupied ant hills. The variable was positively correlated with vegetation density 5 cm above ground ($r_s = 0.92$, $P < 0.001$) and vegetation density 10 cm above ground ($r_s = 0.92$, $P < 0.001$). The eigenvalue of the component was 1.7 and explained 85 % of the variance in the data set. The selection of the final models was based on backward selection using likelihood ratio tests (χ^2-analysis) with a significance level of $\alpha = 0.05$.

The PCA was ascertained using SPSS 22. We used the lme4-package in R 3.2.3 (R Development Core Team 2016) for the calculation of the mixed models.

Results

Habitat preferences of *Lasius flavus*

The mean number of nest mounds inhabited by *L. flavus* per site was 9 ± 4.5 SE. Land use had a significant effect

on the occurrence of *L. flavus* (χ^2: 8.8663; $P < 0.01$; $df = 1$, Fig. 1a). In total, 37.5 % of the occupied sites were abandoned and 62.5 % were grazed, whereas all unoccupied sites were grazed. Moreover, *L. flavus* preferred sites that were less steep and characterized by deeper soils and a lower cover of stones (Table 1).

A similar result was revealed by the LMM (Table 2). The likelihood of finding a high abundance of nest mounds of *L. flavus* was increased in abandoned sites (Fig. 1a) and in sites with deeper soils (Fig. 1b) as well as less steep sites (Fig. 1c, Table 2). However, the explanatory power of the model was low with an adjusted pseudo R^2 [Nagelkerke's] value of 0.09.

Ant hills as oviposition habitats for *Hesperia comma*

A total of 192 of *H. comma* eggs were found at 30 % of all ant hills where *F. ovina* agg. occurred. In contrast, 37 *H. comma* eggs were found within 20 % of the control samples. Sample type (ant hill vs. control samples) had a significant effect on occupation rate per site (mean occupation rate ± SD, ant hills with host plants: 31.6 ± 17.1 %; control samples: 17.8 ± 27.1 %, $\chi 2$: 172.50, $P < 0.001$; $df = 1$). Land use had no significant effect on the occupation rates per site on ant hills (with host plants) (mean occupation rates ± SD, grazed sites: 31.8 ± 16.8 %, abandoned sites: 31.25 ± 18.3 %, χ^2: 0.2068, $P > 0.05$; $df = 1$) and on the occupation rates per site within control samples (grazed sites: 17.3 ± 24.7 %, abandoned sites: 18.6 ± 31.7 %, χ^2: 0.401, $P > 0.05$; $df = 1$).

In comparison with the control samples, ant hills occupied by *H. comma* were characterized by more open vegetation. Occupied ant hills had a lower herb, cryptogam and litter cover and a significantly higher host plant cover (Table 3). Additionally, occupied ant hills exhibited a higher cover of bare ground compared to control samples. From unoccupied ant hills, occupied ant hills by *H. comma* were distinguished by a significantly less dense vegetation (Table 3).

The GLMM revealed that the likelihood of finding an *H. comma* egg on an ant hill was strongly influenced by vegetation structure. A low cover of herbs and a higher cover of bare ground increased the likelihood of finding an egg on ant hills in comparison with the control samples (Fig. 2a, b; Table 4a). The explanatory power of the model was high, with an adjusted pseudo R^2 [Nagelkerke's] of 0.71 %. The likelihood of a certain ant hill used for oviposition was increased when the ant hills were characterized by low vegetation density (Fig. 2c; Table 4b). Nonetheless, the explanatory power of the model was low with an adjusted pseudo R^2 [Nagelkerke's] value of 0.08.
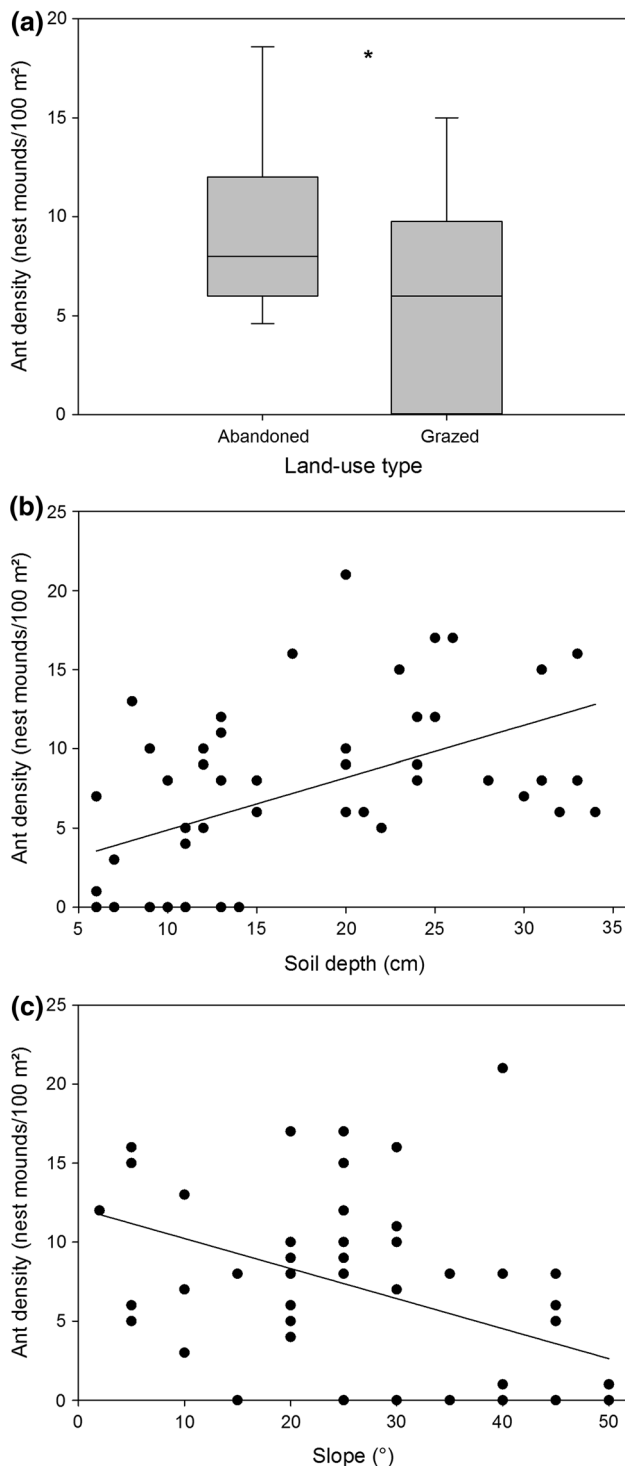
Fig. 1 Results of the LMM: ant density (nest mounds/100 m²) in relation to **a** land-use, **b** soil depth and **c** slope. **a** Result of single predictor LMM: $y = 6.0556 + 3.8111 \times 1$ (*abandonment*), $P < 0.05$, $R_N^2 = 0.02$. The *boxes* show the median and the first and third quartile, the whiskers indicate the 10th and 90th percentile. The regression slopes in (**b**) and (**c**) were fitted by using single predictor LMMs: **b** $y = 1.57029 + 0.33054 \times$ soil depth, $P < 0.001$, $R_N^2 = 0.1$, **c** $y = 12.13181 - 0.19009 \times$ Slope, $P < 0.05$, $R_N^2 = 0.02$. *$P < 0.05$, $R_N =$ Nagelkerke's Pseudo R^2

Discussion

Habitat preferences of *Lasius flavus*

According to this study land use, soil depth and slope were the most important factors explaining the abundance of *L. flavus* in calcareous grasslands. The ants occurred most frequently on abandoned and less steep sites with deeper soils. However, these factors only explained a low variance within the data set. Therefore, further parameters have to be important in the determination of the abundance of *L. flavus*. In addition, nest density was relatively low with a mean of nine nest mounds (with heights above 5 cm) per 100 m² compared with other studies (Dlussky 1981; Dauber and Wolters 2005).

The height and type of a *L. flavus* nest is dependent on several factors, such as subsoil drainage, its age and the surrounding vegetation structure (Waloff and Blackith 1962; Dlussky 1981; Blomqvist et al. 2000). Therefore, it is conceivable that abundance estimations by means of nest mound counts are partially biased. Nonetheless, it is very likely that the calcareous grasslands within our study area only offer sub-optimal habitat conditions for *L. flavus*. Presumably, the soils are too dry and shallow, especially on steeper south-facing slopes, to favour a high abundance of *L. flavus*. According to Seifert (2007), *L. flavus* prefers fresh to wet soils. The importance of deep soils for *L. flavus* was also emphasized by Dean et al. (1997). Hypogeic galleries are excavated by this species within depths of 40–50 cm (Dlussky 1981).

Generally, *L. flavus* prefers sites with low land-use intensity; intensively used or abandoned grasslands are avoided (Feldmann 2009). Abandoned sites may become unsuitable for this species when the vegetation gets too high and dense and precludes insolation of the nests (Waloff and Blackith 1962). However, within our study area, *L. flavus* was especially abundant within abandoned sites. Presumably, these sites still offered a suitable vegetation structure with a warm microclimate due to a relatively low succession speed at the relatively shallow south-facing slopes with high solar irradiation where most of the analyses took place. In contrast, even calcareous grasslands with low-intensity grazing have a very short turf. Hence, they are characterized by a warm microclimate (Stoutjesdijk and Barkman 1992) and soil conditions possibly too dry for *L. flavus*.

In addition to soil depth and land use, food supply is regarded as a further important determinant of *L. flavus* abundance (Dean et al. 1997; Dauber and Wolters 2005). The density of root aphids is higher in sites with a high plant diversity (Pontin 1978; Seifert 1993; Kamczyc and Gwiazdowicz 2013). According to Seifert (1993), *L. flavus*

Table 1 Mean values ± SD of all numerical parameters at sites occupied (N = 40) and unoccupied (N = 11) by *L. flavus*

Parameter	Occupied sites	Unoccupied sites	χ^2	P
Climate				
Elevation (m)	281.3 ± 76.5	238.6 ± 44.5	3.6863	n.s.
Northness	−0.4 ± 0.6	−0.5 ± 0.5	0.2566	n.s.
Eastness	−0.2 ± 0.7	−0.4 ± 0.6	0.7018	n.s.
Slope (°)	23.7 ± 12.2	32.3 ± 9.8	15.311	***
Daily sunshine duration (h)[a]	10.6 ± 1.1	11.3 ± 1.1	1.8145	n.s.
Vegetation cover (%)				
Herb layer	70.3 ± 8.2	69.1 ± 13.6	0.1301	n.s.
Litter	48.3 ± 20.6	39.1 ± 16.9	1.8994	n.s.
Cryptogams	38.4 ± 20.3	26.1 ± 16.6	3.6598	n.s.
Stones	0.6 ± 2.5	6.6 ± 7.6	13.014	***
Turf height (cm)	12.8 ± 3.8	11.9 ± 3.1	0.5721	n.s.
Soil depth (cm)	18.9 ± 8.6	10.0 ± 3.0	12.776	***

Comparison between groups by binomial generalized linear mixed-effect models (cf. methods section for details)

n.s. not significant

*** $P < 0.001$

[a] Mean daily sunshine duration during the growing season

Table 2 Statistics of LMM: relationship between the abundance of *L. flavus* nest mounds and environmental parameters (N = 40 occupied and N = 11 unoccupied sites)

Parameter	Estimate	SE	χ^2	P
Land use				
Abandoned	3.88321	1.41682	7.0077	**
Soil depth	0.25221	0.07252	10.4622	**
Slope	−0.16691	0.05165	9.5005	**

The following variables entered into the analysis were not significant: cover of stones. Non-significant predictors were excluded from the models by stepwise backward selection ($P > 0.05$)

** $P < 0.01$. Pseudo R^2 [Nagelkerke's] = 0.09

is therefore sensitive to fertilization and nitrogen deposition because both lead to a loss of plant-species richness by favouring a few competitive species (Bobbink et al. 1998). However, in our study, a limited food supply due to low plant-species diversity caused by eutrophication is not the reason for the low nest densities. All studied patches are unfertilized (Fartmann 2004), and despite a current atmospheric nitrogen deposition rate of 15–20 kg ha^{-1} y^{-1} (Wichink Kruit et al. 2014), the grasslands are still characterized by high plant-species richness. Plots with a size of 3 m × 3 m usually contain more than 40 species of vascular plants (Fartmann 2004).

Furthermore, the age of a site is an important factor explaining the abundance of *L. flavus*. The ant species is most frequently found within older persistent grasslands with a minimum age of 30 years (Dauber and Wolters

2005; Fagan et al. 2008). All studied patches fulfilled this requirement. They are permanent grasslands and have been used for at least many decades, if not centuries (Fartmann 2004).

In conclusion, the calcareous grasslands of the study area represent only sub-optimal habitats for *L. flavus*. In most parts of the grasslands, the soils are probably too dry and shallow for a high abundance of the ant species. On these grasslands, *L. flavus* mainly occurred on less steep slopes with deeper soils. In contrast to the general preference of the ant species for grasslands with low land-use intensity, abandoned calcareous grasslands were favoured within the study area. While calcareous grasslands with a low-intensity grazing are characterized by a very short turf and a warm microclimate possibly resulting in too dry soil conditions for *L. flavus*, abandoned calcareous grasslands seem to offer more suitable microclimatic conditions.

Ant hills as oviposition habitats for *Hesperia comma*

This study demonstrated that nest mounds of the ant species *L. flavus* represent important oviposition habitats for the endangered butterfly *H. comma*. The mean egg occupancy rate per site was with 32 %, nearly twice as high as at control samples (18 %). These nest mounds were preferred by *H. comma* for oviposition because these microsites have a vegetation structure that strongly differs from the matrix vegetation. In contrast to the surrounding vegetation, the nest mounds of *L. flavus* were characterized by more open vegetation due to lower cover of vegetation, less

Table 3 Mean values ± SD of all numerical parameters at occupied ant hill (N = 90), control (N = 90) and unoccupied ant hill (N = 45) samples of *H. comma*

Parameter	Occupied ant hills	Control samples	χ^2	P	Unoccupied ant hills	χ^{2a}	P^a
Climate							
Northness	−0.4 ± 0.7	−0.5 ± 0.5	2.4855	n.s.	−0.2 ± 0.8	3.8208	n.s.
Eastness	−0.1 ± 0.6	−0.3 ± 0.6	2.9526	n.s.	0.1 ± 0.6	2.0898	n.s.
Slope (°)	22.1 ± 17.3	22.3 ± 9.9	0.0113	n.s.	18.1 ± 15.1	0.971	n.s.
Daily sunshine duration (h)[b]	10.7 ± 1.2	10.5 ± 1.2	0.4324	n.s.	10.7 ± 1.1	0.2912	n.s.
Vegetation cover (%)							
Host plants	10.9 ± 8.3	6.9 ± 6.3	13.393	***	9.9 ± 9.9	0.5959	n.s.
Herb layer	42.1 ± 16.5	64.1 ± 10.5	84.668	***	49.2 ± 15.4	3.5403	n.s.
Litter	28.8 ± 15.7	36.4 ± 15.1	10.749	**	32.4 ± 17.3	1.8186	n.s.
Cryptogams	5.0 ± 11.4	15.5 ± 16.2	25.912	***	6.4 ± 18.2	0.9571	n.s.
Bare ground	34.4 ± 19.7	1.1 ± 4.4	167.89	***	29.2 ± 18.5	3.7414	n.s.
Horizontal cover (%)							
5 cm	42.3 ± 13.9	46.4 ± 17.6	3.0448	n.s.	51.3 ± 14.3	9.8328	**
10 cm	9.9 ± 8.7	9.7 ± 10.1	0.0319	n.s.	16.5 ± 10.6	11.843	**
Turf height (cm)	5.8 ± 8.4	6.4 ± 2.0	0.3939	n.s.	6.4 ± 2.1	1.0192	n.s.
Ant-hill structure (cm)							
Height	23.8 ± 6.3	–	–	–	24.4 ± 7.5	0.3628	n.s.
Diameter	61.3 ± 12.6	–	–	–	59.1 ± 14.4	0.1562	n.s.

Comparisons between groups by binomial generalized linear mixed-effect models (cf. methods section for details)

** $P < 0.01$; *** $P < 0.001$, *n.s.* not significant

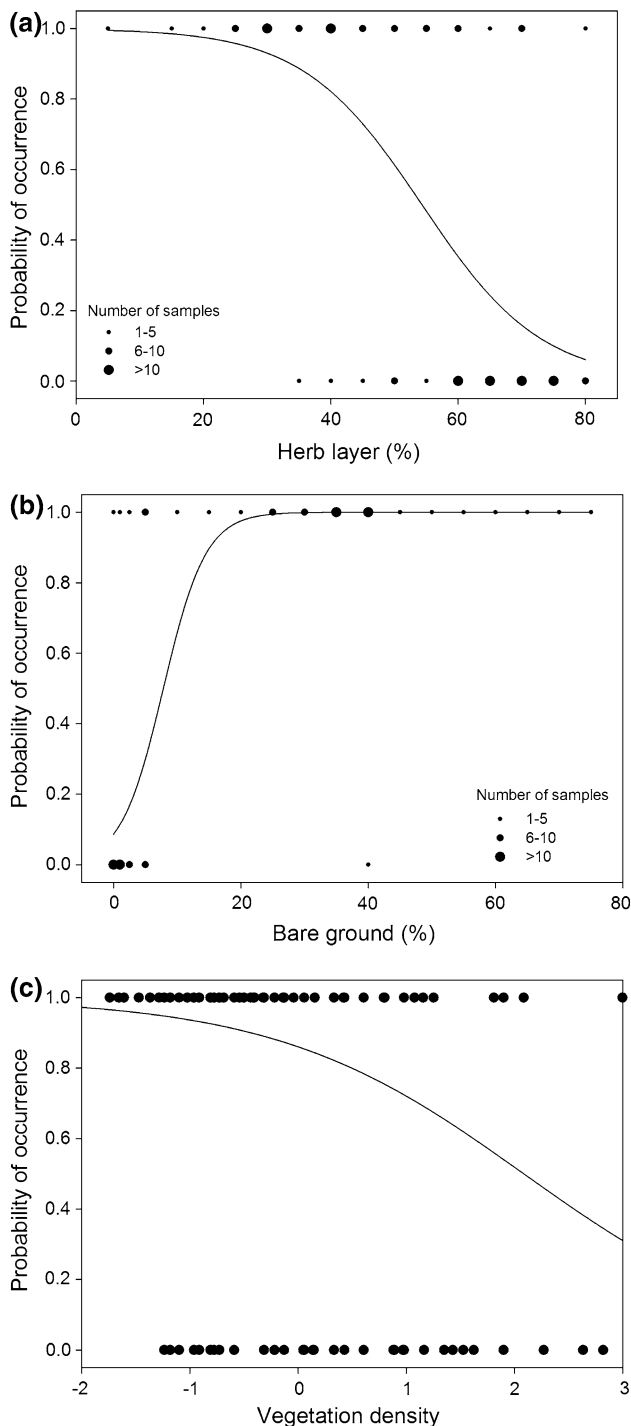[a] Occupied and unoccupied ant hills were tested against each other

[b] Mean daily sunshine duration during August

litter and a higher proportion of bare ground. Furthermore, they had a higher cover of host plants.

In general, microclimate and host-plant abundance are among the most important drivers of habitat selection in butterflies (García-Barros and Fartmann 2009). It is most likely that ant hills are preferred for oviposition by *H. comma* because these sites offer suitable microclimatic conditions for the development of the eggs as a result of the open vegetation. The importance of a warm microclimate for oviposition-site selection by *H. comma* was also emphasized by other studies (Thomas et al. 1986; Fartmann and Mattes 2003). *H. comma* is strongly dependent on grasslands with open turf and a high amount of bare ground due to grazing or disturbance by mammal herbivores (Thomas et al. 1986; Fartmann and Mattes 2003; Lawson et al. 2012). Overall, the larval development of butterflies is increased by warm conditions (Weiss et al. 1988; Roy and Thomas 2003). Several factors determine the microclimate near the ground (Stoutjesdijk and Barkman 1992) and are relevant for the microhabitat selection of butterflies. On the one hand, general characteristics at the landscape level such as aspect or insolation influence microclimatic conditions within sites. For example,

H. comma occurs most frequently within south-facing sites that are characterized by a high degree of solar insolation (Thomas et al. 1986; Fartmann and Mattes 2003; Lawson et al. 2012). Additionally, the structure of the vegetation is an important determinant for microclimatic conditions near the ground (Stoutjesdijk and Barkman 1992). Due to the sparse vegetation and low litter cover on ant hills, solar radiation reaches the ground to a greater extent compared with sites with higher growing matrix vegetation (cf. Stoutjesdijk and Barkman 1992). Additionally, the high amount of bare ground on ant hills favours microclimatic warming of these sites by heat absorption (cf. Stoutjesdijk and Barkman 1992). This was confirmed by Streitberger and Fartmann (2015) who measured significantly higher temperatures (up to 50 °C and more) on ant hills compared with the surrounding vegetation.

Furthermore, sufficient food is indispensable for the successful development of larvae (García-Barros and Fartmann 2009). Typically, many butterfly species prefer microhabitats with a high amount of host plants for oviposition (e.g. Krämer et al. 2012b; Streitberger et al. 2012; Weking et al. 2013). In contrast to the control samples, ant hills had higher host-plant abundance. Due to

◀ **Fig. 2** Results of the binomial GLMMs: the probability of the occurrence of *H. comma* on ant hills in general in relation to **a** cover of herb layer, **b** cover of bare ground and probability of occurrence of *H. comma* on certain ant hills in relation to **c** vegetation density. The regression slopes in (**a**) and (**b**) were fitted by using single predictor GLMMs: **a** $y = 5.78768 - 0.10656 \times$ herb layer, $P < 0.001$, $R_N^2 = 0.34$, **b** $y = -2.35810 + 0.30128 \times$ bare ground, $P < 0.001$, $R_N^2 = 0.67$. **c** Fit of regression slope, cf. Table 4b, intercept = 1.8182. *Vegetation density* represents a synthetic variable that merges horizontal vegetation cover (%) in 5 and 10 cm above ground. *Negative values* represent low vegetation densities (%) (mean values ± SD: vegetation density 5 cm above ground: 35.6 ± 8.8; vegetation density 10 cm above ground: 5.8 ± 4.6) and *positive values* represent high vegetation densities (mean values ± SD: vegetation density 5 cm above ground: 57.5 ± 10.6; vegetation density 10 cm above ground: 20.0 ± 8.9). R_N^2 = Nagelkerke's Pseudo R^2

Table 4 Statistics of GLMM: (a) binomial, prediction of the use of ant hills as oviposition habitats by *H. comma* ($N = 90$ occupied ant hills) in comparison with the control samples ($N = 90$); and (b) binomial, prediction of the use of a certain ant hill as an oviposition habitat ($N = 90$ occupied ant hills) in comparison with unoccupied ant hills ($N = 45$)

Variable	Estimate	SE	χ^2	P	R_N^2
(a) Occupied ant hills versus control samples					0.71
Cover of herb layer	−0.05793	0.02083	8.876	**	
Cover of bare ground	0.27277	0.06369	92.095	***	
(b) Occupied versus unoccupied ant hills					0.08
Vegetation density[a]	−0.8717	0.2609	13.12	***	

The following variables entered into the analysis were not significant: (a) cover of host plants, litter and cryptogams. Non-significant predictors were excluded from the models by stepwise backward selection ($P > 0.05$)

** $P < 0.01$; *** $P < 0.001$. R_N^2 = Nagelkerke's Pseudo R^2

[a] Vegetation density measured 5 and 10 cm above ground was merged into a synthetic variable by PCA due to strong intercorrelations

the small growth form and thin leaves of *F. ovina* agg., it is very likely that densely growing tussocks are especially important for *H. comma* to supply the larvae with sufficient food.

Nonetheless, the GLMM revealed that an open vegetation and, hence, a warm microclimate were more important than host-plant abundance for explaining the use of ant hills for oviposition by *H. comma*. However, there is

evidence that, due to climate change, *H. comma* tends to use a broader range of differently structured microhabitats for oviposition. This was documented at its northern range margin in south-eastern England (Davies et al. 2006). Here, *H. comma* has been continuously expanding northwards since 1982 and, currently, is also found within denser growing habitats or north-facing slopes (Davies et al. 2005, 2006). *Hesperia comma* adapts oviposition-site selection to the present temperature conditions. Davies et al. (2006) demonstrated that there is a negative relationship between microclimate and ambient temperatures in oviposition-site selection by *H. comma*. Therefore, hotter microhabitats are preferred when ambient temperatures

are low. Vice versa, host plants growing within a cooler microhabitat are selected when ambient temperatures are high (Davies et al. 2006). Similar observations were also made on a broader spatial scale (Lawson et al. 2014). Within cooler regions, the oviposition pattern of *H. comma* was more strongly associated with bare ground and a warm microclimate compared to warmer regions. Nonetheless, within our study area, *H. comma* seems to be strictly dependent on a very warm microclimate for oviposition.

Among ant hills, those mounds that had a low vegetation density near the ground were preferred for oviposition by *H. comma*. However, this parameter only explained a minor proportion of ant-hill selection by *H. comma*. A further explanation for the choice of certain ant hills might be the structure of the occurring host plants. Generally, *H. comma* favours low-growing tussocks of *F. ovina* agg. for oviposition, preferentially ones which have been bitten off by grazing animals (Thomas et al. 1986; Fartmann and Mattes 2003). Ant-nest mounds are preferred feeding sites for herbivorous mammals especially within abandoned sites (cf. Veen et al. 2012). Low-growing tussocks bitten off by grazing animals occurred frequently on ant mounds within our study area (own observation). Rabbits and hares are rare within the studied calcareous grasslands, especially within the upper parts of the Diemel Valley (own observation) where most of the analyses took place. In contrast, roe deer (*Capreolus capreolus*) abundance is very high. It is very likely that ant mounds are preferred grazing sites for roe deer. Although roe deer are regarded to be browsers, there is evidence that roe deer feed extensively on grasses within open landscapes (Abbas et al. 2012). According to Fartmann and Mattes (2003), possible explanations for the preference of *H. comma* for tussocks bitten off by mammals are the better accessibility of the leaves compared to long ones, the higher insolation of low-growing tussocks or the better digestibility of regenerating shoots for the larvae due to a lower *C/N*-ratio.

Conclusion

This study showed that ant-nest mounds of *L. flavus* in calcareous grasslands represent important oviposition habitats for *H. comma*. The butterfly species prefers ant hills for oviposition because they offer warm microclimatic conditions for successful development of the eggs due to open vegetation. Our results highlight the important role of *L. flavus* as an ecosystem engineer within central European grasslands because this species increases vegetation heterogeneity due to its mound-building activity. Within our study area, *L. flavus* is especially abundant within abandoned calcareous grasslands. Here, bare ground is rare, and therefore, ant hills are important habitats for

arthropod species dependent on open vegetation. This was underlined by Streitberger and Fartmann (2015) who demonstrated that the larvae of *Z. purpuralis* are frequently found on ant hills within fallow calcareous grasslands.

We recommend the introduction of traditional rough grazing to create small-scale patches of bare ground and an open vegetation for the conservation of *H. comma*. However, with respect to climate change, it is likely that *H. comma* may tend to use denser vegetation for oviposition, especially within extremely hot years (cf. Davies et al. 2006). Thus, it is important to increase vegetation heterogeneity within grassland patches to offer a higher variety of differently structured microhabitats (cf. Fartmann 2006). In terms of climate change, the presence of ant hills is extremely important for *H. comma,* especially within more productive sites with a dense vegetation cover. Here, the presence of ant-nest mounds of *L. flavus* increases the diversity of microhabitats, which enables *H. comma* to adjust oviposition-site selection to climatic conditions.

For the conservation of the ecosystem engineer *L. flavus*, land-use intensification should be avoided, particularly on deep soils where the species is more abundant. Mowing with heavy machinery should also be avoided as it destroys the nest mounds (own observation). However, within less steep or more productive abandoned patches, it is likely that in the long run nest mounds will become too shaded by tall vegetation leading to an abandonment of the nests by *L. flavus*. Therefore, a low-intensive land use, preferably grazing, should be introduced.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

References

Abbas F, Picot D, Merlet J, Cargnelutti B, Lourtet B, Angibault J-M, Daufresne T, Aulagnier S, Verheyden H (2012) A typical browser, the roe deer, may consume substantial quantities of grasses in open landscapes. Eur J Wildl Res 59:69–75. doi:10.1007/s10344-012-0648-9

Augustine DJ, Baker BW (2013) Associations of grassland bird communities with black-tailed prairie dogs in the North American great plains. Conserv Biol 27:324–334. doi:10.1111/cobi.12013

Blomqvist MM, Olff H, Blaauw MB, Bongers T, van der Putten W-H (2000) Interactions between above-and belowground

biota:importance for small-scale vegetation mosaics in a grassland ecosystem. Oikos 90:582–598

Bobbink R, Hornung M, Roelofs JGM (1998) The effects of air-borne nitrogen pollutants on species diversity in natural and semi-natural European vegetation. J Ecol 86:717–738. doi:10.1046/j.1365-2745.1998.8650717.x

Börschig C, Klein AM, von Wehrden H, Krauss J (2013) Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. Bas Appl Ecol 14:547–554. doi:10.1016/j.baae.2013.09.002

Cousins S (2009) Landscape history and soil properties affect grassland decline and plant species richness in rural landscapes. Biol Conserv 142:2752–2758. doi:10.1016/j.biocon.2009.07.001

Cousins SAO, Eriksson O (2008) After the hotspots are gone. Land use history and grassland plant species diversity in a strongly transformed agricultural landscape. Appl Veg Sci 11:365–374. doi:10.3170/2008-7-18480

Critchley CNR, Burke MJW, Stevens DP (2003) Conservation of lowland semi-natural grasslands in the UK: a review of botanical monitoring results from agri-environment schemes. Biol Conserv 115:263–278. doi:10.1016/S0006-3207(03)00146-0

Dauber J, Wolters V (2005) Colonization of temperate grasslands by ants. Bas Appl Ecol 6:83–91. doi:10.1016/j.baae.2004.09.011

Dauber J, Rommeler A, Wolters V (2006) The ant Lasius flavus alters the viable seed bank in pastures. Eur J Soil Biol 42:S157–S163. doi:10.1016/j.ejsobi.2006.06.002

Davidson AD, Lightfood DC (2008) Burrowing rodents increase landscape heterogeneity in a desert grassland. J Arid Environ 72:1133–1145. doi:10.1016/j.jaridenv.2007.12.015

Davies ZG, Wilson RJ, Brereton TM, Thomas CD (2005) The re-expansion and improving status of the silver-spotted skipper butterfly (Hesperia comma) in Britain: a metapopulation success story. Biol Conserv 124:189–198. doi:10.1016/j.biocon.2005.01.029

Davies ZG, Wilson RJ, Coles S, Thomas CD (2006) Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. J Anim Ecol 75:247–256

Dean WRJ, Milton SJ, Klotz S (1997) The role of ant nest-mounds in maintaining small-scale patchiness in dry grasslands in Central Germany. Biodivers Conserv 6:1293–1307

Dlussky GM (1981) Nester von Lasius flavus. Pedobiologia 21:81–99

Drobnik J, Römermann C, Bernhardt-Römermann M, Poschlod P (2011) Adaptation of plant functional group composition to management changes in calcareous grassland. Agric Ecosyst Environ 145:29–37. doi:10.1016/j.agee.2010.12.021

Ebert G, Rennwald E (1991) Die Schmetterlinge Baden-Württembergs. Bd. 2: Tagfalter II. Eugen Ulmer, Stuttgart

Eilers S, Pettersson LB, Ockinger E (2013) Micro-climate determines oviposition site selection and abundance in the butterfly Pyrgus armoricanus at its northern range margin. Ecol Entomol 38:183–192. doi:10.1111/een.12008

Fagan KC, Pywell RF, Bullock JM, Marrs RH (2008) Are ants useful indicators of restoration success in temperate grasslands? Restor Ecol 18:373–379. doi:10.1111/j.1526-100X.2008.00452.x

Fartmann T (2004) Die Schmetterlingsgemeinschaften der Halbtrockenrasen-Komplexe des Diemeltales. Biozönologie von Tagfaltern und Widderchen in einer alten Hudelandschaft. Abh Westf Mus Naturkde 66:1–256

Fartmann T (2006) Oviposition preferences, adjacency of old woodland and isolation explain the distribution of the Duke of Burgundy butterfly (Hamearis lucina) in calcareous grasslands in central Germany. Ann Zool Fenn 43:335–347

Fartmann T, Mattes H (2003) Störungen als ökologischer Schlüsselfaktor beim Komma-Dickkopffalter (Hesperia comma). Abh Westf Mus Naturkde 65:131–148

Feldmann R (2009) Buckelwiesen, Buckelweiden: Häufung von Nesthügeln der Gelben Wiesenameise, Lasius flavus. Ameisenschutz akt 23:1–6

García-Barros E, Fartmann T (2009) Butterfly oviposition: sites, behaviour and modes. In: Settele J, Shreeve TG, Konvicka M, van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 29–42

Grime JP, Hodgson JG, Hunt R (2007) Comparative plant ecology, 2nd edn. Castlepoint Press, Dalbeattie

Hermann G, Steiner R (1997) Eiablage- und Larvalhabitat des Komma-Dickkopffalters (Hesperia comma LINNÉ 1758). Carolinea 55:35–42

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386. doi:10.2307/3545850

Kamczyc J, Gwiazdowicz DJ (2013) The diversity of soil mites (Acari: Mesostigmata) in yellow ant (Lasius flavus) nests along a gradient of land use. Biologia 68:314–318. doi:10.2478/s11756-013-0154-x

King TJ (1977) The plant ecology of ant-hills in calcareous grasslands. I. Patterns of species in relation to ant-hills in southern England. J Ecol 65:235–256. doi:10.2307/2259077

Krämer B, Poniatowski D, Fartmann T (2012a) Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. Biol Conserv 152:253–261. doi:10.1016/j.biocon.2012.03.038

Krämer B, Kämpf I, Enderle J, Poniatowski D, Fartmann T (2012b) Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. J Insect Conserv 16:857–865. doi:10.1007/s10841-012-9473-4

Lawson CR, Bennie JJ, Thomas CD, Hodgson JA, Wilson RJ (2012) Local and landscape management of an expanding range margin under climate change. J Appl Ecol 49:552–561. doi:10.1111/j.1365-2664.2011.02098.x

Lawson CR, Bennie J, Hodgson JA, Thomas CD, Wilson RJ (2014) Topographic microclimates drive microhabitat associations at the range margin of a butterfly. Ecography 37:732–740. doi:10.1111/ecog.00535

Lenoir L (2009) Effects of ants on plant diversity in semi-natural grasslands. Arth-Plant Int 3:163–172. doi:10.1007/s11829-009-9066-7

Löffler F, Stuhldreher G, Fartmann T (2013) How much care does a shrub-feeding hairstreak butterfly, Satyrium spini (Lepidoptera: Lycaenidae), need in calcareous grasslands? Eur J Entomol 110:145–152. doi:10.14411/eje.2013.020

Mariotte P, Buttler A, Kohler F, Gilgen AK, Spiegelberger T (2013) How do subordinate and dominant species in semi-natural mountain grasslands relate to productivity and land-use change? Bas Appl Ecol 14:217–224. doi:10.1016/j.baae.2013.02.003

Möllenbeck V, Hermann G, Fartmann T (2009) Does prescribed burning mean a threat to the rare satyrine butterfly Hipparchia fagi? Larval-habitat preferences give the answer. J Insect Conserv 13:77–87. doi:10.1007/s10841-007-9128-z

Müller-Wille W (1981) Westfalen. Landschaftliche Ordnung und Bindung eines Landes. 2. Auflage. Aschendorffsche Verlagsbuchhandlung, Münster

Munguira M, Garcia-Barros E, Cano JM (2009) Butterfly herbivory and larval ecology. In: Settele J, Shreeve TG, Konvička M, van Dyck H (eds) Ecology of butterflies in Europe. Cambridge University Press, Cambridge, pp 43–54

Pontin AJ (1978) The numbers and distribution of subterranean aphids and their exploitation by the ant Lasius flavus (Fabr.). Ecol Entomol 3:203–207. doi:10.1111/j.1365-2311.1978.tb00920.x

R Development Core Team (2016) R: a language and environment for statistical computing http://www.R-project.org. Accessed 17 Feb 2016

Reinhardt R, Bolz R (2011) Rote Liste und Gesamtartenliste der Tagfalter (Rhopalocera) (Lepidoptera: Papilionoidea et Hesperioidea) Deutschlands. Natursch Biol Vielfalt 70:167–194

Roy DB, Thomas JA (2003) Seasonal variation in the niche, habitat availability and population fluctuations of a bivoltine thermophilous insect near its range margin. Oecologia 134:439–444

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig B, Leemans R, Lodge DM, Mooney HA, Oesterheld M, LeRoy PN, Sykes MT, Walker BH, Walker M, Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287:1770–1774. doi:10.1126/science.287.5459.1770

Seifan M, Tielbörger K, Schloz-Murer D, Seifan T (2010) Contribution of molehill disturbances to grassland community composition along a productivity gradient. Acta Oecol 36:569–577. doi:10.1016/j.actao.2010.08.005

Seifert B (1993) Die freilebenden Ameisenarten Deutschlands (Hymenoptera: Formicidae) und Angaben zu deren Taxonomie und Verbreitung. Abh Ber Naturkundemus Görlitz 67:1–44

Seifert B (2007) Die Ameisen Mittel- und Nordeuropas. Lutra Verlags- und Vertriebsgesellschaft, Boxberg

Stoutjesdijk P, Barkman JJ (1992) Microclimate Vegetation and Fauna. Opulus Press, Uppsala

Streitberger M, Fartmann T (2013) Molehills as important larval habitats for the Grizzled Skipper (*Pyrgus malvae*) in calcareous grasslands. Eur J Entomol 110:643–648

Streitberger M, Fartmann T (2015) Vegetation and climate determine ant-mound occupancy by a declining herbivorous insect in grasslands. Acta Oecol 68:43–49. doi:10.1016/j.actao.2015.07.004

Streitberger M, Hermann G, Kraus W, Fartmann T (2012) Modern forest management and the decline of the woodland brown (*Lopinga achine*) in Central Europe. Forest Ecol Manage 269:239–248. doi:10.1016/j.foreco.2011.12.028

Streitberger M, Rose S, Hermann G, Fartmann T (2014) The role of a mound-building ecosystem engineer for a grassland butterfly. J Insect Conserv 18:745–751. doi:10.1007/s10841-014-9670-4

Thomas JA (1991) Rare species conservation: case studies of European butterflies. In: Spellerberg IF, Goldsmith FB, Morris MG (eds) The scientific management of temperate communities for conservation. Blackwell Scientific, Oxford, pp 149–197

Thomas JA (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. Phil Trans R Soc Lond Ser B Biol Sci 360:339–357. doi:10.1098/rstb.2004.1585

Thomas JA, Thomas CD, Simcox DJ, Clarke RT (1986) Ecology and declining status of the silver-spotted skipper butterfly (*Hesperia comma*) in Britain. J Appl Ecol 23:365–380. doi:10.2307/2404023

Thomas JA, Telfer MG, Roy DB, Preston CD, Greenwood JJD, Asher J, Fox R, Clarke RT, Lawton JH (2004) Comparative losses of British butterflies, birds, and plants and the global extinction crisis. Science 303:1879–1881. doi:10.1126/science.1095046

Tonne F (1954) Besser Bauen mit Besonnungs- und Tageslicht-Planung. Hofmann, Schorndorf

Van Dijk G (1991) The status of semi-natural grasslands in Europe. In: Goriup PD, Batten LA, Norton JA (eds) The conservation of lowland dry grassland birds in Europe. JNCC, Peterborough, pp 15–36

van Swaay CAM (2002) The importance of calcareous grasslands for butterflies in Europe. Biol Conserv 104:315–318. doi:10.1016/S0006-3207(01)00196-3

Van Swaay CAM, Warren M (eds) (2003) Prime Butterfly Areas in Europe: Priority Sites for Conservation. National Reference Centre for Agriculture, Nature and Fisheries, Ministry of Agriculture, Nature Management and Fisheries, Wageningen

Veen P, Jefferson R, de Smidt J, van der Straaten J (eds) (2009) Grasslands in Europe of high nature value. KNNV Publishing, Zeist

Veen GF, Geuverink E, Olff H (2012) Large grazers modify effects of aboveground—belowground interactions on small-scale plant community composition. Oecologia 168:511–518. doi:10.1007/s00442-011-2093-y

Vickery JA, Tallowin JR, Feber RE, Asteraki EJ, Atkinson PW, Fuller RJ, Brown VK (2001) The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. J Appl Ecol 38:647–664. doi:10.1046/j.1365-2664.2001.00626.x

Walker KJ, Preston CD, Boon CR (2009) Fifty years of change in an area of intensive agriculture: plant trait responses to habitat modification and conservation, Bedfordshire, England. Biodivers Conserv 18:3597–3613. doi:10.1007/s10531-009-9662-y

Waloff N, Blackith RE (1962) The growth and distribution of the mounds of *Lasius flavus* (Fabricius) (Hym: Formicidae) in Silwood Park, Berkshire. J Anim Ecol 31:421–437. doi:10.2307/2044

Weiss SB, Murphy DD, White RR (1988) Sun, slope, and butterflies: topographic determinants of habitat quality for *Euphydryas editha*. Ecology 69:1486–1496

Weking S, Hermann G, Fartmann T (2013) Effects of mire type, land use and climate on a strongly declining wetland butterfly. J Insect Conserv 17:1081–1091. doi:10.1007/s10841-013-9585-5

Wichink Kruit R, Schaap M, Segers A, Heslinga D, Builtjes P, Banzhaf S, Scheuschner T (2014) Modelling and mapping of atmospheric nitrogen and sulphur deposition and critical loads for ecosystem specific assessment of threats to biodiversity in Germany – PINETI (Pollutant INput and EcosysTem Impact). Substudy Report 1. Texte Umweltbundesamt 60/2014: 1–170