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ORIGINAL PAPER

Habitat quality determines patch occupancy of two specialist Lepidoptera species in well-connected grasslands

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Abstract
Over the past 150 years, semi-natural grasslands have suffered from either large-scale intensification of land use or abandonment. Lepidoptera are excellent model organisms to study the effects of land-use changes. In this study, we analysed the effects of landscape quality and habitat quality on the patch occupancy of two specialist Lepidoptera species, the butterfly *Erebia medusa* and the burnet moth *Adscita statices*, in small but well-connected semi-natural grasslands ($N=71$) in central Germany. Our study revealed that habitat quality was the main driver of patch occupancy of the two species. The generalized linear model analysis revealed that the occurrence of both species was determined by the litter volume. Additionally, for *A. statices* the cover of the host plants (*Rumex acetosella* and *R. acetosa*) was a further predictor. In contrast, landscape quality had only a minor role on patch occupancy. For both species, the observed population structure resembled a classical metapopulation of the Levins type consisting of many small and highly connected patches. In the short and medium term, abandonment was beneficial for both species, as it maintained the litter layer. In the long run it would lead to vegetation dominated by competitive, high-growing grasses (e.g., *Arrhenatherum elatius*) and a decreasing cover of the less competitive host plants, especially *Festuca ovina* agg. and *R. acetosella*. Hence, we would recommend rotational grazing or mowing, if sufficiently large parts of the habitats were not under management every year.

Keywords *Adscita statices* · *Erebia medusa* · Functional connectivity · Habitat fragmentation · Landscape composition · Vegetation structure

Introduction

Recent biodiversity loss is of global concern. The extinction rates of plant and animal species have risen continuously during recent decades and are nowadays 1000 times higher than would be expected without the influence of humans (De Vos et al. 2014). Despite great efforts in nature conservation, there are currently no signs of a trend reversal (Butchart et al. 2010). Therefore, Barnosky et al. (2011) suggest that we are heading for a sixth global mass extinction. For terrestrial biomes, land-use change is assumed to be the main cause of this biodiversity crisis (Vitousek et al. 1997; Sala et al. 2000; Foley et al. 2005).

Under traditional management with low-intensity grazing or mowing regimes, semi-natural grasslands harboured high biodiversity throughout Europe with a unique flora and fauna (Hoekstra et al. 2005; Veen et al. 2009; Poschlod 2015). Such species-rich semi-natural grasslands once covered large areas of central Europe (Veen et al. 2009; Ellenberg and Leuschner 2010; Poschlod 2015). However, over the past 150 years, semi-natural grasslands have suffered from either large-scale intensification of land use or abandonment (Vitousek 1994; Cousins 2001; Stoate et al. 2001; Baur et al. 2006). Nowadays, semi-natural grasslands are among the most threatened biotope types (Cousins 2001; Hoekstra et al. 2005; Veen et al. 2009), and grassland biodiversity is rapidly declining (Roem and Berendse 2000; Dupré et al. 2010).

Butterflies and burnet moths are excellent model organisms to study the effects of land-use changes at the landscape and habitat level (Franzén and Nilsson 2008; Krämer et al. 2012; Fartmann et al. 2013; Nilsson et al. 2013; Schirmel and

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Fartmann 2014). Most Lepidoptera species have very specific preferences with regard to habitat quality (Fartmann and Hermann 2006; García-Barros and Fartmann 2009). The availability of host plants is among the most important requirements. Microclimate, which is mediated by vegetation structure and local climate, also has a strong impact (García-Barros and Fartmann 2009; Wickmann 2009). The land use of a site influences the above-mentioned parameters, but also affects Lepidoptera directly through the disturbance event (Dover and Settele 2009). Especially habitat specialist species living in metapopulations are affected by habitat fragmentation (Franzén and Ranius 2004; van Swaay et al. 2006; Eichel and Fartmann 2008; Nilsson et al. 2013; Poniatowski et al. 2016). The use of connectivity measures is a reliable method to assess the degree of isolation of metapopulations (Hanski 1999; Moilanen and Nieminen 2002; Brückmann et al. 2010). However, the permeability of the landscape matrix should also be taken into account in patch-occupancy studies. This is possible by using functional (least-cost) rather than Euclidean distances between habitat patches (Stuhldreher and Fartmann 2014a; Poniatowski et al. 2016).

The woodland ringlet butterfly, *Erebia medusa*, and the green forester moth, *Adscita statices*, are both specialised Lepidoptera species which are declining in northern and central Europe (van Swaay and Warren 1999; Fartmann 2004; Sonderegger 2005; Nilsson et al. 2013; Stuhldreher and Fartmann 2014a). Systematic studies on the habitat requirements of *E. medusa* have only recently been conducted (Schmitt 1993; Stuhldreher and Fartmann 2014a, 2015). However, in contrast to our study area, the studied landscape was characterised by a higher degree of patch isolation. Detailed information about the habitat requirements of burnet moths is still scarce (Gutiérrez et al. 2001; Franzén and Ranius 2004; Streitberger and Fartmann 2015), and this is especially true of *A. statices* (Fartmann 2004; Franzén and Ranius 2004).

In this study, we analysed the effects of landscape quality and habitat quality on the patch occupancy of *E. medusa* and *A. statices* in small but still well-connected semi-natural grasslands in central Germany. At the landscape level we studied the effects of patch size, patch connectivity (functional connectivity) and landscape composition on patch occupancy. At the habitat level we analysed the influence of vegetation structure and host plant density on the occurrence of the two Lepidoptera species. Based on our study we make management recommendations for the conservation of both target species.

Materials and methods

Study species

The Lepidoptera species used in this study were *E. medusa* (Denis and Schiffermüller, 1775; Lepidoptera: Nymphalidae) and *A. statices* (Linnaeus, 1758; Lepidoptera: Zygaenidae). Both species have a Palaearctic distribution ranging from Europe to China (Ebert and Rennwald 1991; Ebert 1994; Schraml and Fartmann 2013). Within Europe, *E. medusa* reaches its western range boundary in central and south-eastern Europe (Ebert and Rennwald 1991; Schraml and Fartmann 2013). By contrast, *A. statices* extends into northern Spain and the British Isles (Naumann et al. 1999). In Central Europe, both species are found from the lowlands up to the subalpine belt (Ebert and Rennwald 1991; Ebert 1994; Sonderegger 2005; Schraml and Fartmann 2013). In our study area, the Diemel Valley, they are univoltine (Fartmann 2004). *E. medusa* is on the wing for about four weeks, usually between the beginning of May and mid-June (Fartmann 2004). The flight period of *A. statices* ranges from mid-May to the end of July, usually having a peak at the beginning of June (Fartmann 2004, pers. obs.). Both species are monophagous within the study area and colonize nutrient-poor, open and semi-open habitats with at most low land-use intensity such as wet, mesic, semi-dry calcareous or siliceous grasslands and heathlands as well as sunny woodland glades and clearings (Ebert and Rennwald 1991; Schmitt 1993; Ebert 1994; Fartmann 2004; Schraml and Fartmann 2013). The host plants of *E. medusa* are *Festuca ovina* agg. and *F. rubra* agg. (Fartmann 2004; Stuhldreher and Fartmann 2014a, 2015). In contrast, the larvae of *A. statices* feed on *Rumex acetosella* and *R. acetosa* (Ebert 1994). Both Lepidoptera species hibernate as larva (Ebert 1994; Stuhldreher and Fartmann 2014b) and are considered 'near threatened' in the German red data book (Reinhardt and Bolz 2011; Rennwald et al. 2011).

Study area

The study was carried out in the Diemel Valley (central Germany) stretching in a west-east direction along the border between the federal states of North Rhine-Westphalia and Hesse (Stuhldreher and Fartmann 2015). The study area covered approximately 28 km^2 in the western part of the Upper Diemel Valley (51°18′N/8°43′E and 51°21′N/8°49′E) at an elevation of 380−580 m a.s.l. (Fig. 1). The area has a suboceanic climate (Müller-Wille 1981), with a mean annual temperature of 7.5 °C and mean annual precipitation of 832 mm (Stuhldreher and Fartmann 2015). The study area is dominated by arable land, improved grassland and forest (Poniatowski and Fartmann 2010). However, it still contains a dense network of mesic nutrient-poor grassland patches (Fig. 1). A detailed description of the Diemel Valley is given by Fartmann (2004, 2006).

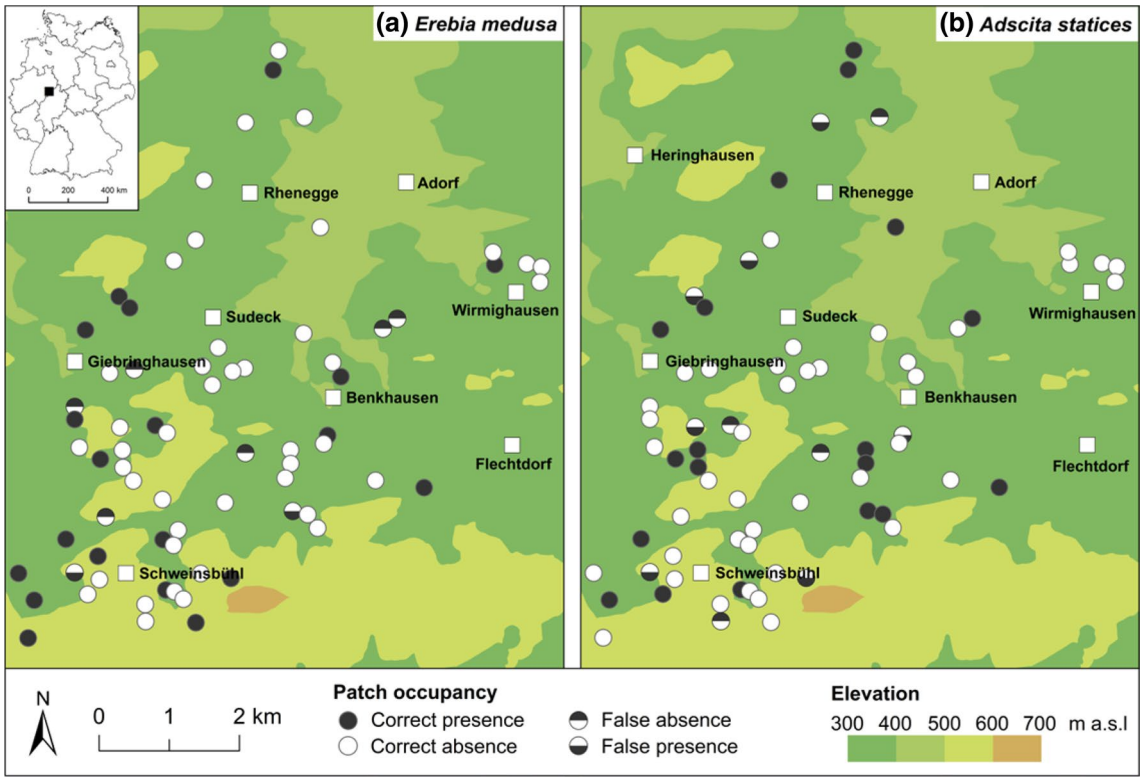

Fig. 1 Distribution of *Erebia medusa* and *Adscita statices* in grassland patches in the study area. Patch occupancy is indicated by shaded circles. Towns are indicated by white squares. *Correct presence* a modelled presence that was occupied, *correct absence* a modelled absence that was unoccupied, *false presence* a modelled presence that was unoccupied, *false absence* a modelled absence that was occupied. Inlay (top left) indicates the location of the study area in Germany. ©GeoBasis-DE/BKG 2013 (modified)

Patch occupancy

Between early May and the end of June 2016, throughout the peaks of the flight periods of *E. medusa* and *A. statices*, sampling was conducted at all 71 nutrient-poor grassland patches of the study area. We checked each patch at least twice for the presence of *E. medusa* and *A. statices* by systematically searching for adults during favourable weather conditions (dry, sunny days with temperatures > 18 °C) Both studied species are conspicuous lepidopterans and visit flowers frequently. Two visits are a commonly used number for the study of the occurrence of single Lepidoptera species (Öckinger 2006; Eichel and Fartmann 2008; Bauerfeind et al. 2009).

Patch size varied between 0.1 and 3.4 ha. Patches were regarded as discrete if they were separated from each other by more than 50 m of non-habitat (e.g., improved grassland, arable fields or forest; Poniatowski and Fartmann 2010; Krämer et al. 2012).

Landscape structure

Landscape-scale parameters were calculated using digital maps (ALKIS-data©) with ArcGIS 10.1 (Table 1). We calculated the percentage of the three dominating land cover types, arable land (mean = 26%), improved grassland (33%) and forest (31%) within a radius of 500 m around each patch (Table 1). Forest and improved grassland were highly intercorrelated ($|r_S| = -0.67$, $P < 0.001$, $N = 71$). Thus, only forest and arable land were used for the statistical analyses (see below).

Functional edge-to-edge distances (least-cost paths) from each patch to all other patches within a radius of 2 km around the patch were measured using the cost-distance tool in ArcGIS 10.1 (Adriaensen et al. 2003; Chardon et al. 2003; Poniatowski et al. 2016). To consider the structure and the different levels of permeability of the landscape matrix for migrating butterflies, resistance values were also entered into the model (Villalba et al. 1998;

Table 1 Mean values (±SD) of all numerical environmental parameters in the habitat patches of *Erebia medusa* and *Adscita statices*

Parameter	*Erebia medusa*			*Adscita statices*			*E.* versus *A.*[a]	r_s	Used variable
	Presence (N = 26)	Absence (N = 45)	*P*	Presence (N = 23)	Absence (N = 48)	*P*	*P*		
Landscape quality									
Patch size (ha)	**0.6 ± 0.7**	**0.4 ± 0.7**	*U	0.7 ± 0.8	0.4 ± 0.6	n.s.	n.s.		
Patch connectivity[b]	32.8 ± 23.9	38.1 ± 41.6	n.s.	31.1 ± 41.9	20.4 ± 31.4	n.s.	n.s.		
Cover (%)									
Arable land	**21.6 ± 12.0**	**28.2 ± 13.4**	*U	28.2 ± 15.0	24.6 ± 12.2	n.s.	n.s.		
Improved grassland	32.6 ± 9.1	32.8 ± 10.6	n.s.	32.9 ± 9.7	32.7 ± 10.3	n.s.	n.s.	− 0.67	▶ Forest
Forest	**36.0 ± 15.6**	**28.9 ± 16.2**	*U	29.9 ± 15.1	32.2 ± 16.9	n.s.	n.s.	1.00	
Habitat quality									
Cover (%)									
Field layer	40.2 ± 18.0	46.2 ± 20.2	n.s.	**53.1 ± 15.3**	**39.6 ± 20.0**	**t	*t		
Festuca ovina agg.[c]	**19.00 ± 23.7**	**3.3 ± 8.3**	* *U	10.8 ± 19.2	8.2 ± 16.6	n.s.	n.s.		
Festuca rubra agg.[c]	28.8 ± 22.8	21.8 ± 19.5	n.s.	25.0 ± 22.1	24.1 ± 20.5	n.s.	n.s.		
Rumex acetosella[d]	5.2 ± 8.7	3.9 ± 6.9	n.s.	**10.1 ± 10.9**	**1.7 ± 2.4**	* **U	*U		
Rumex acetosa[d]	7.1 ± 5.9	8.0 ± 8.0	n.s.	9.8 ± 7.7	6.6 ± 6.9	n.s.	n.s.		
Cryptogam layer	12.4 ± 9.2	23.6 ± 29.2	n.s.	**11.2 ± 16.8**	**23.5 ± 26.5**	*U	n.s.		
Bare ground	12.0 ± 9.6	8.7 ± 12.6	n.s.	11.1 ± 10.3	9.3 ± 12.2	n.s.	n.s.		
Litter layer	**50.4 ± 20.6**	**14.5 ± 15.5**	***U	34.3 ± 28.0	24.5 ± 22.5	n.s.	*U	0.95	▶ Litter volume
Litter height (cm)	**8.5 ± 3.5**	**3.8 ± 3.9**	***U	6.4 ± 4.6	5.1 ± 4.2	n.s.	n.s.	0.93	
Litter volume (m^3)[e]	**1.3 ± 1.0**	**0.28 ± 0.5**	***U	0.9 ± 1.1	0.5 ± 0.7	n.s.	*U	1.00	
Vegetation height (cm)	46.8 ± 16.0	45.3 ± 25.0	n.s.	45.1 ± 17.5	46.2 ± 24.0	n.s.	n.s.		

Comparison between occupied (presence) and unoccupied (absence) patches and between occupied *E. medusa* and occupied *A. statices* patches were analysed with *t* test (*t*) and Mann–Whitney *U* test (*U*), respectively. Significant differences between occupied and unoccupied patches are highlighted by bold type. If several variables were strongly intercorrelated (Spearman's rank correlation [r_S], $|r_S| > 0.6$, $P < 0.05$), only one was used in the subsequent analysis

n.s. not significant

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$

[a]Occupied *E. medusa* and occupied *A. statices* patches were tested against each other

[b]Hanski's connectivity index (Hanski 1999). See Sect. "Landscape structure"

[c]Used only for analyses of patch occupancy of *E. medusa*

[d]Used only for analyses of patch occupancy of *A. statices*

[e]Litter height × litter cover

Adriaensen et al. 2003). As a simple assignment of resistance values provided good results in recent metapopulation analyses (Poniatowski et al. 2016), we differentiated land cover types into one habitat and three non-habitat groups (Table 2). Non-habitat grassland might serve as a corridor for *E. medusa* and *A. statices* favouring migration. Thus, we assigned a resistance value only twice as high as that of habitats. In contrast, forest, shrubbery and settlement could act as physical barriers and therefore, received the highest values. Other land cover types held an intermediate position (Krämer et al. 2012; Helbing et al. 2017; Löffler and Fartmann 2017).

We calculated Hanski's connectivity index I_i (Hanski 1999), modified according to Moilanen and Nieminen (2002), for each patch *i* using the following equation:

$$I_i = \sum_{i \neq j} \exp\left(-\alpha \cdot d_{ij}\right) \cdot A_j^b,$$

where d_{ij} was the distance (in km; the functional distance) between the patch *i* and the neighbouring grassland patch *j* and A_j was the area size (in m^2) of the neighbouring patch *j*. The parameter α was the reciprocal of the average migration distance of a species. In light of the fact that no empirical data for migration distances of the Lepidoptera species were

Table 2 Resistance values of the land-cover types used for the cost-distance model. The percentages of land-cover types are shown in brackets

Land-cover type	Resistance value
Habitat	
Nutrient-poor grassland (<1%)	1
Non-habitat	
Improved grassland (25%)	2
Garden, park, cemetery (<1%)	
Arable land (34%)	4
Road, lane, railway, river (7%)	
Forest, shrubbery (29%)	8
Settlement (3%)	

available, we compared the goodness-of-fit (measured as McFadden's Pseudo R^2) of simple logistic regression models, with patch occupancy as the response and habitat connectivity as the explanatory variable, using different values for α (Stuhldreher and Fartmann 2014a). For *E. medusa*, an average migration distance of 0.8 km resulted in the best model fit. Therefore, we set α at 1.25. The model fit for *A. statices* was best with an average migration distance of 0.5 km (α = 2). The parameter *b* which scales the size of the surrounding habitat patches was set at 0.5. This ensured that the ratio of patch edge to patch area decreased when the patch size increased (Moilanen and Nieminen 2002; Stuhldreher and Fartmann 2014a; Poniatowski et al. 2016). Higher values of the functional connectivity index I_i stood for better connected patches than lower values.

Habitat quality

We sampled habitat quality parameters once in July 2016 (Table 1). On each patch, we recorded structural parameters and abundance of the host plants of *E. medusa* (*F. ovina* agg., *F. rubra* agg.) and *A. statices* (*R. acetosella, R. acetosa*) at three randomly selected plots of 9 m^2. For further analyses, we calculated mean values of the plots.

Statistical analysis

For metric parameters, differences between occupied and unoccupied patches of *E. medusa* and *A. statices* were analysed using a *t* test, provided that data were normally distributed and variances were homogenous by visually checking histograms (Quinn and Keough 2002); otherwise, we performed a Mann–Whitney *U* test.

To determine which landscape-quality and habitat-quality parameters explained patch occupancy of *E. medusa* and *A. statices*, we fitted binomial generalized linear models (GLM). Prior to analysis, we excluded highly intercorrelated variables (Spearman's rank correlation [r_S] $|r_s| > 0.6$; Krämer et al. 2012; Helbing et al. 2014). To avoid overfitting, we performed two different models for *E. medusa* and *A. statices*, respectively, each containing a different set of environmental parameters (landscape quality and habitat quality; Heikkinen et al. 2005; Stuhldreher and Fartmann 2014a). The significant variables from these landscape-quality and habitat-quality models were then used to fit a synthesis model for each studied Lepidoptera species (Stuhldreher and Fartmann 2014a). In order to increase model robustness and identify the most important environmental parameters, we conducted model averaging based on an information-theoretic approach (Burnham and Anderson 2002; Grueber et al. 2011). The 'dredge' function (R package MuMIn, Barton 2018) was used to perform conditional model averaging, and only included top-ranked models within $\Delta AIC_C < 3$ (Grueber et al. 2011). We tested the residuals of all models for spatial autocorrelation by calculating Global Moran's I using the lctools package in R (Kalogirou 2017), but found no significant effects of autocorrelation ($P > 0.05$).

To evaluate model accuracy, we used McFadden's Pseudo R^2 as a goodness-of-fit measure (Menard 2000) and the area under the curve (AUC) of a ROC plot (Fielding and Bell 1997; R package pROC; Robin et al. 2018). The latter was a threshold-independent measure of the overall discriminative ability of logistic regression models (Stuhldreher and Fartmann 2014a). Models with AUC values > 0.7 could be considered as acceptable, > 0.8 as excellent, and > 0.9 as outstanding (Hosmer and Lemeshow 2000). To compare the current distribution of the studied species with model predictions for individual patches, we converted the occurrence probabilities predicted by the synthesis models into presence–absence data. The optimal threshold above which a given probability was classified as a presence was determined by maximising Cohen's Kappa (Cohen 1960), a widely used measure for the proportion of correctly classified cases after accounting for chance effects (Freeman and Moisen 2008). As a measure of classification success, we used the percentage of correctly classified patches (Stuhldreher and Fartmann 2014a).

For statistical analyses, we used R 3.0.2 (R Development Core Team 2017).

Results

In total, 26 grassland patches were occupied by *E. medusa* and 23 by *A. statices* (Table 1). Both species were quite evenly distributed over the study area (Fig. 1). At the landscape level, patches occupied by *E. medusa* were larger and had lower cover of arable land and higher cover of forest in the surrounding than unoccupied patches (Table 1). At the habitat level, occupied patches had higher cover of *F. ovina* agg. and litter, as well as a higher and more voluminous litter

layer. Patches occupied by *A. statices* only differed in habitat quality from unoccupied ones. Occupied patches had lower cover of cryptogams as well as higher cover of the field layer and of *R. acetosella*. The comparison between occupied habitat patches of *E. medusa* and *A. statices* revealed that *A. statices* habitats had higher cover of the field layer and of *R. acetosella*, but lower litter cover and litter volume.

The GLM analysis indicated that both landscape quality and habitat quality influenced the patch occupancy of *E. medusa* (Table 3; Fig. 2). Habitat quality explained most of the variance in the data set. The presence of *E. medusa* was negatively correlated with the cover of arable land in the surrounding of the patches (landscape quality; Table 3a, Fig. 2a) and positively correlated with the litter volume (habitat quality; Table 3b, Fig. 2b). In the synthesis model the litter volume remained as the only predictor (Table 3c). While the explanatory power of the landscape-quality model was very low (McFadden's Pseudo R^2 0.05−0.08, AUC 0.67) the habitat-quality and the synthesis model had a high accuracy (McFadden's Pseudo R^2 0.37−0.45 and 0.31−0.36, respectively) and discriminative ability (AUC 0.93 and 0.89, respectively). Moreover, both models revealed a high rate

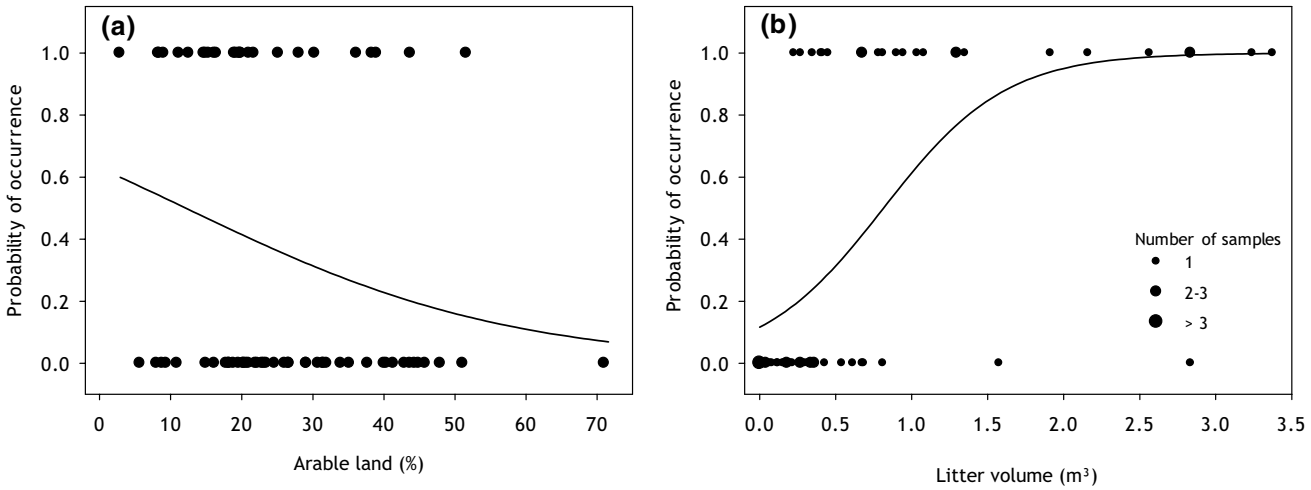

Fig. 2 Results of the binomial GLM analyses: the probability of the occurrence of *Erebia medusa* in relation to **a** cover of arable land in the surrounding and **b** litter volume. The regression slopes were fitted by using single predictor GLM: **a** $y = 1/(1 + \exp(-(0.53058 - 0.04373 \times \text{arable land})))$, $P < 0.05$, $R^2_{MF} = 0.05$; **b** $y = 1/(1 + \exp(-(-2.028 + 2.4897 \times \text{litter volume})))$, $P < 0.001$, $R^2_{MF} = 0.31$. R^2_{MF} = McFadden's Pseudo R^2

Table 3 Statistic of GLM: relationship between patch occupancy of *Erebia medusa* (binomial response variable: presence [$N = 26$] versus absence [$N = 45$]) and several environmental parameters (metric predictor variables)

Parameter	Estimate	SE	Z	*P*	R^2_{MF}	AUC	Cut-off	CCR (%)
(a) Landscape quality					0.05–0.08	0.67	0.30	68
(Intercept)	0.80	0.98	0.81					
Arable land	−0.05	0.02	2.03	*				
Not significant: forest, patch connectivity, patch size								
(b) Habitat quality					0.37–0.45	0.93	0.25	87
(Intercept)	−2.17	1.03	2.09	*				
Litter volume	1.83	0.78	2.30	*				
Not significant: bare ground, cryptogam layer, *Festuca ovina* agg., *Festuca rubra* agg., field layer, vegetation height								
(c) Synthesis model					0.31–0.36	0.89	0.43	88
(Intercept)	−1.00	0.96	1.03					
Litter volume	2.41	0.68	3.47	***				
Not significant: Arable land								

R^2_{MF} McFadden's Pseudo R^2, which is shown as the range of the R^2 values of all top-ranked models, *AUC* area under the curve, *Cut-off* the cut-off value that was used to classify the predicted occurrence probabilities into predicted presences and absences, *CCR* correct classification rate

n.s. not significant

*$P < 0.05$, ***$P < 0.001$

of correct classifications (87% and 88%, respectively) of presences and absences (Table 3b and c; Fig. 1). Patch size, patch connectivity and the cover of forest as well as different further vegetation-structure parameters had no influence on patch occupancy of *E. medusa* (Table 3).

Patch occupancy of *A. statices* was influenced only by habitat-quality parameters (Table 4; Fig. 3). Thus, the habitat-quality model and the synthesis model contained the same parameters and revealed that the cover of *R. acetosella* and *R. acetosa* as well as the litter volume were positively correlated with the presence of *A. statices* (Table 4b and c). Again, the explanatory power and the discriminative ability of the models were very high (McFadden's Pseudo R^2: 0.46−0.55 and 0.37−0.42, respectively; AUC: 0.93 and 0.91, respectively). Additionally, the predicted presences and absences matched the current distribution of *A. statices* in the study area very well (correct classification rate: 85%; Fig. 1).

Discussion

Our study clearly revealed that habitat quality was the main driver of patch occupancy for the two specialist Lepidoptera species, *E. medusa* and *A. statices*, in well-connected grasslands. Occurrence of both species was determined by the litter volume in the GLM analyses. Additionally, for *A. statices*, the cover of the host plants (*R. acetosella* and *R. acetosa*) was a further predictor. In contrast, landscape quality was only a minor factor in patch occupancy. Uniquely, the occurrence of *E. medusa* was negatively affected by a higher cover of arable land in the surrounding of the patches.

Prior studies have shown that the occurrence of butterfly species in cultivated landscapes is mainly determined by (i) habitat quality within patches, (ii) patch size and (iii) patch isolation (Dennis and Eales 1997; Eichel and Fartmann 2008; Stuhldreher and Fartmann 2014a; Poniatowski et al. 2018). However, the relative importance of these factors varies depending on landscape and species. Habitat connectivity was usually less important in well-connected landscapes (Binzenhöfer et al. 2005; Krämer et al. 2012) and became increasingly relevant in highly modified landscapes (Dover and Settele 2009). Consequently, we interpret the lack of influence of connectivity on patch occupancy of both Lepidoptera species by the dense network of habitat patches in the studied area. In contrast, as has recently been shown in an investigation from an adjacent study area, connectivity becomes relevant, at least for *E. medusa*, if the distances between habitat patches are larger (Stuhldreher and Fartmann 2014a).

The minimum patch-size requirements can differ considerably among Lepidoptera species (Crone and Schultz 2003; Salz and Fartmann 2009). Occupied patches of both species in the current study were small with a mean patch size of 0.6 ha for *E. medusa* and 0.7 ha for *A. statices*, respectively (Table 1). Although at least for *E. medusa* occupied patches were larger than unoccupied ones; patch size did not explain patch occupancy of the two species in the GLM analysis.

Table 4 Statistic of GLM: relationship between patch occupancy of *Adscita statices* (binomial response variable: presence [$N=23$] versus absence [$N=48$] and several environmental parameters (metric predictor variables)

Parameter	Estimate	SE	Z	*P*	R^2_{MF}	AUC	Cut-off	CCR (%)
(a) Landscape quality								
n.s.								
Not significant: Arable land, forest, patch connectivity, patch size								
(b) Habitat quality					0.46−0.55	0.93	0.28	90
(Intercept)	−6.00	2.66	2.23	*				
Rumex acetosella	0.37	0.11	3.40	***				
Rumex acetosa	0.17	0.07	2.34	*				
Litter volume	1.17	0.59	1.98	*				
Not significant: Bare ground, cryptogam layer, field layer, vegetation height								
(c) Synthesis model					0.37−0.42	0.91	0.35	85
(Intercept)	−3.96	1.01	3.88	***				
Rumex acetosella	0.36	0.10	3.49	***				
Rumex acetosa	0.14	0.05	2.73	**				
Litter volume	0.87	0.40	2.14	*				
Not significant: −								

R^2_{MF} McFadden's Pseudo R^2, which is shown as the range of the R^2 values of all top-ranked models, *AUC* area under the curve, *Cut-off* the cut-off value that was used to classify the predicted occurrence probabilities into predicted presences and absences, *CCR* correct classification rate

n.s. not significant

*$P<0.05$, **$P<0.01$, ***$P<0.001$

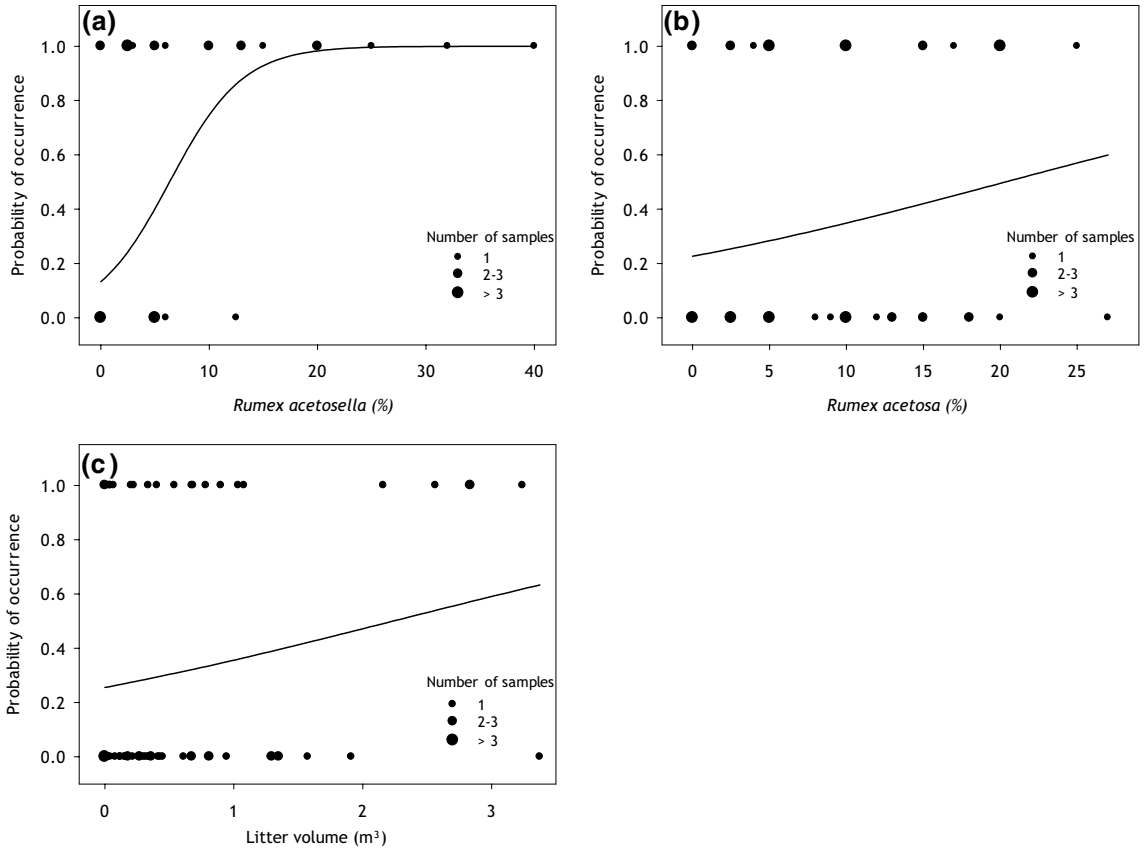

Fig. 3 Results of the binomial GLM analyses: the probability of the occurrence of *Adscita statices* in relation to the cover of **a** *Rumex acetosella* and **b** *Rumex acetosa* and **c** the litter volume. The regression slopes were fitted by using single predictor GLM: **a** $y=1/(1+\exp(-(-1.8749+0.2958\times R.\ acetosella)))$, $P<0.01$, $R^2_{MF}=0.27$; **b** $y=1/(1+\exp(-(-1.22772+0.06041\times R.\ acetosa)))$, n.s., $R^2_{MF}=0.03$; **c** $y=1/(1+\exp(-(-1.0700+0.4791\times \text{litter volume})))$, n.s., $R^2_{MF}=0.03$. R^2_{MF} = McFadden's Pseudo R^2; *n.s.* not significant

Based on our data the population structure of the two studied Lepidoptera species resembled mostly a classical metapopulation of the Levins type consisting of many small and highly connected patches (Hanski et al. 1994; Hanski 1999; Nieminen et al. 2004).

Growing evidence has shown that even in well-connected landscapes the landscape surrounding patches of semi-natural grassland can influence patch occupancy of insect species (Öckinger et al. 2012; Helbing et al. 2017). For *E. medusa*, the cover of arable land was lower around occupied patches in comparison to unoccupied ones and had a negative effect on patch occupancy in the landscape-quality GLM model. Modern-day arable land represents a very hostile environment for Lepidoptera as it usually offers neither host plants nor nectar resources (Nilsson et al. 2013; Konvička et al. 2016). Additionally, the applied pesticides can have directly harmful effects on the insects (Meek et al. 2002; Van Swaay et al. 2009). Furthermore, patches occupied by *E. medusa* had a higher cover of forest in their surrounding than unoccupied ones. Krämer et al. (2012) observed a positive effect of forest cover on a number of habitat specialist butterfly species in semi-natural grassland patches. They concluded that forests acted as a barrier for grassland butterflies and might reduce emigration rates and, hence, the risk of failing to reach a suitable habitat in a hostile environment. In line with this, Schmitt et al. (2000) have shown that forests were an effective barrier for *E. medusa*. Additionally, in contrast to semi-natural grassland patches that border improved grassland or arable land, forests provide barrier protection from the negative effects of fertilizer and pesticides (Meek et al. 2002; Van Swaay et al. 2009).

The main driver of patch occupancy in the well-connected grasslands of our study was habitat quality, and the most important habitat-quality parameter in the GLM analyses of both studied Lepidoptera species was the litter volume. According to Stuhldreher and Fartmann (2014a, 2015), large amounts of litter probably have positive effects on *E. medusa* in two ways: (i) Litter accumulation is an indicator of decreasing land-use intensity. Since females of *E. medusa* mostly attach their eggs 7–14 cm above the ground, they are quite sensitive to land use during the oviposition period in May and June (Fartmann 2004; Stuhldreher and Fartmann

2014a). (ii) The litter layer acts as a microclimatic buffer, reducing temperature and humidity fluctuations (Stuhldreher and Fartmann 2014a, b). This is supposed to enable a more energy-efficient development of the larvae and higher survival rates, compared to more changeable environments (Ruel and Ayres 1999; Stuhldreher and Fartmann 2014a, b). The relationship between patch occupancy of *A. statices* and large amounts of litter observed in the current study might also indicate a similar need for microclimatically buffered microhabitats near the soil surface. However, this hypothesis requires further testing.

Besides a favourable microclimate, larval development depends on sufficient food (Fartmann and Hermann 2006; García-Barros and Fartmann 2009). In line with this, the likelihood of patch occupancy in *A. statices* increased with the cover of the two host plants *R. acetosella* and *R. acetosa*. Additionally, in *E. medusa* the cover of the host plant *F. ovina* agg. was higher on occupied patches than on unoccupied ones.

For *A. statices*, the cover of the cryptogam layer was lower and the cover of the field layer higher in occupied patches compared to unoccupied ones. We explain this pattern based on the increasingly negative effects of ongoing grassland abandonment on *A. statices*. Abandonment of semi-natural grasslands usually results in an increased cover of mosses and litter, while cover of the field layer and small, less competitive plants, such as the host plant *R. acetosella*, decreased (Grime et al. 2007; Ellenberg and Leuschner 2010).

In conclusion, the main driver of patch occupancy of both studied Lepidoptera species in the well-connected grasslands of our study area was habitat quality and the most important habitat-quality parameter was litter volume. In both species, the observed population structure resembled a classical metapopulation of the Levins type consisting of many small and highly connected patches. Large amounts of litter probably favour the occurrence of the species as it indicates decreased land-use intensity and also acts as a microclimatic buffer.

Implications for conservation

Target species often differ in their habitat requirements and, hence, for nature conservationists it is often a challenge to prioritise the appropriate measures. The findings of this study highlighted the importance of habitat quality for the persistence of both studied target species in well-connected grasslands. Habitat requirements for both species were very similar. Both species depend on semi-natural grasslands that were (i) abandoned or have low land-use intensity with a litter layer, and (ii) have a sufficient cover of host plants. In the short and medium term, abandonment was beneficial for both species, as it maintained the litter layer (Stuhldreher and Fartmann 2014a). In the long term this would lead to vegetation dominated by competitive, high-growing grasses (e.g., *Arrhenatherum elatius*) and a decreasing cover of the less competitive host plants, especially *F. ovina* agg. and *R. acetosella* (Grime et al. 2007; Ellenberg and Leuschner 2010). Solutions to this dilemma might include rotational grazing or mowing, if sufficiently large parts of the habitats were left unmanaged every year (Stuhldreher and Fartmann 2014a). Other authors have made similar recommendations for other management-sensitive Lepidoptera species (Balmer and Erhardt 2000; Waring 2001; Goffart et al. 2010; Slamova et al. 2013). Regarding the host plants of *A. statices*, prior studies have shown that *R. acetosella* and *R. acetosa* benefit from the effects of extensive grazing systems (Dolek 2000; Pöyry et al. 2005). Based on our observations in the Diemel Valley, we recommend that any management measures in the habitats of *E. medusa* and *A. statices* should be scheduled as late in the year as possible (Stuhldreher and Fartmann 2014a). At the landscape level, maintaining a network of well-connected habitat patches appears to be crucial, especially in landscapes with a low cover of arable land and a high cover of forests in the surrounding.

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Compliance with ethical standards

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

Research involving animals No butterflies or burnet moths were harmed during the course of this project.

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