



ORIGINAL ARTICLE

Occurrence of an endangered grassland butterfly is mainly driven by habitat heterogeneity, food availability, and microclimate

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Abstract The Marsh Fritillary (*Euphydryas aurinia*) was once widespread in large parts of Central Europe. However, in the course of the last century, populations of the butterfly largely collapsed. Here, we surveyed patch and microhabitat occupancy and its drivers in one of the last vital populations in calcareous grasslands. Our study revealed that environmental conditions at the landscape and habitat level determined the occurrence of *E. aurinia* in a montane agricultural landscape with low land-use intensity. Patch occupancy increased with the cover of Devil's-bit Scabious (*Succisa pratensis*) grasslands in the surroundings of the patches, habitat heterogeneity and host-plant cover. Microhabitat occupancy was driven by a warm microclimate and high availability of host plants. In the well-connected landscape of nutrient-poor grasslands, patch occupancy of *E. aurinia* was driven by parameters defining a high habitat quality. Habitat heterogeneity very likely buffers *E. aurinia* populations against environmental stochasticity and, hence, enhances long-term viability. For the gregariously feeding caterpillars of *E. aurinia*, host-plant biomass is essential. Due to their more luxuriant growth, *S. pratensis* plants were clearly preferred, although the Glossy Scabious (*Scabiosa lucida*) was also widespread. Additionally, the growth of large *Succisa* plants was favored by soil humidity and grassland abandonment. To cope with the adverse macro- and mesoclimatic conditions of the study area, females of the butterfly selected host plants growing in extraordinarily warm microhabitats for oviposition. To secure long-term viability of *E. aurinia* populations, we recommend creating mosaics of traditionally managed grasslands and early stages of abandonment within the patches.

Key words agricultural landscape; calcareous grassland; hay meadow; host-plant abundance; land-use change; traditional management

Introduction

During the last two centuries, humankind has altered environmental conditions across the world at an unprecedented pace (Rockström *et al.*, 2009). As a result,

abundance and species richness of insects has declined dramatically (Sánchez-Bayo & Wyckhuys, 2019; Cardoso *et al.*, 2020). For terrestrial ecosystems, land-use change is considered the main determinant of recent insect decrease (IPBES, 2019; Cardoso *et al.*, 2020; Wagner *et al.*, 2021). Among alterations in land use, especially loss and fragmentation of habitats as well as reduced quality of the remaining habitat patches are responsible for this crisis (Poniatowski *et al.*, 2018; Cardoso *et al.*, 2020).

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Nutrient-poor grasslands on calcareous soils are hotspots of insect diversity (WallisDeVries *et al.*, 2002; Löffler *et al.*, 2020; Helbing *et al.*, 2021). For instance, about half of all indigenous European butterfly species may occur in calcareous grasslands (van Swaay *et al.*, 2006). However, during the last century, these grasslands have suffered from severe loss, fragmentation, and degradation due to agricultural intensification, afforestation, and abandonment of traditional management (WallisDeVries *et al.*, 2002; Veen *et al.*, 2009; Stenoien *et al.*, 2018; Löffler *et al.*, 2020). Calcareous grasslands are legally protected by the EU Habitats Directive (EC, 2007) as a result of both their large significance for biodiversity conservation and their high threat status.

Butterflies mostly exhibit highly specific habitat requirements (García-Barros & Fartmann, 2009; Dennis *et al.*, 2010). Habitat quality for butterflies is usually determined by host-plant availability and microclimate (García-Barros & Fartmann, 2009; Curtis *et al.*, 2015). Additionally, butterflies normally form metapopulations; hence, their distribution in cultivated landscapes also depends on the size and connectivity of habitat patches (WallisDeVries, 2004; Eichel & Fartmann, 2008; Goff *et al.*, 2019).

The Marsh Fritillary (*Euphydryas aurinia*) was once widespread in large parts of Central Europe and adjacent regions (Anthes *et al.*, 2003a). However, in the course of the last century, populations largely collapsed. The ecology of the species in its main habitat, wet grasslands with Devil's-bit Scabious (*Succisa pratensis*) as a primary host plant, has been studied intensively in recent times. At the landscape level, Anthes *et al.* (2003b) showed that *E. aurinia* forms metapopulations of the mainland-island type. At the habitat level, a high abundance of large host plants and warm microclimates was of vital importance (Anthes *et al.*, 2003b; Tjørnløv *et al.*, 2015; Brunbjerg *et al.*, 2017; Pielech *et al.*, 2017). By contrast, our knowledge on the drivers of persistence of the few remaining *E. aurinia* populations in networks of calcareous grasslands is still scarce (Anthes & Nunner, 2006; Bräu *et al.*, 2013). In contrast to wet grasslands, the main host plants in calcareous grasslands, Small Scabious (*Scabiosa columbaria*) and Glossy Scabious (*Scabiosa lucida*) (Anthes & Nunner, 2006), are much smaller than *Succisa* plants (Klotz *et al.*, 2002). Additionally, the relative importance of the three metapopulation parameters isolation, quality, and size of the habitat patches usually differs depending on the degree of habitat fragmentation (Poniatowski *et al.*, 2018).

Here, we surveyed patch and microhabitat occupancy in one of the last vital Central European populations of *E. aurinia* in calcareous grasslands (cf. Bräu *et al.*,

2013). The study area, the Niederwerdenfelser Land in Upper Bavaria (southern Germany), is part of one of the 30 German biodiversity hotspots (Ackermann & Sachteleben, 2012). It is a montane agricultural landscape with low land-use intensity, diverse grassland-woodland mosaics, and mostly well-connected nutrient-poor grasslands (Krämer *et al.*, 2012b; Löffler & Fartmann, 2017). To determine the drivers of occupancy, we assessed environmental parameters at the landscape and habitat level. The most widespread primary host plant within the calcareous grasslands is *S. lucida* (Gutser & Kuhn, 1998; Anthes & Nunner, 2006). Accordingly, we were particularly interested in identifying how *E. aurinia* is able to cope with the poor food availability due to the tiny host plant. Based on the results of our study, we make management recommendations for the conservation of *E. aurinia* in Central European calcareous grasslands.

Material and methods

Study species

The Marsh Fritillary (*Euphydryas aurinia*) is a nymphalid butterfly with Palearctic distribution, occurring from the British Isles throughout Europe and to eastern Asia. It is univoltine, and in Central Europe, adults are on the wing from mid-May to the beginning of July (Bräu *et al.*, 2013). Here, the species colonizes especially wet grasslands with *S. pratensis* as the primary host plant. However, calcareous grasslands with Small Scabious (*Scabiosa columbaria*) as a host plant are another habitat of *E. aurinia* in parts of Central Europe. Especially in the Bavarian pre-Alps and Alps, further Dipsacaceae and Gentianaceae species serve as important host plants (e.g., Glossy Scabious [*Scabiosa lucida*] and Willow Gentian [*Gentiana asclepiadea*]) (Anthes *et al.*, 2003a; Anthes & Nunner, 2006; Bräu *et al.*, 2013) in these two habitat types. The females of *E. aurinia* lay batches of up to 390 eggs on the underside of the leaves of prominent and easily accessible host plants (Anthes *et al.*, 2003b). Larvae feed gregariously until September and overwinter in a dense hibernaculum web (Porter, 1981). Shortly after diapause in March, larvae continue feeding in smaller groups and spend their last two instars solitarily until they pupate in May close to the ground. As a metapopulation species, *E. aurinia* requires a dense network of suitable habitats in close proximity (Wahlberg *et al.*, 2002; Bulman *et al.*, 2007; Zimmermann *et al.*, 2011). The species has dramatically suffered from habitat loss and deterioration during the last century (Asher *et al.*, 2001; Anthes *et al.*, 2003a). As a result, *E.*

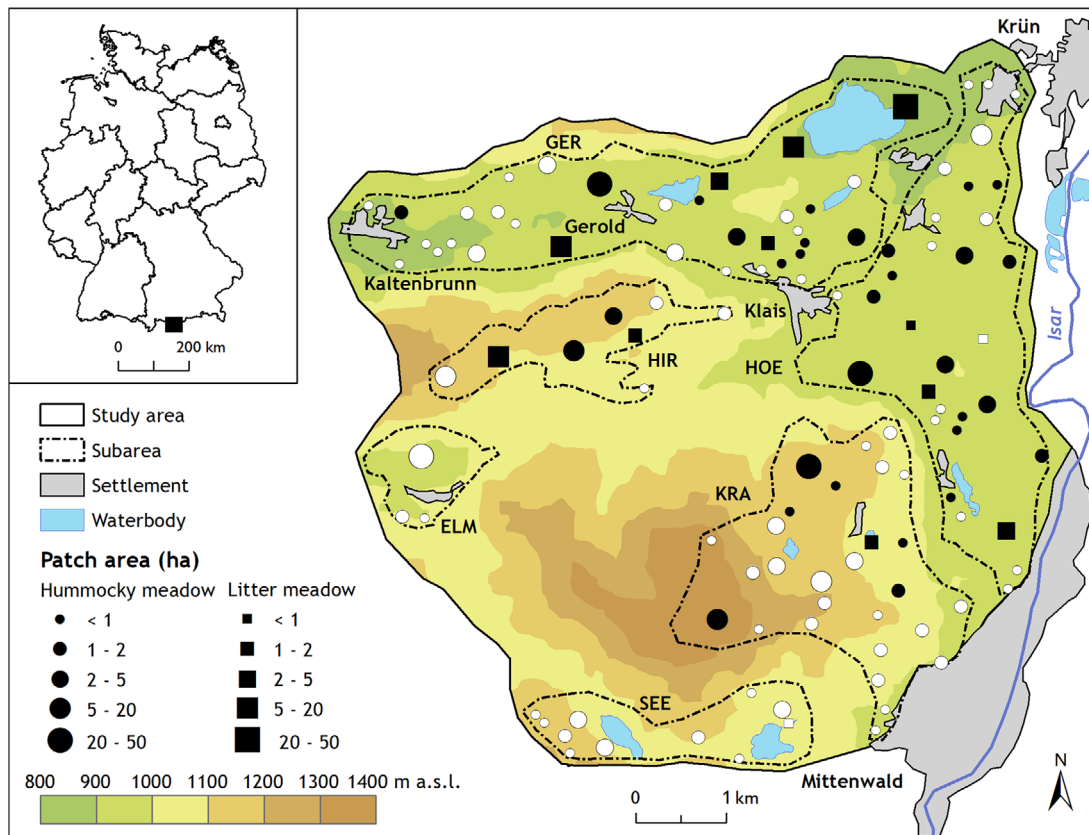


Fig. 1 Location of the study area in Germany and occurrence of hummocky meadows (circles) and moist meadows (squares). Patches occupied by *E. aurinia* are highlighted in black. ELM = Elmau, SEE = Ferchensee and Lautersee, GER = Gerold and Geißschädel, HIR = Hirzeneck, HOE = Hoheebene, KRA = Kranzberg.

aurinia is considered endangered in Germany (Reinhardt & Bolz, 2011) and is protected by the EU Habitats Directive (EC, 2007).

Study area

The study area, the Niederwerdenfelser Land, of about 52 km² and an elevational range of 800–1350 m a.s.l. is located in the Northern Limestone Alps in Upper Bavaria (southern Germany), 100 km south of Munich (47°26'N, 11°10'E und 47°30'N, 11°17'E; Fig. 1). Due to the elevation and its location in the Northern Limestone Alps, which are affected by orographic rainfall, the climate is cold and wet with a mean annual precipitation of 1437 mm and an annual average temperature of 6.7°C (long-term mean: 1961–1990, DWD 2019). However, higher temperatures and periods of reduced precipitation are facilitated by foehn wind and rain-shelter effects caused by the Estergebirge in the north.

The study area is the most important stronghold of the so-called hummocky meadows (“Buckelwiesen”) in Central Europe (~450 ha) (Gutser & Kuhn, 1998; Embleton-Hamann, 2004). Hummocky meadows are pre-Alpine calcareous grasslands with a geomorphological peculiarity: a microrelief consisting of regular pits and mounds. *Scabiosa lucida* is widespread in these grasslands (Gutser & Kuhn, 1998). Due to the elevational gradient of the study area, a wide range of different aspects and slopes within the meadows and the microheterogeneity caused by the pits and mounds, the meso- and microclimatic conditions may differ strongly between and within the grassland patches (Gutser & Kuhn, 1998). Within the pits and depressions of the hummocky meadows, even wet grassland vegetation with *S. pratensis* regularly occurs. For hundreds of years, hummocky meadows have been used with low intensity as hay meadows. However, during the last century, either management has intensified (including flattening of the microrelief and fertilization) or grasslands have

become abandoned and afforested. As a result, the area of hummocky meadows has declined by 95 % (Gutser & Kuhn, 1998). Today, the remaining hummocky meadows are scattered inside a diverse grassland-woodland mosaic and are mostly still well-connected (Krämer *et al.*, 2012b; Löffler & Fartmann, 2017). Besides the hummocky meadows, *E. aurinia* also occurs in the few litter meadows with *S. pratensis* of the study (Fig. 1). Litter meadows are nutrient-poor, periodically wet grasslands mown in autumn to obtain bedding for livestock (Anthes *et al.*, 2003b; Schwarz & Fartmann, 2021).

Study design

In 2019, habitat preferences of *E. aurinia* were studied in all 122 potentially suitable grassland patches (110 hummocky and 12 litter meadows) in the study area. Suitable grassland patches had to be characterized by the occurrence of at least one primary host plant (i.e., in the study area *S. lucida* and *S. pratensis*; Anthes & Nunner, 2006) and be separated by at least 50 m of nonhabitat, for example, improved grassland or coniferous forest (Poniatowski *et al.*, 2018). Size of the patches varied from 0.1 to 43 ha. As patches were spatially clustered, we assigned them to six distinct subareas.

Butterfly sampling To determine patch occupancy of *E. aurinia*, each grassland patch was sampled at least once during the peak of the flight period between late May and early June from 9:00 a.m. to 17:00 p.m. under favorable weather conditions ($>18^{\circ}\text{C}$, sunny weather, hardly windy; Scherer *et al.*, 2021). Per patch, the occurrence of adults was recorded by walking in loops with a distance of 50 m between each loop. If no individual was detected during the first survey, a search was repeated 2 weeks later and, if needed, for a third time in August by looking for larval webs (cf. Anthes *et al.*, 2003b). To cover all habitat structures, especially of small patches, we varied the starting point of each following survey accordingly. A patch was classified as occupied if at least three adults (as an indicator for an indigenous population) or a larval web was detected (Anthes *et al.*, 2003b; Scherer *et al.*, 2021).

Oviposition habitats of *E. aurinia* were surveyed in all occupied patches in the first half of July. We searched for egg batches and webs of first instar larvae by walking in loops with a distance of 2 m between each loop across the patch and checking all host plants (Fartmann, 2006; Krämer *et al.*, 2012a). By contrast, webs of second instar larvae were not considered as these had possibly already moved from the original host plant to another host plant.

Sampling of environmental parameters

Landscape quality Elevation, patch size, and isolation were measured using georeferenced orthophotographs (Table 1). Isolation was assessed by calculating the geometric mean of the Euclidean edge-to-edge distance to the next three occupied patches (Eichel & Fartmann, 2008; Scherer *et al.*, 2021). We also calculated the cover of major habitat types (according to Krämer *et al.*, 2012b) and of grasslands with occurrence of the main host plant in Central Europe, *S. pratensis*, within a buffer of 250 m around each patch using orthophotographs, the real estate cadaster system (ALKIS) and field surveys (Table 1). Mean annual temperature and number of frost days (days with a mean temperature below 0°C) were assessed per patch by using grid-map data (spatial resolution $1 \times 1 \text{ km}$) from the German Meteorological Service (Table 1; reference period 1981–2010; DWD, 2019). All spatial analyses were done using ArcGIS 10.6.

Habitat quality Sampling of the habitat-quality parameters took place from late May to the beginning of June. Sunshine duration in June was measured in the center of each patch using a horizonscope (Table 1) (Scherer *et al.*, 2021). For each grassland patch, three randomly selected plots of 500 m^2 with a relatively homogenous vegetation structure were established. Only in the very smallest patches plots may partly overlap. Per plot, vegetation height was measured three times with a ruler at randomly chosen locations at the level below which about 80% of the vegetation was estimated (Stewart, Bourn & Thomas, 2001) and averaged afterward. The cover of the host plants (*S. pratensis* and *S. lucida*), bare ground, herbs, grasses, and litter were estimated in steps of 5% (Table 1). When cover was above 95% or below 5%, 2.5% steps were used. For further analysis, the three values of each parameter were averaged per patch.

Additionally, for each patch, we calculated a score of habitat heterogeneity (cf. Löffler & Fartmann, 2017). Therefore, we assessed the range in soil humidity (wet, moist, fresh, semidry; score: 1–4), relief (hummocky, flat; score: 1–2), land use (abandoned, mown until the July 31 [mown early], mown from the August 1 onward [mown late] and grazed; score: 1–4), aspect (N, S, plane; score: 1–3) and elevation occurring within a patch (0–50 m, 50–100 m, $>100 \text{ m}$; score: 1–3). Due to a long tradition of partible inheritance in our study area, patches were often divided across multiple land owners. Because land use may slightly differ between land owners, we also considered a score based on the number of land owners per patch (land owners: 1–3, >3 ; score: 1–2). The final score was the sum of the scores for each of the five indicators

Table 1 Overview of sampled metric and ordinal parameters at patches occupied and unoccupied by *E. aurinia*.

Parameter	Factor level	Correlation		Occupied patches ($N = 42$)		Unoccupied patches ($N = 80$)		P
		r_s	used [†]	Mean (\pm SE)	Min. – Max.	Mean (\pm SE)	Min. – Max.	
Landscape level								
Elevation (m a.s.l.)	Metric	–0.8		1,000 \pm 7	(885–1355)	1008 \pm 7	(867–1321)	n.s.
Annual temperature (°C)	Metric	1.0	► Annual temperature	4.7 \pm 0.1	(3.1–5)	4.7 \pm 0.1	(3.4–5)	n.s.
Frost days	Metric	–0.8		128.9 \pm 0.4	(120–149)	129.3 \pm 0.5	(119–146)	n.s.
Isolation (m) [‡]	Metric			313 \pm 18.7	(21–1514)	969 \pm 60	(92–3894)	***
Cover in 250 m radius (%)								
Forest	Metric	1.0		49.3 \pm 3.6	(1–86)	61.3 \pm 2.4	(5–98)	*
Improved grassland	Metric	–0.9	► Forest	33.6 \pm 3.5	(0–86)	22.9 \pm 2.7	(0–85)	n.s.
Grassland with <i>Succisa pratensis</i>	Metric			5.7 \pm 0.8	(0–20)	1.1 \pm 0.1	(0–13)	***
Hummocky meadows	Metric			12.6 \pm 1.2	(0–33)	8.0 \pm 0.7	(0–23)	***
Patch size (ha)	Metric	0.8		8.4 \pm 0.7	(0.3–43)	2.0 \pm 0.2	(0.1–30)	**
Habitat level								
Habitat heterogeneity [§]	Ordinal	1.0	► Habitat heterogeneity	12.5 \pm 0.5	(8–18)	9.8 \pm 0.3	(6–17)	***
Daily sunshine duration (h) [¶]	Metric			12.9 \pm 0.1	(10–15)	11.5 \pm 0.5	(8–15)	**
Cover of host plants	Metric			5.3 \pm 0.3	(1–25)	1.9 \pm 0.1	(1–6)	***
Cover of different layers (%)								
Herbs	Metric			46.8 \pm 0.7	(30–65)	44.1 \pm 1	(15–75)	***
Grasses	Metric			35 \pm 0.7	(18–60)	39.1 \pm 0.7	(20–70)	*
Litter	Metric			8.9 \pm 0.3	(5–25)	8.8 \pm 0.3	(2.5–20)	n.s.
Bare ground	Metric	–0.6		3.6 \pm 0.2	(0–14)	4.9 \pm 0.3	(0–20)	n.s.
Vegetation height (cm)	Metric	1.0	► Vegetation height	15.9 \pm 0.4	(8–31)	16.6 \pm 0.6	(5–50)	n.s.

Note: Differences between occupied and unoccupied patches were tested using GLMM with “subarea” as a random factor. If two or more variables were strongly intercorrelated (Spearman's rank correlation, $|r_s| > 0.6$), only one was used in the subsequent analysis (see Table 2). For further information, see Section Statistical analysis. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; n.s. not significant.

[†]Variables used in the full model (GLMM) of the respective level after correlation analysis.

[‡]Geometric mean of the Euclidean distance to the next three occupied habitats.

[§]For further information, see Section Sampling of environmental parameters.

[¶]Accuracy: 1/2 h (Scherer *et al.*, 2021).

(Löffler & Fartmann, 2017). As an example, a patch that (i) has a fresh and semidry soil (score: 2), (ii) has a hummocky relief, with flat areas in-between (score: 2), (iii) is mown at the July 15 with 10% of the patch left unmown (score: 2), (iv) is facing southward with some plateaus (score: 2), (v) has an elevational range of 20 m (score: 1), and (vi) has five distinct land owners (score: 2) will have an ultimate heterogeneity score of 11. Accordingly, the potential range of heterogeneity values varied from 6 to 18.

Microhabitat quality To assess oviposition preferences, microhabitat characteristics were sampled using the same parameters as mentioned above as well as soil humidity in a radius of 0.5 m around occupied host plants ($n = 90$) (Tables 3 and 4). Soil humidity was measured according to the German Manual of soil mapping (Eckelmann *et al.*, 2006) conducting a finger test. Additionally, we measured the number of host-plant leaves as well as the diameter and height of the host plant (Table 3). To compare the characteristics of occupied and unoccupied host plants within occupied patches, we recorded the same parameters around randomly chosen control samples (i.e., host-plant individuals of the same plant species that were not used by immature stages). These samples represent the nearest unoccupied plant to a randomly thrown stick (cf. Anthes *et al.*, 2003b). The total number of controls corresponded to the number of occupied host plants ($n = 90$). To represent the overall availability of potential microhabitats, the number of control samples per patch was adjusted to its size, with at least one sample per patch (Krämer *et al.*, 2012b; Scherer *et al.*, 2021).

Statistical analysis

In order to detect significant differences in metric environmental parameters (Tables 1 and 3, Fig. 2) between occupied and unoccupied patches/microhabitats, (generalized) linear mixed-effects models (GLMM, LMM) were applied (R packages lme4; Bates *et al.*, 2019) with “sub-area” as a random factor (Crawley, 2007). Patch or microhabitat type (occupied vs. unoccupied) served as a nominal fixed factor, and the analyzed parameters were used as dependent variables. Depending on the distribution of the variables, binomial (percentage data), Poisson (count data), or Gaussian (for square-root- or log-transformed variables with normal distribution) models were applied with the respective standard link functions. In order to reduce overdispersion within the models, observation-level random effects were added as a random factor (Harrison,

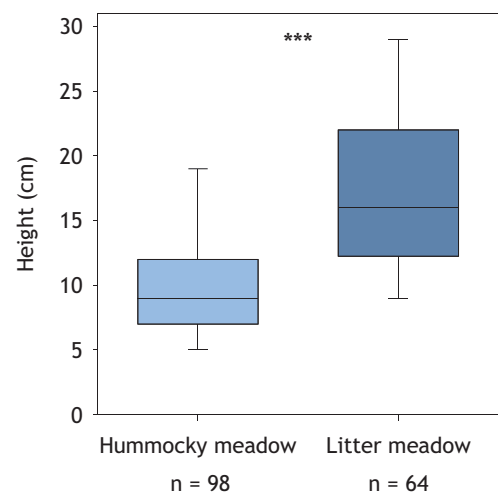


Fig. 2 Height of *Succisa pratensis* plants on hummocky and litter meadows. Differences were tested using GLMM with “sub-area” as a random factor and “patch” within “subarea” as a nested random factor. *** $P < 0.001$.

2014, 2015). The overall effect of the dependent variables on habitat type was analyzed by comparing the full models with reduced models without “patch or microhabitat type” as the fixed factor and applying likelihood-ratio tests. Differences in absolute frequencies between the nominal variables “land-use type” and “soil humidity” of occupied and unoccupied microhabitats were analysed using Fisher’s exact test (Table 4).

To determine which environmental parameters explained patch and microhabitat occupancy of *E. aurinia*, respectively, we fitted GLMM (binomial) with “subarea” as a random factor. The patch occupancy model contained all non-intercorrelated variables of the landscape and habitat level. To avoid model overfitting, we implemented Spearman’s rank correlations (r_s) between all numerical environmental parameters to identify possible intercorrelations. If parameters were strongly intercorrelated ($|r_s| > 0.6$), only the most important variable was used in GLMM analyses (Tables 1–3). Generally, we chose the variable that had the highest explanatory power in the single-predictor GLMM. In case of multicollinearity with more than one other variable or if there was no difference in significance between two variables, we selected the variable that has the highest ecological impact on *E. aurinia*. In order to increase model robustness and identify the most important environmental parameters, we conducted model selection using the “dredge” function (R package MuMIn; Bartón, 2020) followed by model averaging based on an information-theoretic approach (Burnham & Anderson, 2004; Grueber *et al.*

Table 2 Statistics of binomial GLMM (model-averaging).

Parameter	Estimate	SE	Z	P
(a) Patch occupancy				
$R^2_c = 0.66\text{--}0.83$, $R^2_m = 0.76\text{--}0.87$				
Intercept	1.88	10.01	0.19	n.s.
Habitat heterogeneity	0.44	0.15	2.95	**
Cover of grasslands with <i>S. pratensis</i>	0.36	0.14	2.57	*
Cover of host plants	1.05	0.40	2.62	**
(b) Microhabitat occupancy				
$R^2_c = 0.45\text{--}0.83$, $R^2_m = 0.49\text{--}0.84$				
Intercept	−8.66	2.44	−3.53	***
No. of host-plant leaves	0.14	0.04	3.95	***
Cover of host plants	0.05	0.02	2.81	**
Sunshine duration	0.44	0.15	3.03	**

Note: (a) Relationship between patch occupancy of *E. aurinia* and environmental parameters ($N_{\text{occupied}} = 42$ vs. $N_{\text{unoccupied}} = 80$). (b) Relationship between microhabitat occupancy and environmental parameters ($N_{\text{occupied}} = 90$ vs. $N_{\text{unoccupied}} = 90$). “Subarea” was used as a random factor and, additionally, “patch” within “subarea” as a nested random factor in the microhabitat occupancy model. R^2_c = variance explained by fixed effects, R^2_m = variance explained by both fixed and random effects (Nakagawa *et al.*, 2017). ** $P < 0.01$, *** $P < 0.001$; n.s. not significant.

2011). Model averaging only included top-ranked models within $\Delta\text{AIC}_C < 3$ (Grueber *et al.*, 2011). All statistical analyses were performed using R 3.6.2 (R Development Core Team, 2019).

Results

Patch occupancy

In total, one-third of the grassland patches was occupied by *E. aurinia* (42 [34.4%] out of 122 studied patches) (Fig. 1). Except two, all litter meadow patches were colonized (10 [83%] out of 12). By contrast, the species was present only on slightly more than a quarter of the hummocky meadows (32 [29%] out of 110). In the two subareas with the smallest area of hummocky meadows and the almost complete absence of litter meadows, *E. aurinia* was missing. By contrast, in the four other subareas, where both grassland types were widespread and the patches were well-connected, the species regularly occurred.

Occupied patches differed considerably in environmental conditions from unoccupied ones (Table 1). At the landscape level, they were larger and less isolated than unoccupied ones. Additionally, the cover of forests was lower and those of hummocky meadows and grasslands with *S. pratensis* was higher in the surroundings of occupied patches. By contrast, macroclimate (elevation, an-

nual temperature, and frost days) did not differ between occupied and unoccupied patches. At the habitat level, patches with higher habitat heterogeneity, longer sunshine duration, higher cover of host plants and herbs but a lower cover of grasses were preferred. In contrast to occupied patches, unoccupied patches had never a higher cover of host plants than 6% (Fig. 3). By contrast, the cover of litter and bare ground as well as the vegetation height did not differ.

The multivariable synthesis GLMM revealed that patch occupancy of *E. aurinia* was affected by both parameters at the landscape and habitat level (Table 2a). The likelihood of occurrence of *E. aurinia* increased with the cover of grasslands with *S. pratensis* in a radius of 250 m surrounding the patches, habitat heterogeneity and host-plant cover.

Microhabitat occupancy

Altogether, 90 microhabitats containing an egg batch or a first instar larval web were detected within 29 of the 42 occupied patches. The primary host plant was *S. pratensis*; 81 of all occupied host plants (90%) belonged to this species. Although *S. lucida* was also widespread in the hummocky meadows, it was rarely used for oviposition (9 plants, 10%) and was used only if *S. pratensis* was not present on the patch.

Table 3 Overview of sampled metric parameters at microhabitats occupied and unoccupied by *E. aurinia*.

Parameter	Correlation		Occupied microhabitat (<i>N</i> = 90)		Unoccupied microhabitat (<i>N</i> = 90)		<i>P</i>
	<i>r_s</i>	used [†]	Mean (±SE)	Min.–Max.	Mean (±SE)	Min.–Max.	
Daily sunshine duration (h) [‡]			12.8 ± 0.1	(10–15)	11.8 ± 0.2	(1–15)	**
Host-plant characteristics							
Cover (%) [§]			24.5 ± 1.6	(5–70)	14.9 ± 1.5	(2.5–80)	***
No. of leaves			19.9 ± 1.2	(6–86)	12.6 ± 0.7	(2–38)	***
Diameter (cm)	0.6		20.4 ± 0.9	(3–53)	16.7 ± 0.7	(6–39)	**
Height (cm)	0.8	▲ Vegetation height	13.2 ± 0.7	(3–36)	11.9 ± 0.7	(3–31)	n.s.
Vegetation height (cm)	1.0		17.0 ± 0.9	(6–56)	17.6 ± 0.8	(7–39)	n.s.
Cover of different layers (%)							
Herbs	1.0	▲ Herbs	48.8 ± 1.5	(15–80)	46.3 ± 1.6	(10–80)	n.s.
Grasses	–0.7		32.1 ± 1.4	(5–65)	35.8 ± 1.6	(10–80)	n.s.
Litter			11.8 ± 0.7	(5–40)	10.4 ± 0.5	(5–30)	n.s.
Bare ground			4.4 ± 0.9	(0–60)	2.9 ± 0.3	(0–20)	n.s.

Note: Differences between occupied and unoccupied microhabitats were tested using GLMM with “subarea” as a random factor and “patch” within “subarea” as a nested random factor. If two or more variables were strongly intercorrelated (Spearman’s rank correlation, $|r_s| > 0.6$), only one was used in the subsequent analysis (see Table 2). For further information, see section Materials and methods, Statistical analysis. ***P* < 0.01, ****P* < 0.001; n.s., not significant.

[†] Variables used in the full model (GLMM) of the respective level after correlation analysis.

[‡] Accuracy: 1/2 h (Scherer *et al.*, 2021).

[§] Cover of all host plants within a radius of 50 cm around the focal host plant.

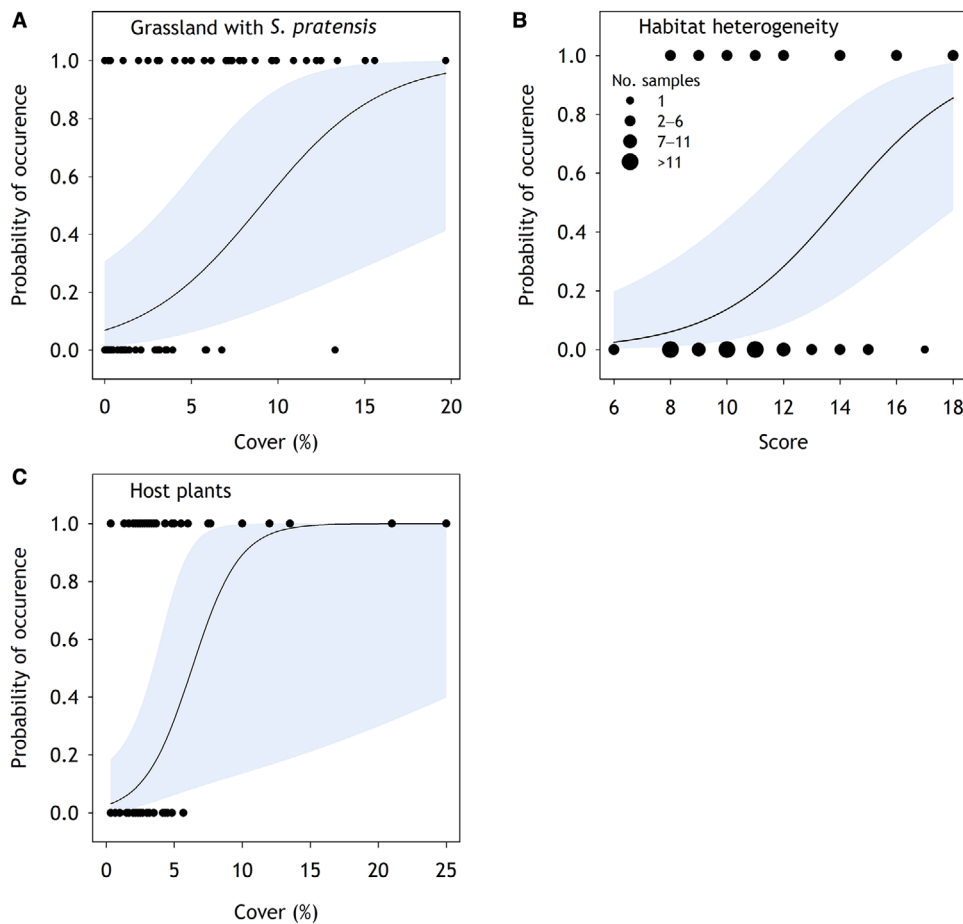


Fig. 3 Relationship between patch occupancy of *E. aurinia* and significant environmental parameters ($N_{\text{occupied}} = 42$ vs. $N_{\text{unoccupied}} = 80$; see Table 2 for detailed GLMM statistics).

Occupied microhabitats differed from unoccupied ones by a higher sunshine duration (Table 3). In contrast to unoccupied microhabitats, we found no occupied microhabitats that received less than 10 h of solar radiation (Fig. 4). Additionally, host-plant characteristics had a strong influence on microhabitat occupancy. Microhabitats with a higher cover of host plants and host plants providing more biomass (more leaves, greater diameter) were preferred for oviposition. By contrast, vegetation height and the cover of the vegetation layers did not differ between occupied and unoccupied microhabitats. Land use also influenced microhabitat occupancy (Table 4). Within the occupied patches, abandoned microhabitats were preferred for oviposition. The vast majority of occupied host plants was found in moist, followed by wet and then by fresh microhabitats. By contrast, semidry microhabitats were of low importance for oviposition. However, soil humidity did not differ between occupied and unoccupied microhabitats. *Succisa pratensis* plants

growing in litter meadows were generally taller than those in hummocky meadows (Fig. 2).

The multivariable GLMM revealed that microhabitat occupancy increased with host-plant biomass (number of leaves), cover of host plants and sunshine duration (Table 2b).

Discussion

Our study revealed that environmental conditions at the landscape and habitat level determined the occurrence of *E. aurinia* in a montane agricultural landscape with low land-use intensity. Patch occupancy increased with the cover of *S. pratensis* grasslands in the surroundings of the patches, habitat heterogeneity, and host-plant cover. Microhabitat occupancy was driven by a warm microclimate and high availability of host plants. The performance of the GLMMs was outstanding.

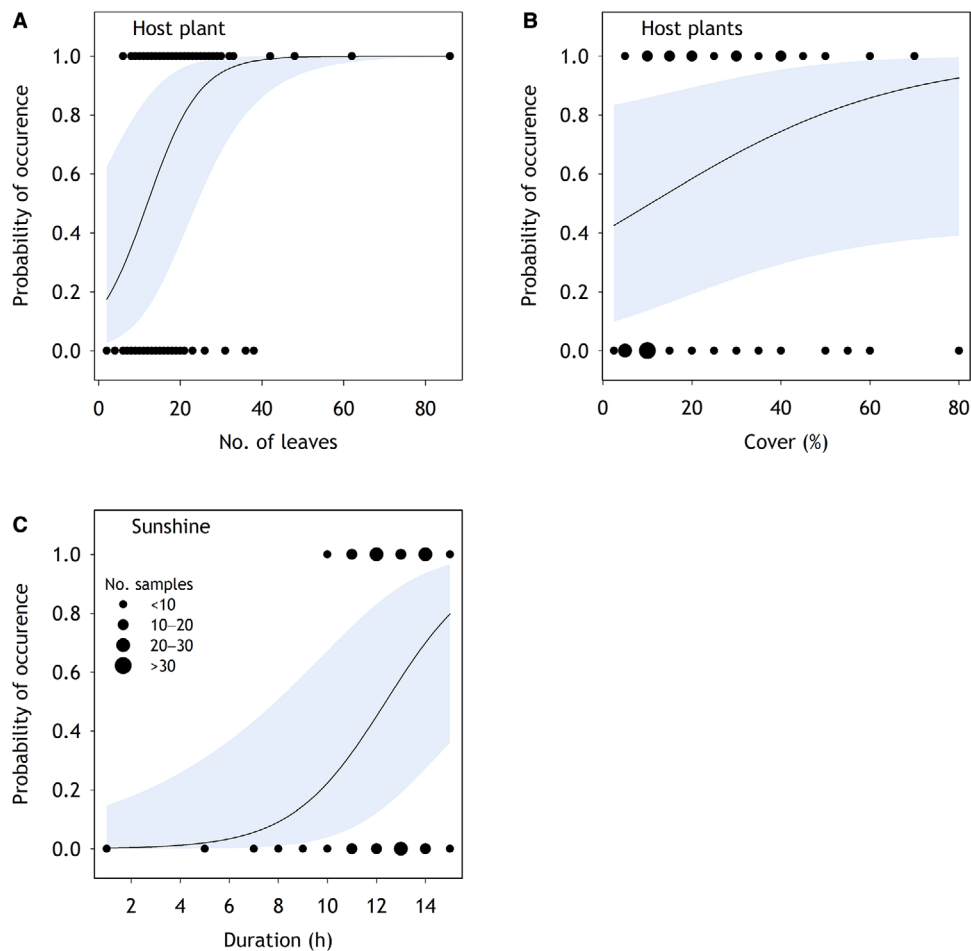


Fig. 4 Relationship between microhabitat occupancy of *E. aurinia* and significant environmental parameters ($N_{\text{occupied}} = 90$ vs. $N_{\text{unoccupied}} = 90$; see Table 2 for detailed GLMM statistics).

The persistence of species forming metapopulations, such as *E. aurinia* (Wahlberg *et al.*, 2002; Anthes *et al.*, 2003b; Bulman *et al.*, 2007), in our landscapes is driven by the isolation, quality and size of the habitat patches (WallisDeVries, 2004; Eichel & Fartmann, 2008; Stuhldreher & Fartmann, 2014). However, the relative importance of the three metapopulation parameters usually differs depending on the degree of habitat fragmentation (Poniatowski *et al.*, 2018). Especially in well-connected landscapes with large habitat patches, which is the case in the study area, habitat quality is mostly the main driver of patch occupancy (Krämer *et al.*, 2012b; Poniatowski *et al.*, 2018; Münch *et al.*, 2019). In line with this assumption, isolation had no effect on patch occupancy of the butterfly species in the synthesis model. Nevertheless, occupied patches were less isolated than unoccupied ones. Furthermore, can the cover of *S. pratensis* grass-

lands in the near surroundings of the patches also be considered as a measure of habitat connectivity. This is especially true for a less dispersive species like *E. aurinia*. By contrast, habitat quality strongly explained the occurrence of *E. aurinia*. Patch occupancy increased with habitat heterogeneity and the cover of host plants on different spatial scales. For many other butterfly species, it has also been shown that habitat heterogeneity promotes population stability (Oliver *et al.*, 2010). This is especially true in times of global warming, where extreme climatic events become increasingly more likely (Stuhldreher & Fartmann, 2018; Suggitt *et al.*, 2018). Habitat heterogeneity and patch size are often interrelated (Poniatowski *et al.*, 2018). This relationship has already been detected for the hummocky meadows of the study area (Löffler & Fartmann, 2017) and was also the case in this study. Accordingly, our results corroborate

Table 4 Absolute and relative frequencies of the categorical variables land-use type and soil humidity at microhabitats occupied and unoccupied by *E. aurinia*.

Parameter	Occupied microhabitat (<i>N</i> = 90)		Unoccupied microhabitat (<i>N</i> = 90)		<i>P</i>
	<i>N</i>	%	<i>N</i>	%	
Land-use type					*
Mown early	11	12	18	20	
Mown late	43	49	48	55	
Grazed	0	0	2	2	
Abandoned	34	39	20	23	
Soil humidity					n.s.
Wet	23	26	32	37	
Moist	45	52	38	43	
Fresh	17	19	16	18	
Semidry	3	3	2	2	

Note: Differences were analyzed using the Fisher's exact test. **P* < 0.05; n.s., not significant.

previous findings, showing that the population structure of *E. aurinia* resembles mostly the mainland-island type of metapopulation (Wahlberg *et al.*, 2002; Anthes *et al.*, 2003b).

Sufficient food is of vital importance for the survival of the larvae, in particular for cluster-building species with gregarious caterpillars so as to avoid intraspecific competition (García-Barros & Fartmann, 2009). In our study, both patch and microhabitat occupancy of *E. aurinia* increased with the cover of host plants; additionally, host plants with many leaves were preferred for oviposition. The great significance of a high host-plant biomass for patch and microhabitat selection in *E. aurinia* has also been observed for pure wet grassland populations (Anthes *et al.*, 2003b; Konvicka *et al.*, 2003; Tjørnølv *et al.*, 2015; Brunbjerg *et al.*, 2017). By far the most important host plant in our study was *S. pratensis*; 90% of all occupied plants belonged to this species. Additionally, patch occupancy increased with the cover of *S. pratensis* grasslands in a radius of 250 m around the patches. The second host plant, *S. lucida*, was common in the hummocky meadows (cf. Gutser & Kuhn, 1998). However, it was rarely used for oviposition and was used only if *S. pratensis* was not present in the patch. We explain the clear preference for *S. pratensis* by the higher biomass of the species due to a more luxuriant growth compared to *S. lucida* (cf. Klotz *et al.*, 2002). However, plant size did not only differ between the two host-plant species but also within *S. pratensis* populations. *Succisa* plants in litter meadows were larger than those in the less productive hummocky meadows on usually much drier soils. As a result, we explain the clearly higher

occupancy of litter meadows compared to hummocky meadows as well as the preference for moist and wet microhabitats for oviposition also by a higher availability of biomass per host plant.

Anthes *et al.* (2003b) showed that land use also had a strong impact on host-plant size and, hence, plant biomass. Early stages of abandonment favored the growth of large host plants in wet grasslands. Accordingly, the authors identified the occurrence of luxuriant host plants as the key factor for the preferred oviposition by *E. aurinia* in young abandoned grasslands. Our study revealed similar findings. Within occupied patches, abandoned microhabitats were preferred for oviposition. However, with ongoing succession, even under the very nutrient-poor conditions in the studied grasslands, host plants will become overgrown (cf. Anthes *et al.*, 2003b). Our study also provides evidence for negative effects of long-term abandonment on *E. aurinia*. Occupied patches were characterized by a higher cover of herbs and a lower cover of grasses than unoccupied ones. By contrast, abandonment of grasslands favors the expansion of competitive grasses at the expense of herbs (Ellenberg & Leuschner, 2010). In the studied grasslands, especially *Brachypodium rpestre*, *Calamagrostis varia* and *Molinia arundinacea* typically become dominant after long-term succession (Gutser & Kuhn, 1998; Streitberger *et al.*, 2012).

Microclimatic conditions also play an important role in determining habitat quality for butterflies (Roy & Thomas, 2003; WallisDeVries & van Swaay, 2006; Dennis *et al.*, 2010; Stuhldreher & Fartmann, 2018). If larvae of *E. aurinia* develop under warm microclimatic conditions during prehibernation, the chance of reach-

ing the 4th instar before hibernation increases (Porter, 1982, 1983). As a result, after hibernation in spring, caterpillars become less parasitized by braconid wasps (*Cotesia* spp.). In accordance with this, *E. aurinia* is known to prefer warm microhabitats exposed to the sun for oviposition (Anthes *et al.*, 2003b; Pielech *et al.*, 2017). Therefore, in cool montane habitats with a pronounced relief, such as in the pre-Alps, a preference for warm microhabitats should be particularly pronounced. Indeed, our results indicate that *E. aurinia* is able to cope with the adverse macro- and mesoclimatic conditions in the study area by choosing extraordinarily warm microhabitats for oviposition characterized by high solar radiation.

In conclusion, in the well-connected landscape with large patches of nutrient-poor grasslands, habitat quality was the main driver of patch occupancy in *E. aurinia*. Habitats of high quality were defined by (i) a high habitat heterogeneity, (ii) sufficient food for the larvae, and (iii) a warm microclimate. Habitat heterogeneity very likely buffers *E. aurinia* populations against environmental stochasticity and, hence, enhances long-term population viability. Although both *S. lucida* and *S. pratensis* were widespread in the studied grasslands, the latter was clearly preferred as a host plant. Due to the more luxuriant growth, *S. pratensis* plants offered generally more biomass to the caterpillars than *S. lucida* plants. Additionally, the growth of large *Succisa* plants was favored by wet or moist soils (litter meadows) and early stages of grassland abandonment. To cope with the adverse macro- and mesoclimatic conditions of the study area, females selected host plants growing in extraordinarily warm microhabitats for oviposition.

Implications for conservation

As shown by our study, a high abundance of luxuriant *Succisa* plants within the nutrient-poor grasslands of the study area is of vital importance for the long-term survival of *E. aurinia*. Such conditions are found in early stages of abandonment in both litter meadows and the wettest parts of hummocky meadows. Interestingly, all patches with a higher cover of host plants than 6% were occupied by *E. aurinia*. This might be an important threshold that should especially be considered for habitat restoration and the re-establishment of *S. pratensis*. However, to counteract the suppression of the host plants through ongoing succession (Gutser & Kuhn, 1998; Streitberger *et al.*, 2012) and to favor richness of plant and insect species in general, even these very nutrient-poor grasslands depend at least from time to time on low-

intensity management (Krämer *et al.*, 2012b; Löffler & Fartmann, 2017). Accordingly, we recommend creating mosaics of traditionally managed grasslands and early stages of abandonment within the patches. Traditionally the hummocky and litter meadows are mown once per year, not before July (Gutser & Kuhn, 1998). Consequently, the stage most sensitive to direct effects of land use, the immobile egg stage, is usually not affected by this kind of land use (cf. Section Materials and methods, Study species). Accordingly, we recommend maintaining the traditional mowing regime and reintroducing it in hummocky and litter meadows with long-term abandonment (cf. Krämer *et al.*, 2012b; Löffler & Fartmann, 2017; Schwarz & Fartmann, 2021). Large and heterogeneous grassland patches played a decisive role as habitats for *E. aurinia*. Consequently, these patches should have priority for conservation management. During the last century, the area of hummocky meadows has markedly declined (Gutser & Kuhn, 1998). Hence, to increase the long-term viability of *E. aurinia* populations further and to counteract a potential extinction debt (Bulman *et al.*, 2007; Löffler *et al.*, 2020), we suggest restoring former hummocky meadows.

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