# Abandonment of traditional land use and climate change threaten the survival of an endangered relict butterfly species

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**Abstract.** 1. The decline of butterflies exceeds those of many other animal taxa due to their high sensitivity to habitat alterations driven by land-use change. Moreover, cold-adapted species frequently suffer severe range retractions due to rising temperatures at their trailing-edge range margins.

2. In this study, we aim to identify drivers of occupancy of the post-glacial relict species *Lycaena helle* at three spatial scales – (i) landscape, (ii) habitat, and (iii) microhabitat – in one of its last refuges in central Europe.

3. In our study in the Eifel low mountain range (western Germany), the occurrence of *L. helle* was mainly driven by the (i) isolation, (ii) size, and (iii) quality of habitat patches. *Lycaena helle* formed metapopulations that were dependent on networks of interconnected but often small habitat patches.

4. Habitat quality within the semi-natural grasslands was determined by (i) macro- and mesoclimate, (ii) host-plant abundance, and (iii) vegetation structure, which was interrelated with microclimate. *Lycaena helle* preferred moist, nutrient-poor grasslands in deep, narrow valleys at the highest elevations of the study area, which were characterised by (i) cold winters, (ii) high abundance of the host plant, and (iii) short and sparse swards providing a warm microclimate in summer.

5. According to these findings, abandonment of traditional land use and climate change are considered the most severe threats for long-term survival of the species. Hence, conservation measures should aim at maintaining and restoring networks of large and well-connected habitat patches of high quality, preferably in cold-air depressions within mountain systems.

**Key words.** Global warming, habitat fragmentation, host-plant abundance, land-use change, *Lycaena helle*, microclimate.

## Introduction

Insects are the most diverse taxonomic group worldwide (Stork, 2018). Due to their outstanding conservation value, as well as their importance for ecosystem functioning and agricultural production, they are of crucial importance for future generations (Powney *et al*., 2019; Samways *et al*., 2020). However, many insects are facing extinction (Sánchez-Bayo &

Wyckhuys, 2019; Cardoso *et al*., 2020). Hence, conservation of insect diversity has received increasing attention in recent years (Harvey *et al*., 2020; Samways *et al*., 2020). Nevertheless, evidence-based conservation strategies addressing all relevant spatial scales are still lacking for many insect taxa, even among charismatic insect groups such as butterflies (Dennis & Sparks, 2006; Eichel & Fartmann, 2008; Dennis, 2010; Thomas *et al*., 2010).

The decline in butterfly diversity and abundance exceeds those of plants and many other animal taxa (Thomas *et al*., 2004; Thomas, 2005). Since the 1950s, agricultural intensification and abandonment have led to a strong decline and

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degradation of semi-natural habitats, especially grassland eco-systems across Europe (Stoate *et al.*, 2009; WallisDeVries *et al.*, 2002; Habel *et al.*, 2019; Löffler *et al.*, 2020). Consequently, populations of many grassland butterflies have strongly decreased, and thus, they are now often restricted to a few habitat fragments, situated in hostile landscape matrixes (Maes & Van Dyck, 2001; van Swaay *et al.*, 2009; Brückmann *et al.*, 2010; Poniatowski *et al.*, 2018; Warren *et al.*, 2021). Moreover, there is increasing evidence that global warming alters the population size and distribution of butterflies. While many thermophilic species benefit from climate change (Parmesan *et al.*, 1999; Chen *et al.*, 2011; Devictor *et al.*, 2012), cold-adapted species with a boreo-montane distribution often suffer severe range retractions due to rising temperatures at their trailing-edge range margins (Konvička *et al.*, 2003; Thomas *et al.*, 2006; Stuhldreher & Fartmann, 2018). Consequently, they are among the most sensitive species to recent environmental change and, thus, need particular consideration in conservation strategies and management (Wilson *et al.*, 2007; Habel & Assmann, 2010; van Swaay *et al.*, 2010).

Isolation and habitat patch size have been identified as important drivers of grassland butterfly persistence at the landscape scale (Hanski, 1998; Anthes *et al.*, 2003; Krämer *et al.*, 2012a; Poniatowski *et al.*, 2018; Belitz *et al.*, 2020). In particular, mobile species depending on a metapopulation network are vulnerable to habitat fragmentation (e.g. Anthes *et al.*, 2003; Eichel & Fartmann, 2008; van Strien *et al.*, 2011). However, climate-sensitive species with lower mobility may also strongly depend on high connectivity, as it increases their ability to evade detrimental environmental conditions under global warming (Bauerfeind *et al.*, 2009; Modin & Öckinger, 2020). Furthermore, habitat quality is another important driver of butterfly patch occupancy (Thomas *et al.*, 2001; Poniatowski *et al.*, 2018; Münsch *et al.*, 2019). Maintenance of high habitat quality in semi-natural habitats usually requires proper management practices (Krämer *et al.*, 2012a; Münsch *et al.*, 2019). Habitat quality, specifically, is determined by ecological requirements of the immature stages because they are more sensitive to habitat alterations than more mobile and, usually, less-specific adults (García-Barros & Fartmann, 2009). Availability of sufficient food and a suitable microclimate are of prime importance for the successful development of immature stages.

In this study, we aim to identify the occupancy drivers of the relict species *Lycaena helle* at three spatial scales – (i) landscape, (ii) habitat and (iii) microhabitat scale (see 'Environmental parameters' section) – in one of its last refuges in central Europe. Previous studies have revealed that *L. helle* is highly sensitive to both land-use and climate change and, thus, is one of the most severely threatened butterfly species in Europe (Fischer *et al.*, 1999; Bauerfeind *et al.*, 2009; Habel & Assmann, 2010; van Swaay *et al.*, 2010; Maes *et al.*, 2019). Consequently, it is now a protected species of Annex II and IV of the EU Habitats Directive [European Commission (EC), 1992]. Despite increased conservation efforts, recent studies suggest that the remaining populations are still declining and suffer a decrease of genetic diversity due to global warming (Habel & Assmann, 2010; Nabielec & Nowicki, 2015). As there is still uncertainty to what extent these declines are driven by habitat

fragmentation, degradation of habitat quality, or global warming, more studies considering all relevant spatial scales are needed to improve management strategies in a rapidly changing environment. Moreover, conservation measures should more strongly address potential interactions between the effects of habitat fragmentation and climate change (cf. Oliver *et al.*, 2016).

The results of our analyses provide profound insights into habitat preferences of *L. helle* and are used to derive implications for future management, which may help the species cope with climate change. We expect that a dense habitat network will increase the long-term viability of the remaining central European *L. helle* populations in times of global warming. Moreover, we assume that long-term persistence of the species in these refuges depends on periodic, low-intensity land use to maintain high habitat quality, that is, moist grasslands with short swards and high host-plant abundance (cf. Bauerfeind *et al.*, 2009). In contrast, agricultural abandonment inevitably leads to local extinctions of the species in the long run. Microhabitat characteristics are critical for *L. helle*, and, thus, likely need particular attention in conservation management. Due to its sensitivity to global warming, the availability of suitable microhabitats with a well-developed litter layer may help the species to buffer temperature fluctuations in winter, which could be detrimental for hibernating pupae (cf. Stuhldreher *et al.*, 2014; Turlure *et al.*, 2014).

## Materials and methods

### Study species

The Violet Copper (*L. helle*) is a post-glacial relict species with a boreo-montane distribution in the Palearctic (Habel & Assmann, 2010; Kudrna *et al.*, 2011). The species has a low mobility, generally with dispersal distances less than 1 km (Fischer *et al.*, 1999). While this lycaenid butterfly was widespread in temperate Europe during the glacial and post-glacial era, it has become scarce across large parts of its European range during post-glacial warming (Habel & Assmann, 2010). The occurrence of the species in western and central Europe is now largely restricted to a few isolated remnant metapopulations, mostly located in cold mountain areas (Fischer *et al.*, 1999; Nunner, 2006; Habel & Assmann, 2010), but lowland populations still exist in more continental and boreal Europe (Skórka *et al.*, 2007; Kudrna *et al.*, 2011). During recent decades, the remaining populations of *L. helle* have strongly declined, primarily due to habitat deterioration and climate change (van Strien *et al.*, 2011; Nabielec & Nowicki, 2015). Consequently, the species is now considered endangered at a continental scale (van Swaay *et al.*, 2010).

*Lycaena helle* mainly occurs in cool and damp abandoned semi-natural grasslands (Fischer *et al.*, 1999; Skórka *et al.*, 2007). However, regionally, it also occupies other wetland habitats, such as spring-fed swamps, bogs, and forest clearings (Steiner *et al.*, 2006; Bauerfeind *et al.*, 2009; Bräu *et al.*, 2013). In central Europe, *L. helle* is monophagous with larvae only feeding on the Common Bistort (*Bistorta officinalis*;

Fischer *et al.*, 1999). In addition to the occurrence of its host plant, *L. helle* requires very specific habitat conditions providing climatically suitable microhabitats in well-connected habitat patches (Fischer *et al.*, 1999; Nunner, 2006; Steiner *et al.*, 2006; Bauerfeind *et al.*, 2009; Goffart *et al.*, 2014). The western and central European populations of *L. helle* are univoltine with a flight period from the beginning of May to early July (Ebert & Rennwald, 1991; Bräu *et al.*, 2013). In contrast to larvae, adults have less-specific feeding preferences and usually use several available nectar resources in their habitats (Ebert & Rennwald, 1991; Fischer *et al.*, 1999).

### Study area

The study area is located in western Germany, approximately 50 km southwest of the city of Cologne (52°31′N/13°24′E to 50°29′N/6°37′E). With an area of approximately 500 km², it comprises the north-western part of the Eifel low mountain range, stretching from 370 to 690 m above sea level (a.s.l.). The climate in the study area is sub-oceanic with relatively cool summers and moderately cold winters (mean annual temperature: 8.0 °C) and high levels of precipitation (mean annual precipitation: 857 mm) [weather station Kall Sistig; 505 m a.s.l.; reference period: 1981–2010; German Meteorological Service (DWD), 2020]. The

study area is characterised by an undulating terrain, crossed by deep, narrow stream valleys which are usually affected by cold air draining (Löffler *et al.*, 2019). While mountain ridges and steep slopes are usually forested, the damp valley floors are traditionally used as nutrient-poor meadows or pastures. However, due to the adverse environmental conditions for agriculture, many wet grasslands on the damp valley floors have been abandoned over the last decades.

### Sampling design

The effects of landscape and habitat quality on patch occupancy of *L. helle* were studied within 67 semi-natural grassland patches with occurrence of the host plant (*B. officinalis*) (patch size: 0.1–2.6 ha). All patches were situated in valleys close to small streams within six distinct study subareas; the majority of these valleys were deep and narrow. Patches were regarded as discrete when they were isolated from the nearest neighbouring patch by >50 m of non-habitat, such as forest or improved grassland (Krämer *et al.*, 2012a; Poniatowski *et al.*, 2018). Microhabitat occupancy was studied within all occupied patches (*n* = 25).

*Butterfly sampling.* Patch occupancy of *L. helle* was assessed using standardised transect counts (Pollard &

**Table 1.** Metric environmental parameters at patches occupied by *L. helle* (*n* = 25) and unoccupied ones (*n* = 42). Differences were analysed using GLMM with a binomial error structure. Study subarea was used as a random factor in all models. Statistical significances of the predictors were assessed using the likelihood ratio test. Significance levels are indicated as follows: n.s., not significant, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

| Parameter | Occupied (*n* = 25) | | Unoccupied (*n* = 42) | | |
| --- | --- | --- | --- | --- | --- |
| | Mean ± SE | Min.–Max. | Mean ± SE | Min.–Max. | *P* value |
| (a) *Landscape scale* | | | | | |
| Isolation (km)* | 0.9 ± 0.3 | (0.1–8.0) | 4.5 ± 0.6 | (0.1–14.0) | *** |
| Patch size (ha) | 0.9 ± 0.2 | (0.1–5.0) | 0.6 ± 0.1 | (0.1–2.6) | * |
| Elevation (m a.s.l.) | 534.4 ± 11.3 | (425–610) | 511.9 ± 8.0 | (395–605) | ** |
| Mean annual temperature (°C) | 6.9 ± 0.1 | (6.4–7.5) | 7.0 ± 0.1 | (6.2–7.9) | n.s. |
| Number of frost days | 103.8 ± 0.8 | (96–110) | 101.6 ± 0.9 | (88–114) | n.s. |
| Cover of habitat types (%)† | | | | | |
| Arable land | 0.0 ± 0.0 | (0–0) | 0.6 ± 0.4 | (0–20) | n.s. |
| Managed grassland | 16.2 ± 2.2 | (0–40) | 16.8 ± 2.8 | (0–65) | n.s. |
| Abandoned grassland | 13.6 ± 1.5 | (5–30) | 9.2 ± 0.8 | (0–25) | * |
| Clear cut | 3.8 ± 0.9 | (0–10) | 3.7 ± 1.2 | (0–35) | n.s. |
| Forest | 60.2 ± 3.2 | (30–80) | 61.3 ± 3.1 | (15–90) | n.s. |
| (b) *Habitat scale* | | | | | |
| Host-plant cover (%) | 30.4 ± 2.9 | (10–65) | 24.2 ± 2.9 | (5–85) | n.s. |
| Sunshine duration (h) | 10.5 ± 0.4 | (6–15) | 9.8 ± 0.4 | (4–15) | n.s. |
| Cover of vegetation layers (%) | | | | | |
| Bare ground | 4.8 ± 0.6 | (0–15) | 4.9 ± 0.6 | (0–20) | n.s. |
| Total vegetation | 89.0 ± 1.5 | (65–95) | 91.8 ± 0.8 | (80–100) | n.s. |
| Shrubs | 7.2 ± 0.9 | (0–20) | 9.0 ± 1.1 | (0–30) | n.s. |
| Herbs | 57.0 ± 2.9 | (30–80) | 60.7 ± 2.5 | (35–90) | n.s. |
| Grass | 37.4 ± 2.0 | (10–60) | 35.6 ± 2.4 | (10–70) | n.s. |
| Litter | 8.5 ± 0.8 | (2.5–20) | 10.5 ± 1.8 | (2.5–25) | n.s. |
| Mosses | 6.1 ± 0.8 | (0–20) | 4.8 ± 0.5 | (0–15) | n.s. |

*Mean Euclidean distance to nearest three occupied patches (Bauerfeind *et al.*, 2009).
†250 m around the patch.

Yates, 1993). Patches were sampled up to three times between the beginning of May and the end of June 2017, with a time interval of at least 3 weeks between each survey. Transect walks were done between 10:00 and 17:00 hours under suitable weather conditions (i.e. temperature > 15 °C, cloud cover <50%, wind <4 Beaufort; Pollard, 1977). In each patch, adults of *L. helle* were recorded walking in loops covering the whole patch with a width of 5 m between the loops. Only patches without evidence for occupancy of *L. helle* during the first survey were investigated a second or even a third time. According to Poniatowski *et al.* (2018), a patch was classified as occupied if at least three adults (as an indicator for an indigenous population) were detected.

Microhabitat occupancy of *L. helle* was assessed by systematically searching for immature stages (eggs or larvae) on the host plants in June 2017 by pacing each occupied habitat patch in loops with a distance of 5 m between each loop. A host plant (i.e. microhabitat) was considered occupied if at least one egg or larva was found (Krämer *et al.*, 2012a).

### Environmental parameters

*Landscape, habitat, and microhabitat scale.*   At the landscape scale, we measured elevation, isolation, and size of all patches (Table 1). The isolation of a patch was calculated as the mean distance from the focal patch to the three nearest occupied habitat patches, which is among the most frequently used connectivity measures (Moilanen & Nieminen, 2002). According to Krämer *et al.* (2012b), we also calculated the cover of major habitat types within a buffer of 250 m around each patch (Table 1). Moreover, mean annual temperature and number of frost days were derived for each patch using grid-map data (spatial resolution 1 × 1 km) from the German Meteorological Service [Table 1; reference period 1981–2010; German Meteorological Service (DWD), 2020]. All spatial analyses were done using ArcGIS 10.4.

Habitat quality at the habitat scale (i.e. patch scale) was assessed at the end of May, which is the peak flight period of *L. helle* in central Europe (cf. 'Study species' section). For each patch, we recorded land use (managed vs. abandoned) and potential daily sunshine duration for June – the month with the highest potential solar radiation – in the centre of the patch using a horizontoscope (Krämer *et al.*, 2012a; Tables 1 and 2). Furthermore, we measured vegetation structure [for details, see column

(b) in Table 1], soil humidity, and abundance of the host plant (*B. officinalis*) in three randomly chosen plots within the patches, each covering 9 m² (3 m × 3 m; for details, see Tables 1 and 2). Mean values of the parameters assessed from the three plots were used for all further analyses.

Microhabitat characteristics were studied using the same parameters as mentioned above within a buffer of 0.5 m around occupied host plants (*n* = 56) (Tables 3 and 4). Additionally, we measured average vegetation height in the microhabitats (Table 3). To contrast the characteristics of occupied and unoccupied host plants, we recorded the same parameters around randomly chosen control samples (i.e. host-plant individuals that were not used by immature stages). These samples represent the nearest unoccupied plant to a randomly thrown stick (cf. Anthes *et al.*, 2003). The total number of control samples corresponded to the number of occupied host plants (*n* = 56). To represent the overall availability of potential microhabitats, the number of control samples per habitat patch was adjusted to its size, with at least one sample per patch.

*Microclimatic measurements.*   To investigate microclimatic preferences, we recorded summer and winter temperatures within a random selection of occupied (*n* = 10) and unoccupied patches (*n* = 10) using temperature loggers (MicroLogPRO II). The loggers were installed 10 cm above the ground in the centre of the patch, and measurements took place during a period of high solar radiation. Summer temperatures were measured from the 18th to 21st of July, 2017 and winter temperatures from the 15th to 16th of February, 2018. Temperatures were recorded hourly with an accuracy of 0.1 °C. For further analyses, we distinguished between daytime (summer: 09:00–21:00 hours; winter: 10:00–17:00 hours) and night-time (summer: 21:00–09:00 hours; winter: 17:00–10:00 hours) using the mean temperature values of each logger within these periods.

### Statistical analysis

Landscape, habitat, and microhabitat characteristics of occupied and unoccupied patches were compared using univariable generalised linear mixed-effect models (GLMM) (R package multcomp, Hothorn *et al.*, 2020). We conducted multivariable GLMM to reveal environmental parameters that crucially determine the occupancy of

**Table 2.** Categorical environmental parameters at patches occupied by *L. helle* (*n* = 25) and unoccupied ones (*n* = 42). Differences were analysed using GLMM with a binomial error structure. Study subarea was used as a random factor in all models. Statistical significances of predictors were assessed using the likelihood ratio test. Significance levels are indicated as follows: n.s., not significant, *P < 0.05.

| Parameter | Occupied (*n* = 25) | | Unoccupied (*n* = 42) | | |
| --- | --- | --- | --- | --- | --- |
| | *n* | % | *n* | % | *P* value |
| Land use | | | | | |
| Managed (baseline) | 9 | 36.0 | 16 | 38.1 | |
| Abandoned | 16 | 64.0 | 26 | 61.9 | n.s. |
| Soil humidity | | | | | |
| Fresh (baseline) | 3 | 12.0 | 11 | 26.2 | |
| Moist | 18 | 72.0 | 17 | 40.5 | * |
| Wet | 4 | 16.0 | 14 | 33.3 | n.s. |

**Table 3.** Metric environmental parameters at microhabitats occupied by *L. helle* (*n* = 56) and randomly selected control sites (*n* = 56). Differences were analysed using GLMM with a binomial error structure. Patches nested within the study subarea were used as a random factor in all models. Statistical significances of the predictors were assessed using the likelihood ratio test. Significance levels are indicated as follows: n.s., not significant, **$P < 0.01$, ***$P < 0.001$.

| Parameter | Occupied (*n* = 56) | | Control (*n* = 56) | | |
|---|---|---|---|---|---|
| | Mean (±SE) | Min.–Max. | Mean (±SE) | Min.–Max. | *P* value |
| Host-plant cover (%) | 47.5 ± 2.2 | (20–90) | 28.3 ± 2.2 | (5–70) | *** |
| Vegetation height (cm) | 48.5 ± 1.8 | (30–81) | 83.5 ± 3.0 | (30–123) | *** |
| Sunshine duration (h) | 10.1 ± 0.2 | (7.5–15) | 10.3 ± 0.2 | (5–15) | n.s. |
| Cover of vegetation layers (%) | | | | | |
| Bare ground | 4.6 ± 0.6 | (0–25) | 2.4 ± 0.4 | (0–20) | ** |
| Total vegetation | 81.3 ± 2.2 | (35–95) | 89.8 ± 0.9 | (50–95) | *** |
| Shrubs | 1.0 ± 0.4 | (0–10) | 0.0 ± 0.0 | (0–0) | n.s. |
| Herbs | 61.4 ± 2.5 | (30–95) | 62.2 ± 2.2 | (30–90) | n.s. |
| Grasses | 25.4 ± 2.0 | (5–60) | 27.7 ± 2.1 | (2.5–60) | n.s. |
| Litter | 15.6 ± 2.0 | (5–60) | 7.3 ± 0.5 | (2.5–20) | *** |
| Mosses | 3.9 ± 0.4 | (0–15) | 3.4 ± 0.4 | (0–15) | n.s. |

**Table 4.** Categorial environmental parameters at microhabitats occupied by *L. helle* (*n* = 56) and randomly selected controls (*n* = 56). Absolute (*n*) and relative frequencies (%) of the categories across the whole number of samples are given. Differences were analysed using GLMM with a binomial error structure. Patches nested within the study subarea were used as a random factor in all models. Statistical significances of the predictors were assessed using the likelihood ratio test. Significance levels are indicated as follows: n.s., not significant.

| Parameter | Occupied (*n* = 56) | | Unoccupied (*n* = 56) | | |
|---|---|---|---|---|---|
| | *n* | % | *n* | % | *P* value |
| Land use | | | | | |
| Managed (baseline) | 15 | 26.8 | 10 | 17.9 | |
| Abandoned | 41 | 73.2 | 46 | 82.1 | n.s. |
| Soil humidity | | | | | |
| Fresh (baseline) | 15 | 26.8 | 15 | 26.8 | |
| Moist | 38 | 67.9 | 37 | 66.1 | n.s. |
| Wet | 3 | 5.4 | 4 | 7.1 | n.s. |

*L. helle* at the (i) landscape, (ii) habitat, and (iii) microhabitat scale (R package lme4, Bates *et al*., 2019). To increase model robustness and identify the most important environmental parameters, we applied model averaging based on an information-theoretic approach (Grueber *et al*., 2011). Model averaging was done using the 'dredge' function (R package MuMIn, Bartón, 2020) and included only top-ranked models within $\Delta AIC_C < 3$ (Grueber *et al*., 2011). To avoid multicollinearity in the models, strongly inter-correlated variables were excluded from the analyses (Spearman rank correlations [$r_s$] values >|0.6|) (cf. Graham, 2003; Löffler & Fartmann, 2017). At the landscape scale, elevation ($r_s = -0.76$) and the number of frost days ($r_s = -0.92$) were excluded due to its strong correlation with temperature, forest cover due to its correlation with the cover of managed grasslands ($r_s = -0.74$). At the habitat and microhabitat scale, bare-ground cover was strongly inter-correlated with vegetation cover ($r_s = -0.61$ and $-0.60$, respectively). In addition, herb cover was excluded from the habitat and microhabitat models due to its strong correlation with grass cover ($r_s = -0.73$ and $-0.66$, respectively).

Models at the landscape and habitat scale were conducted with 'subarea' as a random factor. In models at the microhabitat scale,

'patch' was used as a nested random factor within 'subarea' (cf. Bolker *et al*., 2009). All statistical analyses were done using R 3.5.1 (R Development Core Team, 2020).

## Results

### Landscape scale

In total, *L. helle* was present at 25 (37%) of the 67 studied patches. Occupied patches were situated at higher elevations than unoccupied ones (Table 1). Moreover, they were larger, less isolated, and surrounded by a greater area of abandoned semi-natural grasslands compared to unoccupied patches. All other metric variables at the landscape scale did not differ between occupied and unoccupied patches. The multivariable GLMM analyses at the landscape scale revealed that patch occupancy of *L. helle* was positively affected by patch size, but was restricted by patch isolation [column (a) in Table 5; Fig. 2a].

**Table 5.** Model-averaging results (GLMM, binomial error structure). Relationship between patch occupancy of *L. helle* ($n_{occupied} = 25$ vs. $n_{unoccupied} = 42$) at the (a) landscape scale and (b) habitat scale, as well as microhabitat selection by *L. helle* ($n_{occupied} = 56$ vs. $n_{unoccupied} = 56$) at the (c) microhabitat scale and environmental parameters. In models (a) and (b), the study subarea was used as a random factor. In model (c), patches nested within the study subarea were used as a random factor. Model-averaged coefficients (conditional average) were derived from the top-ranked models ($\Delta AIC_C < 3$). Significance levels are indicated as follows: n.s. $P > 0.05$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

| Parameter | Estimate | SE | z | P value |
|---|---|---|---|---|
| (a) *Landscape scale (AUC [Area under the curve] = 0.90)* | | | | |
| Isolation (km) | −0.77 | 0.26 | −2.94 | ** |
| Patch size (ha) | 2.71 | 1.28 | 2.09 | * |
| Mean annual temperature (°C) | 2.22 | 1.36 | 1.60 | n.s. |
| Managed grassland (%) | −0.01 | 0.02 | −0.38 | n.s. |
| Abandoned grassland (%) | 0.07 | 0.06 | 1.10 | n.s. |
| (b) *Habitat scale (AUC = 0.91)* | | | | |
| Host-plant cover (%) | 0.05 | 0.02 | 1.97 | * |
| Total vegetation cover (%) | −0.18 | 0.07 | −2.53 | * |
| Sunshine duration (h) | 0.34 | 0.17 | 1.97 | * |
| Soil humidity (moist) | 2.74 | 1.12 | 2.40 | * |
| Grass cover (%) | 0.01 | 0.01 | 0.19 | n.s. |
| Litter cover (%) | −0.03 | 0.04 | −0.55 | n.s. |
| (c) *Microhabitat scale (AUC = 0.95)* | | | | |
| Vegetation height (cm) | −0.09 | 0.03 | −3.39 | *** |
| Host-plant cover (%) | 0.05 | 0.02 | 2.14 | * |
| Litter cover (%) | 0.24 | 0.11 | 2.04 | * |
| Grass cover (%) | −0.02 | 0.02 | −0.77 | n.s. |
| Sunshine duration (h) | 0.10 | 0.19 | 0.48 | n.s. |

### Habitat scale

Land use did not differ between occupied and unoccupied patches (Table 2). In total, 63% of the studied patches were abandoned, whereas the remaining 37% were managed by low-intensity grazing or mowing once per year. Moist patches were clearly preferred; 72% of all occupied patches had moist soil conditions (Table 2). In contrast, this was only true for 40% of the unoccupied patches.

In winter, occupied patches were characterised by lower temperatures during both day and night (Fig. 1). In contrast, in summer, lower temperatures in occupied patches were only detected during night-time.

The multivariable GLMM analyses at the habitat scale showed that the likelihood of patch occupancy increased with host-plant cover, sunshine duration and was positively affected by moist conditions within the patches [column (b) in Table 5; Fig. 2b]. In contrast, total vegetation cover had a negative effect on patch occupancy.

### Microhabitat scale

Altogether, 56 host plants were occupied by immature stages of *L. helle*. Occupied microhabitats had a higher cover of host plants, litter, and bare ground than unoccupied ones (Table 3). Additionally, they were characterised by shorter and sparser vegetation. All other environmental parameters at the habitat scale did not differ between occupied and unoccupied microhabitats (Tables 3 and 4).

The multivariable GLMM analyses at the microhabitat scale revealed that both host-plant and litter cover had positive effects on the occurrence of immature stages, while vegetation height negatively affected microhabitat occupancy of *L. helle* [column (c) in Table 5; Fig. 2c].

## Discussion

In our study in the Eifel low mountain range (western Germany), we identified significant predictors of *L. helle* occupancy at all relevant spatial scales. At the landscape scale, the occurrence of *L. helle* was determined by (i) the isolation and (ii) size of habitat patches. At the habitat and microhabitat scale, key habitat-quality parameters were the (i) cover of host plants (*B. officinalis*) and (ii) vegetation structure. Further drivers of occupancy at the habitat scale were a high sunshine duration and an intermediate soil humidity.

Persistence of butterflies in fragmented landscapes is known to depend on the isolation, size, and quality of habitat patches (Hanski, 1999; Thomas *et al.*, 2001; Anthes *et al.*, 2003; Poniatowski *et al.*, 2018). However, the relative importance of each of these parameters usually varies between species (Poniatowski *et al.*, 2018). A study by Öckinger *et al.* (2012) revealed that small butterfly species (i.e. species having a low dispersal capacity) with specific habitat requirements are most sensitive to habitat fragmentation. *Lycaena helle* is a small and short-lived butterfly species with maximum dispersal distances rarely exceeding 1 km (Fischer *et al.*, 1999; Turlure *et al.*, 2014; Modin & Öckinger, 2020). Bauerfeind *et al.* (2009) showed that
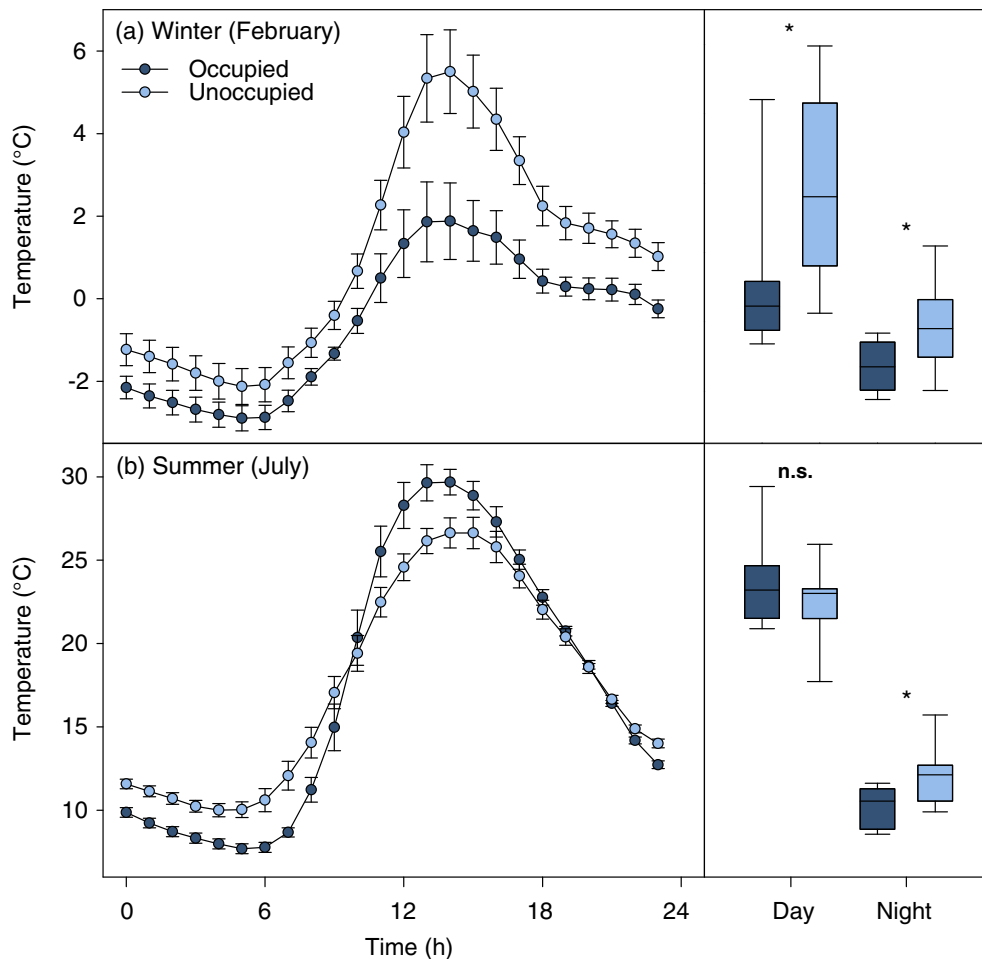
**Fig 1.** Diurnal variation of air temperature at occupied habitats of *L. helle* (dark blue, *n* = 10) and unoccupied habitats (light blue, *n* = 10) in (a) winter (measurement period: 15th to 16th of February, 2018) and (b) summer (measurement period: 18th to 21st of July, 2017). The left graphs show hourly averages (±SE). The boxplots on the right indicate differences between mean day (i.e. winter: 10:00–17:00 hours, summer: 09:00–21:00 hours) and night (winter: 17:00–10:00 hours, summer: 21:00–09:00 hours) temperatures at occupied (dark blue) and unoccupied habitats (light blue, Median, 1st and 3rd quartile [boxes] and the 10th and 90th percentiles [whiskers]). Differences between occupied and unoccupied habitats were assessed using *t* tests. Significance levels are indicated as follows: n.s., not significant, *$P < 0.05$. [Color figure can be viewed at wileyonlinelibrary.com]

*L. helle* depend on well-connected habitat patches for long-term survival. Although we found that patch occupancy was negatively affected by isolation, the mean isolation distance between occupied patches (0.9 km) was close to the species' maximum dispersal capacity (see Fischer *et al.*, 1999), which might pose a threat to the remaining local populations.

The role of patch size for butterfly persistence in fragmented landscapes has often been emphasised (e.g. Thomas *et al.*, 2001; Bauerfeind *et al.*, 2009; Poniatowski *et al.*, 2018). It is generally expected that larger patches harbour larger populations of a species, and, thus, have a lower extinction risk (Thomas *et al.*, 2001). In line with this assumption, patch occupancy of *L. helle* was positively affected by patch size in our study, indicating that smaller patches often cannot sustain viable populations of the species in the long run (Nabielec & Nowicki, 2015). However, minimum patch-size requirements usually differ among species (Crone & Schultz, 2003; Salz &

Fartmann, 2009; Baguette & Stevens, 2013). In our study, patches occupied by *L. helle* were relatively small, with a mean size of $0.9 \pm 0.3$ ha (Table 1), compared to many other specialised butterfly species (cf. Brückmann *et al.*, 2010). This is in accordance with the study of Bauerfeind *et al.* (2009), which showed that occupied patches in the Westerwald low mountain range (western Germany) had a very similar size of $0.8 \pm 0.2$ ha and also had a higher connectivity. Consequently, it can be suggested that the population structure of *L. helle* in Central European habitat fragments can be characterised as a classic metapopulation, composed of small but sufficiently connected habitat patches (cf. Hanski, 1999; Nieminen *et al.*, 2004; Münsch *et al.*, 2019).

Besides isolation and size of habitat patches, the composition of the landscape matrix can be another factor that affects patch occupancy of insects in fragmented habitats (Krauss *et al.*, 2003; Öckinger *et al.*, 2012; Poniatowski *et al.*, 2016;
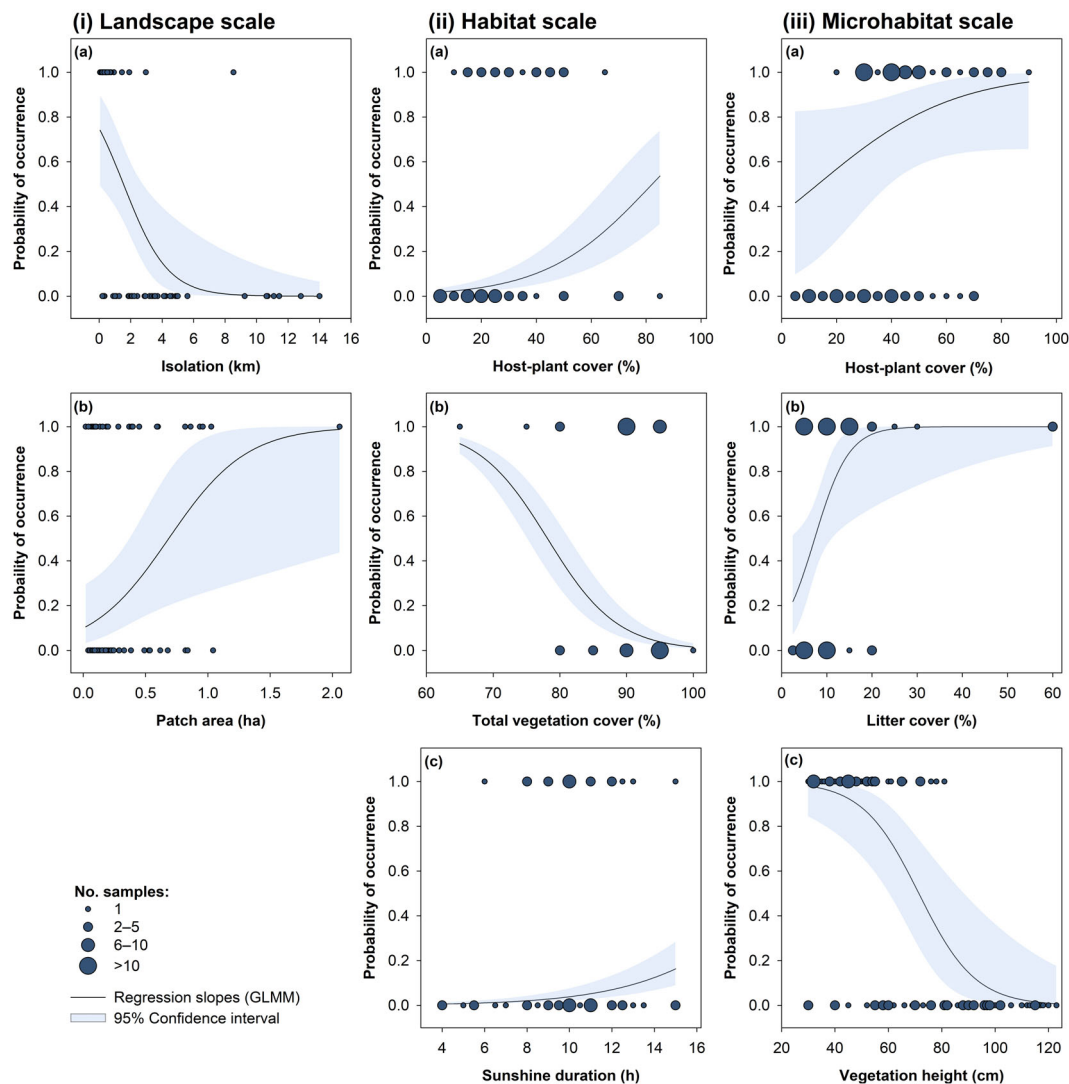
**Fig 2.** Relationship between patch occupancy of *L. helle* ($n_{occupied} = 25$ vs. $n_{unoccupied} = 42$) at the (a) landscape and (b) habitat scale, as well as microhabitat selection by *L. helle* ($n_{occupied} = 56$ vs. $n_{unoccupied} = 56$) at the (c) microhabitat scale and significant metric environmental parameters (see Table 5 for detailed GLMM statistics). [Color figure can be viewed at wileyonlinelibrary.com]

Helbing *et al*., 2017). The landscape surrounding habitat patches can (i) be directly harmful for dispersing insects (e.g. pesticides applied on arable land; Meek *et al*., 2002; van Swaay *et al*., 2009), (ii) act as a dispersal barrier (e.g. forests for grassland species; Dover & Settele, 2009), or (iii) even support dispersal (e.g. semi-natural grasslands for grassland species; Poniatowski *et al*., 2016). The study area is characterised by generally low land-use intensity with traditionally used meadows or pastures but also large areas of abandoned grasslands in narrow valley floors, as well as forests on the ridges and steep slopes (see 'Study area' section, Table 1). In contrast, the area of arable land is negligible. The surroundings of the occupied patches had a higher cover of abandoned grasslands than unoccupied ones, which likely facilitates the dispersal of *L. helle* in the linear valley systems (cf. Modin & Öckinger, 2020).

*Lycaena helle* is a boreo-montane species with distribution depending on a cold macroclimate, at least in winter (Fischer *et al*., 1999; Goffart *et al*., 2014; Modin & Öckinger, 2020). In fact, at the landscape scale, occupied patches were situated at higher elevations than unoccupied ones. Elevation was negatively correlated with temperature and positively with the number of frost days (Table 5). Additionally, all studied patches were situated in deep and narrow valleys (see 'Study area' section). Here, especially in winter, solar radiation rarely reaches the valley floors and cold air accumulates, forming cold-air depressions (Stoutjesdijk & Barkman, 1992). In accordance with this, winter temperatures were lower during both day- and night-time at occupied habitats compared to unoccupied ones. In contrast, for summer temperatures, this was only true during night-time.

The most important parameters defining habitat quality at the habitat and microhabitat scale were the (i) cover of host plants and (ii) vegetation structure, which is usually interrelated with microclimate (Stoutjesdijk & Barkman, 1992). A sufficient amount of food is a prerequisite for successful larval development. Therefore, everything else being equal, butterflies should prefer a high cover of host plants over a low one at oviposition sites (García-Barros & Fartmann, 2009; Pschera & Warren, 2018). As shown by Bauerfeind *et al.* (2009) and our study, this is also true for *L. helle*. *Bistorta officinalis* is a characteristic plant species in moist soils (Ellenberg *et al.*, 2001). Accordingly, the habitat requirements of the host plant may explain why *L. helle* also preferred moist habitats in our study.

According to the results of our study, *L. helle* depends on a cold climate during winter. Constantly cool winter temperatures might be essential for the survival of the hibernating pupae of *L. helle* (cf. Stuhldreher *et al.*, 2014). However, warm microhabitats seem to be of crucial importance for larval development during summer (cf. Fischer *et al.*, 1999; Nunner, 2006), especially in areas with cool macro- or mesoclimates (cf. Modin & Öckinger, 2020). In our study, patch occupancy increased with sunshine duration in June and microhabitat occupancy with litter cover and shorter swards. Moreover, occupied microhabitats were characterised by sparser swards with more bare ground than unoccupied ones. Consequently, they provided conditions that generally favour a warm microclimate through daytime (Stoutjesdijk & Barkman, 1992; Krämer *et al.*, 2012a; Streitberger *et al.*, 2014). Moreover, a higher litter cover may act as a microclimatic buffer during winter by reducing temperature fluctuations, which could be detrimental for the survival of hibernating pupae (cf. Stuhldreher & Fartmann, 2014; Turlure *et al.*, 2014).

Previous studies showed that inappropriate habitat management can rapidly lead to local extinctions of *L. helle*, and the populations are favoured by abandonment, at least in the short term (Skórka *et al.*, 2007; Bauerfeind *et al.*, 2009; Goffart *et al.*, 2014). Indeed, the majority of occupied patches in our study area were abandoned. However, we frequently recorded the species in managed habitats, too, demonstrating that *L. helle* is able to persist under traditional land-use practices, such as low-intensity grazing (Steiner *et al.*, 2006). The habitats of *L. helle* were characterised by high cover of the host plant (*B. officinalis*), as well as shorter and more open swards with high sunshine during the time of caterpillar development. Although the occupied habitats traditionally had relatively low nutrient levels (see 'Study area' section) without any disturbance, they will likely become overgrown by nitrophilous tall-forb communities or shrubs (cf. Grime *et al.*, 2007; Ellenberg & Leuschner, 2010). Hence, some kind of management, at least from time to time, is of vital importance to sustain viable populations of *L. helle* (cf. Fischer *et al.*, 1999; Bauerfeind *et al.*, 2009; Modin & Öckinger, 2020).

To summarise, in our study, the occurrence of *L. helle* was mainly driven by the (i) isolation, (ii) size, and (iii) quality of the habitat patches. Habitat quality within the semi-natural grasslands was determined by (i) macro- and mesoclimate, (ii) host-plant abundance, and (iii) vegetation structure, which is known to have a crucial impact on microclimate (Stoutjesdijk & Barkman, 1992; Stuhldreher & Fartmann, 2014). *Lycaena helle* preferred moist, nutrient-poor grasslands in deep and narrow valleys at the highest elevations of the study area, characterised by (i) cold winters, (ii) high abundance of the host plant, and (iii) shorter and more open swards with a warm microclimate in summer. As a result, abandonment of traditional land use and climate change are considered the most severe threats for long-term survival of the species (see also Bauerfeind *et al.*, 2009; Habel *et al.*, 2011).

## Implications for conservation

Since the occurrence of *L. helle* in the studied grasslands was negatively related to the isolation and positively to the size of the patches, conservation measures should aim at maintaining and restoring networks of large and well-connected habitat patches with high habitat quality. To improve habitat quality within habitat patches, we recommend establishing an alternating habitat management system, which should be applied every 3–5 years, as either rough grazing for large habitats (i.e. <0.2 livestock units ha$^{-1}$; cf. Goffart *et al.*, 2014; Bubová *et al.*, 2015) or rotational mowing during late summer or autumn in small habitat fragments (cf. Goffart *et al.*, 2014).

Recent studies revealed that insect species with low dispersal ability will hardly be able to cope with climate change in fragmented landscapes (Pöyry *et al.*, 2009; Poniatowski *et al.*, 2020). According to the low mobility of *L. helle* (Fischer *et al.*, 1999), this might especially apply to its central European populations which are mostly restricted to low-mountain ranges (Kudrna *et al.*, 2011; Wachlin, 2020). Therefore, the capacity of uphill distribution shifts for the species in response to recent global warming is very limited (cf. Konvička *et al.*, 2003). Nevertheless, long-term viability of the relict populations will likely increase if the aforementioned measures are aimed at maintaining and restoring suitable habitats in cold-air depressions within the mountain systems.

## Conflict of interest

The authors declare that they have no conflict of interest.

## Data availability statement

Data available on request from the authors.

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