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

GWYDION SCHERER, FRANZ LÖFFLER and THOMAS FARTMANN

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) macroand 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
degradation of semi-natural habitats, especially grassland ecosystems 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 matrices (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 (Konvicka 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 Lycæna 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).

Lycæna 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; Braun 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) | P value |
|------------------------------------|-------------------|---------------------|---------|
|                                    | Mean ± SE         | Min.–Max.           | Mean ± SE | Min.–Max. |         |
| (a) Landscape scale                |                   |                     |         |
| Isolation (km²)                    | 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 horizontal scope (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.

Microclimatc 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

| Parameter           | Occupied (n = 25) | Unoccupied (n = 42) | P value |
|---------------------|-------------------|---------------------|---------|
|                     | n         | %      | n         | %      |         |
| 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 2. Categorial 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.
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 ΔAIC<sub>C</sub> < 3 (Grueber et al., 2011). To avoid multicollinearity in the models, strongly inter-correlated variables were excluded from the analyses (Spearman rank correlations [r<sub>S</sub>] values >|0.6|) (cf. Graham, 2003; Löffler & Fartmann, 2017). At the landscape scale, elevation (r<sub>S</sub> = −0.76) and the number of frost days (r<sub>S</sub> = −0.92) were excluded due to its strong correlation with temperature, forest cover due to its correlation with the cover of managed grasslands (r<sub>S</sub> = −0.74). At the habitat and microhabitat scale, bare-ground cover was strongly inter-correlated with vegetation cover (r<sub>S</sub> = −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<sub>S</sub> = −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 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) | P value |
|------------------------------------|------------------|-----------------|---------|
|                                    | Mean (±SE)       | Min.–Max.       |         |
| Host-plant cover (%)               | 47.5 ± 2.2       | (20–90)         | ***     |
| Vegetation height (cm)             | 48.5 ± 1.8       | (30–81)         | ***     |
| Sunshine duration (h)              | 10.1 ± 0.2       | (7.5–15)        | n.s.    |
| Cover of vegetation layers (%)     |                  |                 |         |
| Bare ground                        | 4.6 ± 0.6        | (0–25)          | **      |
| Total vegetation                   | 81.3 ± 2.2       | (35–95)         | ***     |
| Shrubs                             | 1.0 ± 0.4        | (0–10)          | n.s.    |
| Herbs                              | 61.4 ± 2.5       | (30–95)         | n.s.    |
| Grasses                            | 25.4 ± 2.0       | (5–60)          | n.s.    |
| Litter                             | 15.6 ± 2.0       | (5–60)          | ***     |
| Mosses                             | 3.9 ± 0.4        | (0–15)          | n.s.    |

**Table 4.** Categorical 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) | Control (n = 56) | P value |
|-------------|------------------|-----------------|---------|
|             | n                | %               |         |
| Land use    |                  |                 |         |
| Managed     | 15               | 26.8            |         |
| Abandoned   | 41               | 73.2            | n.s.    |
| Soil humidity |               |                 |         |
| Fresh       | 15               | 26.8            |         |
| Moist       | 38               | 67.9            |         |
| Wet         | 3                | 5.4             | n.s.    |
**Table 5.** Model-averaging results (GLMM, binomial error structure). Relationship between patch occupancy of *L. helle* (*n*<sub>occupied</sub> = 25 vs. *n*<sub>unoccupied</sub> = 42) at the (a) landscape scale and (b) habitat scale, as well as microhabitat selection by *L. helle* (*n*<sub>occupied</sub> = 56 vs. *n*<sub>unoccupied</sub> = 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 (*ΔAIC* < 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 = 0.90) |           |     |       |           |
| Isolation (km)                   | −0.77    | 0.26| −2.94 | **        |
| Patch size (ha)                  | 2.71     | 1.28| 2.69  | *         |
| 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; Poniatoowski *et al.*, 2018). However, the relative importance of each of these parameters usually varies between species (Poniatoowski *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. *L. 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...
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 ± 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 ± 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).

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]
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 Lycaena helle in the linear valley systems (cf. Modin & Öckinger, 2020).

**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]

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.

© 2021 The Authors. Insect Conservation and Diversity published by John Wiley & Sons Ltd on behalf of Royal Entomological Society., Insect Conservation and Diversity, doi: 10.1111/icad.12485
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; Runner, 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; Tururile 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 forbs 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 mesoclimates, (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 (Kudrnà 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.

Acknowledgements

We are grateful to Stefan Meisberger and Julia Zehlius for their assistance in study-site selection. The study was partly funded by a PhD scholarship of the German National Academic Foundation allocated to G. Scherer and a PhD scholarship of the German Environmental Foundation (DBU) allocated to F. Löffler. Open access funding enabled and organized by Projekt DEAL.

Conflict of interest

The authors declare that they have no conflict of interest.

Data availability statement

Data available on request from the authors.

© 2021 The Authors. Insect Conservation and Diversity published by John Wiley & Sons Ltd on behalf of Royal Entomological Society., Insect Conservation and Diversity, doi: 10.1111/icad.12485
References

Anthes, N., Hartmann, T., Hermann, G. & Kaule, G. (2003) Combining larval habitat quality and metapopulation structure – the key for successful management of prealpine Euphydryas aurinia colonies. Journal of Insect Conservation, 7, 175–185.

Baguette, M. & Stevens, V.M. (2013) Predicting minimum area requirements of butterflies using life-history traits. Journal of Insect Conservation, 17, 645–652.

Bartón, K. (2020) Multi-Model Inference (Package MuMIn: version 1.43.17). <https://www.r-project.org> accessed 10th October 2020.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2019) lme4: Linear Mixed-Effects Models Using 'Eigen' and 'S4'. Package: lme4 version 1.1-19. <http://CRAN.R-project.org/web/packages/lme4/> 20th November 2019.

Bauerfeind, S.S., Theisen, A. & Fischer, K. (2009) Patch occupancy in the endangered butterfly Lycaena helle in a fragmented landscape: effects of habitat quality, patch size and isolation. Journal of Insect Conservation, 13, 271–277.

Belitz, M.W., Monß, M.J., Cuthrell, D.L. & Monß, A.K. (2020) Landscape-level environmental stressors contributing to the decline of Poweshiek skipperling (Oarisma poweshiek). Insect Conservation and Diversity, 13, 187–200.

Bolker, B.M., Brooks, M.E., Clark, C.J., Geange, S.W., Poulsen, J.R., Stevens, M.H.H. & White, J.S.S. (2011) LMEM: Linear Mixed-Effects Models Using 'Eigen' and 'S4'. Package: lme4 version 1.1-19. <https://CRAN.R-project.org/web/packages/lme4/> 20th November 2019.

Bubová, T., Vrabec, V., Kulma, M. & Nowicki, P. (2015) Landscape-level environmental stressors contributing to the decline of Poweshiek skipperling (Oarisma poweshiek). Insect Conservation and Diversity, 13, 271–277.

Dewicke, V., van Swaay, C., Berest, L., Treston, D., Chamberlain, D., Heliolia, J., Herrando, S., Julliard, R., Kuussaari, M., Lindström, Å., Reif, J., Roy, D.B., Schweiger, O., Settele, J., Stefanescu, C., Van Strien, A., Vandevenhoven, C., WallisDeVries, M., Wynhoff, I. & Jiguet, F. (2012) Differences in the climatic debts of birds and butterflies at a continental scale. Nature Climate Change, 2, 121–124.

Dover, J. & Settele, J. (2009) The influences of landscape structure on butterfly distribution and movement: a review. Journal of Insect Conservation, 13, 3–27.

© 2021 The Authors. Insect Conservation and Diversity published by John Wiley & Sons Ltd on behalf of Royal Entomological Society., Insect Conservation and Diversity, doi: 10.1111/icad.12485
Global change threatens a relict butterfly

Vujic, A., Wagner, D.L., WallisDeVries, M.F., Westphal, C., White, T.E., Wilkins, V.I., Williams, P.H., Wyckhuys, K.A.G., Zhu, Z.-R. & de Kroon, H. (2020) International scientists formulate a roadmap for insect conservation and recovery. *Nature Ecology & Evolution*, 4, 174–176.

Helbing, F., Fartmann, T., Löfler, F. & Poniatowski, D. (2017) Effects of local climate, landscape structure and habitat quality on leathopassel assemblies of acidic grasslands. *Agriculture, Ecosystems & Environment*, 246, 94–101.

Hoithorn, T., Bretz, F., Westfall, P., Heiberger, R.M., Schützenmeister, A. & Scheibe, S. (2020) *Simultaneous Inference in General Parametric Models* (Package: multcomp version 1.4-15). <https://www.r-project.org> accessed 3rd September 2020.

Konvička, M., Maradova, M., Beneš, J., Fric, Z. & Kepka, P. (2003) Uphill shifts in distribution of butterflies in The Czech Republic: effects of changing climate detected on a regional scale. *Global Ecology and Biogeography*, 12, 403–410.

Krämer, B., Köpf, I., Enderle, J., Poniatowski, D. & Fartmann, T. (2012a) Microhabitat selection in a grassland butterfly: a trade-off between microclimate and food availability. *Journal of Insect Conservation*, 16, 857–865.

Krämer, B., Poniatowski, D. & Fartmann, T. (2012b) Effects of landscape and habitat quality on butterfly communities in pre-alpine calcareous grasslands. *Biological Conservation*, 152, 253–261.

Krauss, J., Steffen-Dewenter, I. & Tscharnkte, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography*, 30, 889–900.

Kudra, O., Harpke, A., Lux, K., Pennerstorfer, J., Schweiger, O., Settele, I. & Wiemers, M. (2011) *Distribution Atlas of Butterflies in Europe*. Gesellschaft für Schmetterlingsschutz, Halle, Germany.

Löfler, F. & Fartmann, T. (2017) Effects of landscape and habitat quality on Orthoptera assemblages of pre-alpine calcareous grasslands. *Agriculture, Ecosystems & Environment*, 248, 71–81.

Löfler, F., Poniatowski, D. & Fartmann, T. (2019) Orthoptera community shifts in response to land-use and climate change – lessons from a long-term study across different grassland habitats. *Biological Conservation*, 236, 315–323.

Löfler, F., Poniatowski, D. & Fartmann, T. (2020) Extinction debt across three taxa in well-connected calcareous grasslands. *Biological Conservation*, 246, 108588.

Maes, D. & Van Dyck, H. (2001) Butterfly diversity loss in Flanders (north Belgium): Europe’s worst case scenario? *Biological Conservation*, 99, 263–276.

Maes, D., Verovnik, R., Wiemers, M., Brosens, D., Beshkov, S., Bonelli, S., Buszko, J., Cantu-Salazar, L., Cassar, L.F., Collins, S., Dincă, V., Djuric, M., Dušej, G., Elven, H., Franeta, F., Garcia-Pereira, P., Geryak, Y., Goffart, P., Gör, Á., Hiernaux, U., Höttinger, H., Huemer, P., Iakši, J., John, E., Kalivoda, H., Kati, V., Kirkland, P., Komac, B., Krämer, B., Kumpf, I., Krámer, M., Krämer, R., Krásilová, M., Král, K., Kuussaari, M., L’Hoste, L., Lele, S., Mestdagh, X., Mickevich, N., Milhoci, I., Mihut, S., Monasterio-León, Y., Morgan, D.V., Munugira, M.L., Murray, T., Nielsen, P.S., Ölafsson, E., Önup, E., Panperis, E.N., Pavlíčko, A., Pettersson, L.B., Popov, S., Popovič, M., Pöyry, J., Prentice, M., Reyserhove, L., Ryhrholm, N., Šašić, M., Saenko, V., Settele, J., Sieczewski, M., Sinev, S., Stefanescu, C., Švitra, G., Tammaru, T., Tiitsaar, A., Titkáll, E., Tzortzakaki, O., van Swaay, C.A.M., Viborg, A.L., Wynhoff, I., Zografou, K. & Warren, M.S. (2019) Integrating National Red Lists for prioritizing conservation actions for European butterflies. *Journal of Insect Conservation*, 23, 301–310.

Meek, B., Loxton, D., Sparks, T., Pywell, R., Pickett, H. & Nowakowski, M. (2002) The effect of arable field margin composition on invertebrate biodiversity. *Biological Conservation*, 106, 259–271.

Modin, H. & Öckinger, E. (2020) Mobility, habitat selection and population connectivity of the butterfly *Lycaena helle* in central Sweden. *Journal of Insect Conservation*, 24, 821–831.

Molilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology*, 83, 1131–1145.

Münsch, T., Helbing, F. & Fartmann, T. (2019) Habitat quality determines patch occupancy of two specialist Lepidoptera species in well-connected grasslands. *Journal of Insect Conservation*, 23, 247–258.

Nabielec, J. & Nowicki, P. (2015) Drivers of local densities of endangered *Lycaena helle* butterflies in a fragmented landscape. *Population Ecology*, 57, 649–656.

Nieminen, M., Siljander, M. & Hanski, I. (2004) Structure and dynamics of *Melitaea cinxia* metapopulations. In *The Wings of Checkerspots: A Model System for Population Biology*, (ed. by P.R. Ehrlich and I. Hanski), pp. 63–91.Oxford University Press, Oxford, UK.

Nunner, A. (2006) Zur Verbreitung, Bestandssituation und Habitatbildung des Blauschillernden Feuerfalters (*Lycaena helle*) in Bayern. *Larvalökologie von Tagfaltern und Widderchen in Mitteleuropa*. Abhandlungen aus dem Westfälischen Museum für Naturkunde (ed. by T. Fartmann and G. Hermann), Vol. 68, pp. p. Münster, Germany: 153–170.

Öckinger, E., Lindborg, R., Sjödin, N.E. & Bommarco, R. (2012) Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, 35, 259–267.

Oliver, T.H., Smithers, R.J., Beale, C.M. & Watts, K. (2016) Are existing biodiversity conservation strategies appropriate in a changing climate? *Biological Conservation*, 193, 17–26.

Parnes, C., Ryholm, N., Stefanescu, C., Hill, J.K., Thomas, C.D., Descimon, H., Huntley, B., Kaila, L., Kullberg, J., Tammaru, T., Tennent, W.J., Thomas, J.A. & Warren, M. (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, 399, 579–583.

Pollard, E. (1977) A method for assessing changes in abundance of butterflies. *Biological Conservation*, 12, 115–134.

Pollard, E. & Yates, T.J. (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman and Hall, London, UK.

Poniatowski, D., Beckmann, C., Löfler, F., Münch, T., Helbing, F., Samways, M.J. & Fartmann, T. (2020) Relative impacts of land-use and climate change on grasshopper range shifts have changed over time. *Global Ecology and Biogeography*, 29, 2190–2202.

Poniatowski, D., Löfler, F., Stuhlthreger, G., Borchard, F., Krämer, B. & Fartmann, T. (2016) Functional connectivity as an indicator for patch occupancy in grassland specialists. *Ecological Indicators*, 67, 735–742.

Poniatowski, D., Stuhlthreger, G., Löfler, F. & Fartmann, T. (2018) Patch occupancy of grassland specialists: habitat quality matters more than habitat connectivity. *Biological Conservation*, 225, 237–244.

Powney, G.D., Carvell, C., Edwards, M., Morris, R.G.K., Roy, H.E., Woodcock, B.A. & Isaac, N.J.B. (2019) Widespread losses of pollinating insects in Britain. *Nature Communications*, 10, 1018.

Pöyry, J., Luoto, M., Heikkinen, R.K., Kuussaari, M. & Saarinen, K. (2009) Species traits explain recent range shifts of Finnish butterflies. *Global Change Biology*, 15, 732–743.

Pschera, J. & Warren, M.J. (2018) Microhabitat selection by ovipositing females and pre-diapause larvae of a Welsh population of *Euphydryas aurinia* (Lepidoptera: Nymphalidae). *Journal of Insect Conservation*, 22, 571–579.

R Development Core Team (2020). *R: A Language and Environment for Statistical Computing*, Version 3.4.3. <http://www.r-project.org>.

© 2021 The Authors. *Insect Conservation and Diversity* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society. *Insect Conservation and Diversity*, doi: 10.1111/icad.12485
Salz, A. & Farmann, T. (2009) Coastal dunes as important strongholds for the survival of the rare Niobe fritillary (Argynnis niobe). *Journal of Insect Conservation*, 13, 643–654.

Samways, M.J., Barton, P.S., Birkhofer, K., Chichorro, F., Deacon, C., Farmann, T., Fukushima, C.S., Gaigher, R., Habel, J.C., Hallmann, C.A., Hill, M.J., Hochkirch, A., Kaila, L., Kwak, M.L., Maes, D., Mammola, S., Norieja, J.A., Orfinger, A.B., Pedraza, F., Pycke, J.S., Roque, F.O., Settele, J., Simaika, J.P., Stork, N.E., Suhling, F., Vorster, C. & Cardoso, P. (2020) Solutions for humanity on how to conserve insects. *Biological Conservation*, 242, 108-127.

Sánchez-Bayo, F. & Wyckhuys, K.A.G. (2019) Worldwide decline of insects in Europe – a review of its drivers. *Biological Conservation*, 232, 8–27.

Skórka, P., Settele, J. & Woyciechowski, M. (2007) Effects of management cessation on grassland butterflies in southern Poland. *Agriculture, Ecosystems & Environment*, 121, 319–324.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., Maes, D., Mammola, S., Norieja, J.A., Orfinger, A.B., Pedraza, F., Pycke, J.S., Roque, F.O., Settele, J., Saimaka, J.P., Stork, N.E., Suhling, F., Vorster, C. & Cardoso, P. (2020) Solutions for humanity on how to conserve insects. *Biological Conservation*, 242, 108-127.

Stoate, C., Báldi, A., Beja, P., Boatman, N.D., Herzon, I., van Doorn, A., de Snoo, G.R., Rakosy, L. & Ramwell, C. (2009) Ecological impacts of early 21st century agricultural change in Europe – a review. *Journal of Environmental Management*, 91, 22–46.

Stöck, N.E. (2018) How many species of insects and other terrestrial arthropods are there on Earth? *Annual Review of Entomology*, 63, 31–45.

Stoutjesdijk, P. & Barkman, J.J. (1992) *Microclimate, Vegetation and Fauna*. Opulus Press, Uppsala, Sweden.

Streitberger, M., Rose, S., Herrmann, G. & Farmann, T. (2014) The role of a mound-building ecosystem engineer for a grassland butterfly. *Journal of Insect Conservation*, 18, 745–751.

Stuhlreher, G. & Farmann, T. (2014) When habitat management can be a bad thing: effects of habitat quality, isolation and climate on a declining grassland butterfly. *Journal of Insect Conservation*, 18, 965–979.

Stuhlreher, G. & Farmann, T. (2018) Threatened grassland butterflies as indicators of microclimatic niches along an elevational gradient – implications for conservation in times of climate change. *Ecological Indicators*, 94, 83–98.

Stuhlreher, G., Herrmann, G. & Farmann, T. (2014) Cold-adapted species in a warming world – an explorative study on the impact of high winter temperatures on a continental butterfly. *Entomologia Experimentalis et Applicata*, 151, 270–279.

Thomas, C.D., Franco, A.M. & Hill, J.K. (2006) Range retractions and extinction in the face of climate warming. *Trends in Ecology & Evolution*, 21, 415–416.

Thomas, J.A. (2005) Monitoring change in the abundance and distribution of insects using butterflies and other indicator groups. *Philosophical Transactions of the Royal Society B*, 360, 339–357.

Thomas, J.A., Bourn, N.A.D., Clarke, R.T., Stewart, K.E., Simcox, D.J., Pearman, G.S., Curtis, R. & Goodger, B. (2001) The quality and isolation of habitat patches both determine where butterflies persist in fragmented landscapes. *Proceedings of the Royal Society of London B*, 268, 1791–1796.

Thomas, J.A., Simcox, D.J. & Hovestadt, T. (2010) Evidence-based conservation of butterflies. *Journal of Insect Conservation*, 15, 241–258.

Thomas, J.A., Telfer, M.G., Roy, D.B., Preston, C.D., Greenwood, J.J., Asher, J., Fox, R., Clarke, R.T. & Lawton, J.H. (2004) Comparative losses of British butterflies, birds and plants and the global extinction crisis. *Science*, 303, 1871–1881.

Turlure, C., Van Dyck, H., Goffart, P. & Schtickzelle, N. (2014) Resource-based habitat use in *Lycaena helle*: significance of a functional, ecological niche-oriented approach. *Jewels in the Mist: A Synopses on the Endangered Violet Copper Butterfly Lycaena helle*. (ed. by J.C. Habel, M. Meyer and T. Schmitt), pp. p. 67–86. Pensoft Publishers, Sofia-Moscow, Bulgaria.

van Strien, A.J., van Swaay, C. & Kéry, M. (2011) Metapopulation dynamics in the butterfly *Hipparchia semele* changed decades before occupancy declined in The Netherlands. *Ecological Applications*, 21, 2510–2520.

van Swaay, C., Cuttelod, A., Collins, S., Maes, D., López Munguira, M., Šašić, M., Settele, J., Verovnik, R., Verstraël, T., Warren, M., Wiemers, M. & Wynhof, I. (2010) *European Red List of Butterflies*. Publications Office of the European Union, Luxembourg City, Luxembourg.

van Swaay, C., Maes, D. & Warren, M.S. (2009) Conservation status of European butterflies. *Ecology of Butterflies in Europe*. (ed. by J. Settele, T.G. Shreeve, M. Konvička and H. Van Dyck), pp. p. 322–338. Cambridge University Press, Cambridge, UK.

Wachlin, V. (2020) *Lycaena helle* (Denis & Schiffermüller, 1775) – Blauschillernder Feuerfalter. *Verbreitungstasat der Tagfalter und Widderchen Deutschlands*. (ed. by R. Reinhardt, A. Harpke, S. Caspari, M. Dolek, E. Kühn, M. Musche, Trusch, R., Wiemers, M. & Settele, J.), pp. p. 132–133. Stuttgart, Germany, Ulmer.

WallisDeVries, M.F., Poschloid, P. & Willems, J.H. (2002) Challenges for the conservation of calcareous grasslands in northwestern Europe: integrating the requirements of flora and fauna. *Biological Conservation*, 104, 265–273.

Warren, M.S., Maes, D., van Swaay, C.A.M., Goffart, P., Van Dyck, H., Bourn, N.A.D., Wynhoff, I., Hoare, D. & Ellis, S. (2021) The decline of butterflies in Europe: problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences of the United States of America*, 118, e2002551117.

Wilson, R.J., Gutiérrez, D., Gutiérrez, J. & Monserrat, V.J. (2007) An elevational shift in butterfly species richness and composition accompanying recent climate change. *Global Change Biology*, 13, 1873–1887.

Accepted 22 February 2021

Editor/associate editor: Karsten Schonrogge

© 2021 The Authors. *Insect Conservation and Diversity* published by John Wiley & Sons Ltd on behalf of Royal Entomological Society, *Insect Conservation and Diversity*, doi: 10.1111/icad.12485