Population status of the highly endangered *Lycaena helle* (Papilionoidea, Lycaenidae) in the Šumava Mts. two decades after establishment

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Abstract. The process of translocation of endangered species represents a useful conservation tool, but subsequent monitoring of translocated populations is often neglected, although it may supply critical information for conservation work. The EU-protected glacial relic *Lycaena helle* (Lycaenidae) went extinct in the Czech Republic, where a few lowland populations historically existed, in the 1950s. In 2002, a mountain-dwelling population was established in Šumava Mts., among grasslands and fenlands surrounding the abandoned village of Nové Údolí, from 2/33 ♂♂/♀♀ originating in the Türnitz Alps, Austria. The transferred population was surveyed a decade later and again 21 years after the transfer. During the second (2023) survey, we visited 212 grassland patches to record the species' presence and relative abundance, and to ascertain its habitat preferences. A third of the surveyed patches were occupied by *L. helle*, in a total area of occupied grasslands was 66.6 ha scattered over 4.5 km^2, with approximately 2,400 adult individuals, recorded up to 4.2 km from the original release point. *L. helle* typically occupies wet tussocky grasslands with closed edges, minimum management and high cover of its larval host plant, the mid-to late-successional forb *Bistorta officinalis*. It avoids drier managed grasslands rich in flowering plants. The expansion rate from the release point (0.1 km/year during the first decade, 0.2 km/year over two decades) was slower than in two earlier *L. helle* transfers, targeting Morvan and Forez Mts., France (≈ 0.5 km/year in both cases). We attribute this to the relief of the release locality, a shallow depression surrounded by higher-elevated forested ridges, but we expect faster expansion once the continuous woodlands are crossed.

Introduction

Owing to their aesthetic appeal, popularity, good life history knowledge and armies of enthusiasts, butterflies have always ranked high among animals intentionally translocated to novel localities (Oates and Warren 1990; Schultz et al. 2008; Sedláček and Kadlec 2019). While a vast majority of such translocations had been unsuccessful, not resulting in long-term population establishment, some successful translocations significantly expanded the target species' ranges (Schmitt et al. 2005; Wildman 2023). Motives of the translocations have varied from intention to enrich the faunas of target regions (Oates and Warren 1990), through scientific curiosity (Soffner 1967; Barascud et al. 1999), to returns of extirpated species to historical sites (Lukášek 1997; Thomas et al. 2009; Wildman 2023).

The perception of butterfly translocations by experts also varies greatly. On the one hand, deliberate unauthorised translocations are discouraged because they interfere with species' natural ranges and evolutionary processes (Hodder and Bullock 1997; Konvička 2005). On the other hand, rationally prepared re/introductions aiming to expand populations of declining species, are increasingly advocated in the contexts of habitats loss and climate change (IUCN/SSC 2013), as a means to assist species to cope with habitat loss and dispersal limitations ("assisted translocations": Willis et al. 2009; Sedláček and Kadlec 2019; Kracke et al. 2021; Sucháčková-Bartoňová et al. 2021). Following translocations, it is essential to closely monitor the fates of newly established populations, as these unique experiments may contribute to resolving such issues as genetics and demography of populations' establishment (Schmitt et al. 2005; Wildman et al. 2024), drivers of habitat selection (Van Langevelde and Wynhoff 2009), and dispersal/colonisation in novel environments (Néve et al. 1996; Cizek et al. 2003).

For the Violet Cooper, *Lycaena helle* (Denis & Schiffermüller, 1775) (Lepidoptera: Lycaenidae), a species protected by the EU Habitats Directive (Biewald and Nunner 2005, van Swaay et al. 2010; Habel et al. 2014), two documented transfers had been carried out in France (Descimon and Bachelard 2014), while the third, from the Austrian Alps to the Hercynian mountains in the Czech Republic, is described here.

The Eurosiberian range of *L. helle* encompasses the Hercynian mountains in Western Europe (Westerwald, Eifel, Ardennes, Vosges, Black Forest, Jura, Madeleine), Massif Central, Pyrenees and the Alps (a few scattered populations) (Biewald and Nunner 2005; Habel et al. 2010b), both lowlands and Carpathian Mts. in Romania (Craioveanu et al. 2014; Ion et al. 2023) and high altitudes of Stara Planina Mts., Serbia (Popovic et al. 2014). The distribution is more contiguous in northeastern European lowlands, from Mecklenburg-Vorpommern through Poland to the Baltic states (Chrzanowski et al. 2013; Nabielec and Nowicki 2015; Reinhardt et al. 2020). Recent declines were reported from Fennoscandia (Ryrholm 2014; Modin and Ockinger 2020). The range then continues through boreal eastern Europe to Siberia, Mongolia and Transbaikalia to Northern China (Tolman and Lewington 1997; Chuluunbaatar et al. 2008). Combined with molecular evidence (Finger et al. 2009; Habel et al. 2010a, b; Kebaïli et al. 2023) this distribution indicates that *L. helle* is a glacial relict in temperate Europe, which was widely distributed during cooler periods of the Quaternary and ascended to high elevations during Holocene. The loss from lower elevations has been relatively recent, coinciding with loss of lowland fenlands due to drainage, farming intensification, or building developments (Benes and Kuras 1998; Beneš et al. 2002; Craioveanu et al. 2014; Reinhardt et al. 2020) (Fig. 1).

Larvae develop on the the bistorts *Bistorta officinalis* Delarbre, or *B. vivipara* (L.) Delarbre in the extreme North. When used as the larval host, *B. officinalis* is also the main nectar source (Turlure et al. 2014). This competitively strong forb prospers in waterlogged tussocky grasslands and fens in advanced stages of succession (Pecháčková and Krahulec 1995; Krahulec et al. 1997), which complicates *L. helle* conservation management (Fischer et al. 1999, 2014). Both regular

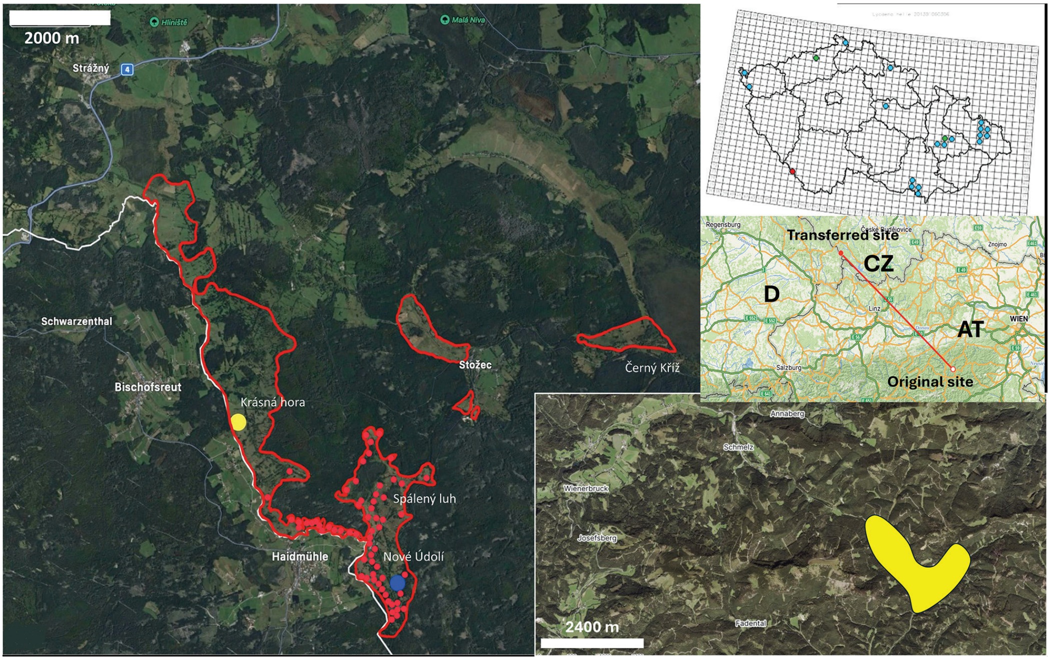

Figure 1. Left: Aerial map of the section of Šumava National Park showing Czechia/Germany state border (narrow white line), the sections of the park surveyed for presence of the transferred butterfly *Lycaena helle* (bounded by narrow red lines), the original release site (blue dot), the most distant observation in 2023 (yellow dot), and all the occupied grassland patches (red dots). Right, top: Distribution map of *L. helle* in the Czech Republic, with blue dots standing for pre-1950 records, green dots for pre-1980 records, and red dots the introduced Šumava NP population. Right, middle, shows a section of Central Europe with sites of origin and release of the *L. helle* transfer. Right, bottom shows approximate distribution of the donor population in Türnitz Alps, Austria. All maps are from mapy.cz, licenced by Creative Commons.

cutting or grazing regimes, and successional overgrowth, deplete the host plant, ultimately harming the butterfly. It is desirable to maintain some proportions of the inhabited grasslands in the advanced successional stage beneficial for *B. officinalis*, while preventing taller vegetation or woody encroachment (Goffart et al. 2010, 2014; Ion 2023).

In Czech Republic, only lowland populations of *L. helle* existed historically, inhabiting fens along major rivers (Kašpar 1939; Benes and Kuras 1998). The species was recorded from 20 grid mapping cells (out of 675 in the country) prior to the 1950s, but the last colony fell victim to aquifer drainage in 1952 near Olomouc (Beneš et al. 2002). In 2002, a mountain population was established in the Šumava Mts. by transfer of 35 adults from a geographically close population in the Austrian Alps.

Here, we report results of a survey, carried out in 2023, i.e., two decades after the transfer, targeting distribution extent and habitat selection of the transferred population. We aim to answer two specific questions: 1) What habitat is selected by the population, does it differ from other populations in Western and Central Europe, and what implications emerge for habitat management? 2) What is the size of currently occupied area and how rapidly had the population expanded, if compared with the two previous transfers?

Material and methods

Study species

Lycaena helle is univoltine in mountains, with adults on wings in May–June, but forms two to three generations in lowlands (Kašpar 1939; Blaik 2014; Plazio and Nowicki 2021). Males perch on prominent plants in wild-sheltered positions to acquire females (Craioveanu et al. 2014). Shrubs or small trees amidst inhabited sites are used for overnight roosting (Kašpar 1939; Goffart et al. 2010). Mobility is rather restricted, with maximum published movement <1 km, and with longer distances travelled by females (Fischer et al. 1999; Chuluunbaatar et al. 2008; Nabielec and Nowicki 2015; Modin and Öckinger 2020; Plazio and Nowicki 2021). Larval development lasts 4–6 weeks and is followed by pupation in plant litter (Nunner 2006; Blaik 2014). The pupa either overwinters or develops directly into the next generation (Plazio and Nowicki 2021).

Establishment of the Czech population

The source of the transferred butterflies was a population inhabiting a mountain valley in Türnitz Alps, part of Northern limestone Alps, Austria (along local road L101 Schmelz – Ulreichberg; 47.84N, 15.41E, elevation 900 m; "Alps: Mariazell" in Habel et al. 2010b). Mountain fens with a high representation of *B. officinalis* are situated at the narrow valley bottom. In the late 1990s, a proportion of the fens was afforested by spruce, which prompted the idea to transfer part of the population into a novel environment. A total of 35 adults (2♂♂, 33♀♀) were captured in early June 2002, and immediately transferred to the release site in the Šumava Mts., Czech Republic.

The release site (Nové Údolí, 48.82N, 13.80E, 860 m elevation; 160 km aerial distance from the source locality; Figs 1, 2) consists of a mix of grasslands and fens around a former village, deserted while establishing the depopulated border between (Eastern bloc) Czechoslovakia and (Western) Germany in the early 1950s. Former inhabitants (34 households, 271 persons according to 1910 census) made their living in forestry, or as cattle ranchers (Kozák 2003). The grasslands (partly natural at waterlogged sites, partly obtained by forest clearance) were utilised as summer pastures, or for producing winter fodder. Following desertion of the village, meadows and pasture-woodlands were unmanaged and gradually succumbed to succession. This development supported *B. officinalis*, which currently dominates wetter parts of the area. Since the establishment of the Šumava National Park (1992), some management was established, aiming to retain the grasslands in the advanced stage of succession while preventing woody encroachment. Drier allotments are occasionally grazed by sheep or machine-mown in prolonged intervals, while the waterlogged fens are mostly unmanaged, with only periodic clearance of woody regrowth (Albrecht 2003).

The transferred butterflies were released at two grassland patches with abundant *B. officinalis*, separated by 200 m. The central point between them (48.8243 N, 13.8014 E) is hereafter considered as the "release point". The presence of the butterfly was checked annually by A.P., who is a local resident. Until the third year after the transfer, the butterflies were only observed at the release sites. Subsequently, they expanded to adjacent grasslands. In 2011 and 2012, a decade after the transfer, Předotová (2013) carried out mark-recapture at four distinct grassland patches of summed area 3 ha and estimated that ≈110 adults inhabited the area (2-years average). She also detected the furthest individuals 900 m from the original release point and estimated that the occupied area was ≈2 km^2.

Figure 2. Habitats of the newly established population of *Lycaena helle* in the Šumava Mts. Left: A grassland patch in most suitable stage, with high representation of blooming host plant *Bistorta officinalis*. Right, top: A grassland patch in more advanced stage of succession, with progressing encroachment by *Salix* spp. shrubs. Right, bottom: Patch at the banks of Studená Vltava River with *Carex brisoides* sedges suppressing *B. officinalis*.

Field survey

As we aimed on both ascertaining the current distribution extent and elucidating habitat selection of the transferred population, we selected a minimalistic approach, which allowed addressing both questions during the short flight period of the butterfly. Hence, each grassland in our area of interests was visited only once, by zigzagging its entire area (cf. Thomas 1983), and visit date was considered in statistical models as a potential covariate.

The survey covered all grasslands and fenlands in wider environs of the release site: around the Nové Údolí deserted village, downstream (eastwards) and upstream (westwards) along Studená Vltava River, along its right-side tributary Hraniční potok brook, and still further north along the state border. We also surveyed grasslands and fenlands around Stožec village (4 km NE aerial distance from the release site, separated by 1.2 km of mature spruce forests) and Černý Kříž homestead (6.4 km E, through 4.7 km of mature forests) (Fig. 1).

The surveys were carried out June 1–10, 2023, 9–16 hours CEST, if weather was suitable for butterfly activity. As a "grassland patch", we understand a patch of grassland or fenland discernible in the field by clear borders (woodland edge, a strip of shrubs or trees, a brook, road, stone wall), or by a distinct management (a fenced pasture, unmanaged fen). Using detailed aerial maps, we surveyed 212 such patches. The centroid of each patch was marked into mapy.cz mobile application, and the patch was zigzagged to detect the butterfly and assess its abundance (ordinal scale, 1: single individual, 2: ≤5, 3: ≤10, 4: ≤20, 5: >20 individuals). Each visit to a patch was further characterised by: Julian Date; closest Hour; Clouds (ordinal 1–3 scale, from clear sky to overcast); Wind (1: none, 2: some wind, 3: light breeze); Woody cover (trees or shrubs >1.5 m, % of total area); Slope (1: flat, 2: mild, 3: steep); Impenetrability (subjective assessment considering tussocks, height of sward and litter accumulation, ordinal 1–3); Wetness (1–3, from dry to waterlogged); *Bistorta* cover (% projection of total patch area); Nectar abundance (1: none, 2: some nectar, 3: abundant nectar); Nectar diversity (the number of flowering forbs' species, ordinal scale, 1: ≤5 spp., 2: ≤10 spp., 3: >10 spp.); and Management (1/0, site mown or grazed vs. unmanaged; for this we utilised local knowledge of A.P.). Following fieldwork, we measured the area of each grassland patch (in square metres, square roots were used in computations); and the lengths of its edges distinguishing open, partly closed and closed edges (expressed as % of the entire perimeter length). Finally, we measured the distance of each patch centroid from the original release site (in metres).

Statistical analyses

Two response variables analysed in parallel were *L. helle* presence during the survey, coded binomially (present/absent), and abundance, coded at ordinal 1–5 scale.

Prior to analyses, we transformed all numeric and ordinal predictors to zero means and unit variance. We then visualised the relationships among thus transformed predictors using the principal component analysis (PCA) in Canoco, v. 5 (Ter Braak and Šmilauer 2018). Individual grassland patches were treated as samples, and *L. helle* presence and abundance were visualised as supplementary species data.

We then used the general linear models (glm) in R 4.2.2 to model responses of *L. helle* presence and abundance to properties of the grassland patches. We used binomial link for presence and Poisson link for abundance and followed the information theory approach (= AIC values, which detect optimal points between competing models' precision and complexity) for comparing the models' performance.

We first constructed single-term regressions $y \sim x$, plus polynomial terms for Serial date and Hour, with all the potential predictors. Next, we defined two covariate models, the first accounting for mutual positions of the sites in space (Positional model: built by backward elimination from latitude, longitude and altitude, their interactions, and polynomials), the second just considering aerial distances from the release point (Distance model). Then, we assessed the predictors with "significant" effects (ΔAIC between null and fitted model ≤2.0) in single-term regressions against these two covariate models. Finally, we constructed multiple regressions, using stepwise elimination (*drop1* function in R) from models, containing either Position or Distance, plus all predictors which were significant in the single- term regressions, until we obtained models with the lowest AICs.

Results

We surveyed 212 grassland patches with a summed area of 285.7 ha (average patch 1.4 ± 1.04 SD, range 0.1–5.9 ha) (Figs 1, 2). *Lycaena helle* was encountered at 71 of them (33.5% of patches surveyed, 23.3% of the area surveyed), in a summed number of 557 observations. It was abundantly present around the former Nové Údolí village, along Studená Vltava River and in the environs of Spálený luh bog (furthest record 48.848N, 13.796E, aerial 2800 m NE from the release point). Northwards, the density of positive records gradually diminished, with the furthest record at 48.850N, 13.758E, i.e., 4210 m NW from the release point). The butterfly has not colonised the fenlands around Stožec village and Černý Kříž homestead. The current distribution range was ≈4.5 km^2, while the summed area of grassland patches with a positive record was 66.6 ha.

The PCA ordination (Fig. 3; total variation 2533.0, eigenvalues 0.231, 0.169, 0.143, 0.087; pseudo-canonical correlations with supplementary variables 0.365, 0.115, 0.116, 0.088) associated *L. helle* presence and abundance with wet, impenetrable and unmanaged grassland patches at flat terrain, with closed edges, and high *Bistorta* cover, from drier, easily penetrable and managed patches of large area, and with high nectar abundance and diversity.

The regression models corroborated this. Both presence and abundance of the butterfly (Table 1) were affected by 2nd-degree polynomial of Serial date, indicating that our survey covered increase, peak and decrease of adult flight period. They declined with Clouds and Wind, but also with patch Area, Slope, active Management and Nectar diversity. They increased with Wetness, closed edges, and high *Bistorta* cover. The latter reached 49.6 ± 28.51 vs. 23.4 ± 28.43 SD percentual cover at occupied vs. unoccupied patches, respectively, and accounted for 11.9/17.3% of variation in the presence/abundance models.

Position and Distance models explained even higher amounts of variation (Table 2). Regarding the former, the hump-shaped relationships to latitude and longitude suggested gradual decrease in occupied grasslands with increasing distance from the release point (cf. Fig. 1). Regarding the latter, both presence and abundance decreased with distance from the release point. Adding further predictors to Position and Distance models (Table 2) corroborated more likely presence and higher abundance of *L. helle* at waterlogged grasslands with high *Bistorta* cover. Abundance also decreased at actively managed patches. The multiple-regression models corroborated the positive effects of *Bistorta* cover and wetness, and negative effects of slope, even after considering sites Position, or Distance from the expansion source (Fig. 4).

Table 1. Results of single-term regressions, relating presence and ordinally coded abundance of adult *Lycaena helle* butterflies to predictors describing the 212 visited grassland patches around the Nové údolí site of release in Šumava Mts. Models with ΔAIC ≥2.0 compared with the null model are shown in **bold.**

Model	Presence					Abundance				
	Coefficients	D.f.	Dev.	D²%	AIC	Coefficients	D.f.	Dev.	D²%	AIC
Null (y ~+1)	–	211	270.3		272.3	–	211	382.4		574.1
~Serial date	-1.47x	210	198.2	26.7	**202.2**	-1.15x	210	245.6	35.8	**439.2**
~ Serial date²	$-23.52x -5.20x^2$	209	194.6	28.0	**200.6**	$-18.72x -2.60x^2$	209	241.7	36.8	**437.4**
~Hour	-0.02x	210	270.3	0.00	274.3	0.06x	210	381.9	0.1	575.5
~Hour²	$-0.32x +3.17x^2$	209	268.0	0.9	274.0	$0.71x +1.50x^2$	209	380.0	0.6	575.6
~Cloudiness	-0.65x	210	254.1	6.0	**258.1**	-0.56x	210	346.3	9.4	**540.0**
~Wind	-0.34x	210	265.1	1.9	**269.1**	-0.35x	210	363.2	5.0	**556.8**
~Area	-0.92x	210	248.9	7.9	**252.9**	-0.82x	210	334.2	12.6	**527.8**
~*Bistorta* cover	0.89x	210	236.0	12.7	**240.0**	0.62x	210	316.2	17.3	**509.9**
~Nectar abundance	-0.82x	210	246.5	8.8	**250.5**	-0.55x	210	346.9	9.3	**540.5**
~Impenetrability	0.17x	210	268.9	0.5	272.9	0.08x	210	381.2	0.3	574.9
~Slope	-0.30x	210	266.2	1.5	**270.2**	-0.14x	210	379.4	0.8	573.0
~Woody cover	0.08x	210	270.0	0.1	274.0	0.08x	210	381.3	0.3	574.9
~Wetness	0.41x	210	262.6	2.9	**266.6**	0.32x	210	365.9	4.3	**559.5**
~Management	-1.42x	210	258.6	4.3	**262.6**	-1.05x	210	363.4	5.0	**557.0**
~Nectar diversity	-0.54x	210	259.1	4.1	**263.1**	-0.35x	210	366.8	4.1	**560.4**
~Closed edges	1.36x	210	264.3	2.2	**268.3**	0.23x	210	373.7	2.3	**567.3**
~Partly closed edges	-0.27x	210	267.1	1.2	271.1	-0.15x	210	379.2	0.8	572.8
~Open edges	-0.07x	210	270.1	0.1	274.1	-0.09x	210	381.3	0.3	574.9

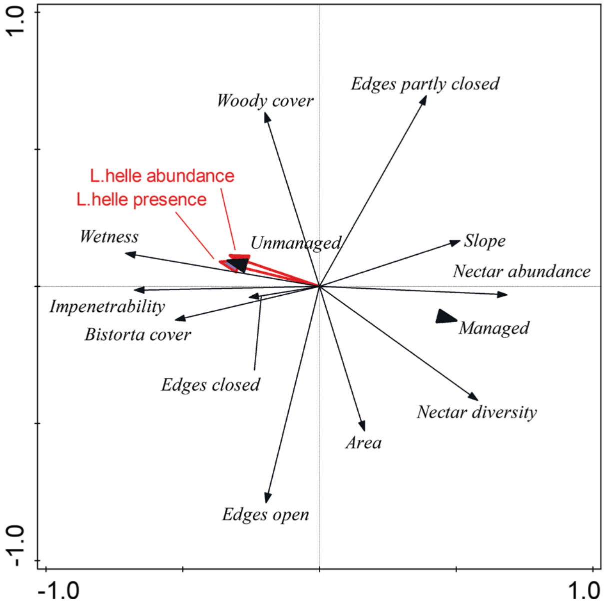

Figure 3. PCA ordination biplot showing the mutual relationships among characteristics of the 212 individual grassland patches surveyed for presence and abundance of *Lycaena helle* in Šumava National Park. The narrow black arrows (and triangles, for the factor Management) are predictors used in subsequent regression analysis. The red arrows, dependent variables in the regressions, are visualised as "supplementary variables", not influencing the mutual positions of predictors.

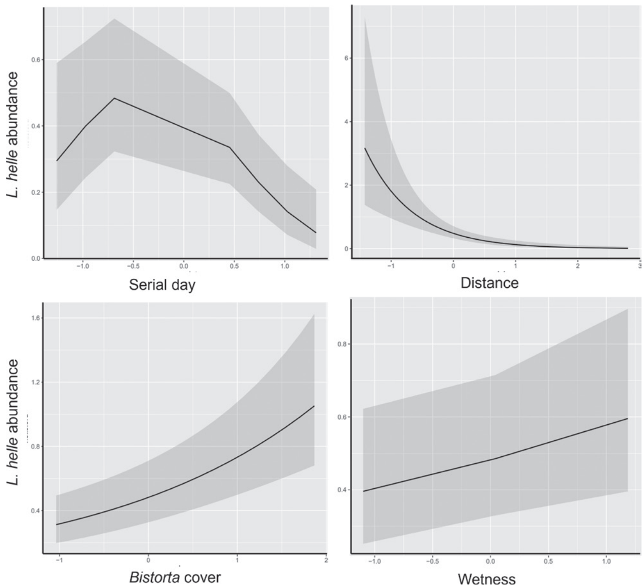

Figure 4. Components of the multiple-regression model *Lycaena helle* presence ~ Distance + Serial day +Serial day^2 +*Bistorta* cover +Wetness. Serial day and Distance from the transfer site were input a priori, before stepwise elimination from all predictors that achieved ΔAIC >2.0 in single-term regressions presented in Table 1. Table 2 presents the model's characteristics.

Table 2. Results of multiple regression models, relating presence and ordinal abundance of *Lycaena helle* to characteristics of 212 grassland patches in the Šumava Mts. distribution area of the introduced populations. The table shows both terms of position and distance models, used as covariates in further analysis; results of adding single predictors onto the covariate models, and resulting multiple-regression models.

Model	Presence					Abundance				
	Terms coefficients	D.f.	Dev.	D^2%	AIC	Terms coefficients	D.f.	Dev.	D^2%	AIC
Null	–	211	270.3		272.3	–	211	382.4		574.1
Positional	-28.59 Latitude -14.29 Latitude^2 +2.14 Longitude -47.29 Longitude^2	207	169.3	37.4	**179.3**	-19.93 Latitude -7.06 Latitude^2 -0.35 Longitude -34.83 Longitude^2	**207**	**203.0**	46.9	**402.6**
Serial date	-0.82 Serial date	206	165.1	38.9	**177.1**	–				
Bistorta cover	1.39 *Bistorta* cover	206	132.0	51.2	**144.0**	0.49 *Bistorta* cover	206	163.0	57.4	**364.7**
Wetness	0.53 Wetness	206	162.6	39.8	**174.6**	0.29 Wetness	206	191.5	49.9	**393.1**
Multiple regression	-25.40 Latitude -16.83 Latitude^2 -4.48 Longitude -58.66 Longitude^2 -0.93 Serial date +1.43 *Bistorta* cover	205	127.7	53.1	**141.7**	-15.92 Latitude -4.62 Latitude^2 +0.09 Longitude -32.19 Longitude^2 +0.49 *Bistorta* cover	206	163.0	57.4	**364.7**
Distance	-2.05 Distance	210	183.0	32.3	**187.0**	-1.37 Distance	210	228.2	40.3	**421.8**
Date^2	-9.58 Serial date -11.04 Serial date^2	208	171.7	36.5	**179.7**	-7.81 Serial date -6.43 Serial date^2	208	208.9	45.4	**406.6**
Bistorta cover	1.27 *Bistorta* cover	209	146.6	45.8	**152.6**	0.49 *Bistorta* cover	209	185.7	51.4	**381.4**
Nectar abundance	–					-0.23 Nectar abundance	209	223.6	41.5	**419.2**
Penetrability	–					0.19 Penetrability	209	222.9	41.6	**418.6**
Wetness	0.60 Wetness	209	173.2	35.9	**179.2**	0.33 Wetness	209	211.0	44.8	**406.6**
Slope	-0.33 Slope	209	179.9	1.8	185.9	–				
Management	-1.21 Management	209	178.8	33.8	**184.8**	-0.64 Management	209	222.0	42.0	**417.7**
Multiple regression	-2.98 Distance -10.28 Serial date -13.54 Serial date^2 -0.41 Slope +1.32 *Bistorta* cover	206	134.1	50.4	**146.1**	-1.32 Distance -6.64 Serial date -4.77 Serial date^2 +0.42 *Bistorta* cover +0.18 Wetness	206	168.1	56.0	**369.7**

Discussion

Twenty years after its establishment, the transferred Šumava Mts. population of *L. helle* inhabits 66.6 ha of waterlogged grassland patches, scattered across 4.5 km^2 of mountain grasslands. Identically to other occupied areas in Western and Central Europe, the Šumava *L. helle* prefers waterlogged grasslands with high representation of its host plant, *Bistorta officinalis*, sheltered from winds by contiguous woody boundaries, typically with flat relief and no active management. It avoids drier grasslands on steeper slopes managed by grazing or mowing and containing higher diversity of nectaring forbs. Surveying grasslands in wider environs revealed that the butterfly has not yet expanded through wider stretches of contiguous forests.

The association with waterlogged sheltered grasslands with high host plant supply corroborates the findings from other regions such as Westerwald and Eifel Mts., Germany (Fischer et al. 1999; Bauerfeind et al. 2009; Scherer et al. 2021), Ardennes, Belgium (Turlure 2009; Goffart et al. 2010; Turlure et al. 2014), Poland (Blaik 2014; Nabielec and Nowicki 2015), Lăpuș river valley, Romania (Craioveanu et al. 2014), or Khentey Mts., Mongolia (Chuluunbaatar et al. 2009). In agreement with other authors, the negative response to management highlights the practical difficulties with supporting the butterfly. Regular mowing or grazing the inhabited grasslands rapidly decreases *B. officinalis* supply (Fischer et al. 1999; Goffart et al. 2010; Hart and Bowles 2014), while total abandonment leads to prevalence of competitively dominant grasses and sedges, and ultimately woody encroachment (Goffart et al. 2014; Scherer et al. 2021). It follows that *B. officinalis*/*L. helle* sites should by managed over rather long periods, with the aim to retain advanced-successional dominance of the host plant. A need of active intervention is well indicated by advance of woody plants, which must be kept in check (Fischer et al. 1999; Goffart et al. 2010).

Interestingly, nectar diversity correlated positively with active management and negatively with high *Bistorta* cover. This suggests that management interventions increase the number of flowering plants, while suppressing the *L. helle* host plant (cf. Krahulec et al. 1997). In Ardennes, Turlure et al. (2009) observed that *L. helle* adults sometimes utilise other nectar sources besides *B. officinalis*. This implies that presence of some alternative nectar is beneficial for the butterfly, but over rich supply of other flowers indicates decreased site suitability. It is also notable that patch area, which had a positive effect on *L. helle* occupancy in several studies (Bauerfeind et al. 2009; Nabielec and Nowicki 2015), had a negative effect in our regressions. Possibly, these authors considered only *Bistorta*-rich habitat patches, whereas our survey included all grasslands existing in our study area. The larger patches were more likely to be regularly managed, and thus unsuitable for the butterfly.

In 2011 and 2012, i.e. one decade after establishment the Šumava population, Předotová (2013) estimated adult numbers using mark-recapture at four separate patches with a summed area of ≈ 3 ha. She did not estimate a total area of inhabited grasslands, which would allow extrapolating her estimates to adult numbers in those years, but she reported her most distant record from the original release point (48.8287 N, 13.7925 E, 900 m aerial distance) and total extent of occupied area (≈2 km^2). Our estimate of actually occupied grasslands area (66.6 ha) combined with 2011 and 2012 two-year average (≈70 adults in 2010, ≈150 adults in 2011) gives a total estimated adult number of ≈2400 individuals (66.6/3 * 110) in 2023. This number may be inflated because Předotová (2013) carried out her mark-recapture at high density patches. However, given that we counted >500 individuals during the 2023 survey, adult numbers in their lower thousands of appear a realistic population estimate. The population thus increased by two orders of magnitude since its establishment.

Perhaps more interesting is the expansion rate following the transfer. Compared to the 900 m reported by Předotová (2013), our most distant record was 4210 m from the release point. The expansion rate was therefore 0.1 km/year during the first decade, and 0.2 km/year over both decades, indicating an acceleration. Situations in which non-native species initially expand slowly, and then its expansion accelerates, were described, e.g., for the invasive Cane Toad (*Rhinella marina* (Linnaeus, 1758)) in Australia (Phillips et al. 2006), or from experiments with the chrysomelid beetle *Callosobruchus maculatus* (Fabricius, 1775) (Ochocki and Miller 2017), and the Red Flour Beetle *Tribolium castaneum* (Herbst, 1797) (Weiss-Lehman et al. 2017).

The 0.2 km/year expansion rate calls for comparing with the two earlier *L. helle* transfers, both carried out in France, to Morvan Mts. (Bourgogne-Franche-Comté, highest point Haut-Folin, 901 m elevation) and to Forez Mts. (northern projection of the Massif Central, highest point Pierre-sur-Haute, 1,631 m elevation) (Descimon and Bachelard 2014). In 1975 and 1992, respectively, 6♀♀ were transferred from Ardennes to Morvan, and 15♀♀ + 3♂♂ from Madeleine Mts. (southern part of Vosges Mts.) to Forez. In Morvan, *L. helle* expanded 11 km in 21 years, i.e. with a rate of 0.52 km/year. In Forez, it crossed 9 km in 20 years, i.e. 0.45 km/year. The expansion in Šumava Mts. is thus twice slower. Habel et al. (2010b, 2011) reported the levels of observed/expected genetic heterozygosity (H_o/H_e) for the relevant populations: Madeleine 49/68, Ardennes 65/76, Türnitz Alps 54/77 (the source of the Šumava population), Morvan 40/59 (a population established from 6♀♀). This rules out genetic impoverishment as a reason for the slower expansion in Šumava Mts. while documenting that even the genetically impoverished Morvan population expanded quite rapidly.

The situation also deserves comparison with Bog Fritillary *Boloria eunomia* (Esper, 1800) (Nymphalidae), another glacial relic (Maresova et al. 2019) developing on *Bistorta officinalis*, which shares habitats with *L. helle* (Sawchik et al. 2005; Turlure 2009; Goffart et al. 2010; Turlure et al. 2014), and is similarly intolerant of frequent mowing or grazing (Goffart et al. 2010; Hart and Bowles 2014). Native to Šumava Mts., *B. eunomia* expanded there in the recent past from a few sites along the Vltava River to almost the entire mountain system (Ebenhöh 1972; Pavlíčko 1996a). This expansion was likely facilitated by post-war decline of grassland management followed by increase of *B. officinalis* (Pavlíčko 1996b). Néve et al. (2009) used allozyme markers to evaluate the expansion. Their results supported the putative location of the source population, and documented decrease of genetic diversity with distance from the source. Similarly to *L. helle*, *B. eunomia* was also transferred to previously unoccupied Morvan Mts., France (Baguette and Néve 1994; Néve et al. 1996). The translocated populations expanded with a speed of 0.4 km/year, i.e. at an identical rate to *L. helle* in Morvan and Forez, and to *B. eunomia* in the Šumava Mts. (≈20 km from source population to distribution limits in ≈50 years: Néve et al. 2009).

The newly established *L. helle* population in the Šumava Mts. thus has been expanding at a slower rate than the previously transferred populations of the same species and both transferred and natural populations of an unrelated butterfly with similar habitat requirements. The Šumava *L. helle* has not yet trespassed barriers of contiguous spruce forests (cf. Fig. 1), whereas Descimon and Bachelard (2014) explicitly mention transgressing contiguous forests by *L. helle* in Morvan. The slower rate than in the case of *B. eunomia* may be due to more restricted *L. helle* mobility (Fischer et al. 1999; Craioveanu et al. 2014; Modin and Öckinger 2020) if compared to *B. eunomia*, for which movements >2 km are routinely recorded (Néve et al. 1996; Schtickzelle et al. 2012). A contributing factor also may be *L. helle*'s preference for sheltered sites, associated with its perching mate-locating activity (Beneš et al. 2002; Craioveanu et al. 2014); the adults are practically inactive in stronger winds. In contrast, *B. eunomia* exhibits patrolling mate-locating activity, which encompasses active flight even in moderately windy conditions.

Still, such species-specific circumstances do not explain the slower expansion of Šumava *L. helle*, when compared to the translocated populations in Morvan and Forez. A possible reason relates to geomorphology of the release localities. The Nové Údolí area discussed here is a shallow pan with high representation of grasslands, surrounded at all sites by higher and mostly forest-covered ridges. Comparing this with Morvan and Forez would require a detailed analysis of local orographies. Likely it took *L. helle* 20 seasons to colonise all the suitable grasslands within this area. Given that in 2023, *L. helle* was recorded at the highest point of the grasslands between Nové Údolí and Strážný, the further expansion to the northwardly situated grasslands will likely accelerate.

As the introduced population inhabits sites directly adjoining the border with Germany, expansion into Germany is fully expectable, and was indeed confirmed by records of *L. helle* from the village Haidmühle in 2021. The landscape and spatial configuration of habitats at the German side of the border differ from the Czech side, however, as there were no post-war transfers of inhabitants, a majority of the area is farmed, and potential habitats are more fragmented. A detailed survey of *L. helle* performance on the German side of the border is desirable and can provide an interesting comparison to its performance on abandoned land.

Conclusion

The newly established population of *Lycaena helle* in Šumava Mts., Czech Republic, is apparently viable, having expanded from the original release point to a wide area along the course of Studená Vltava River, and has potential for further expansion. Its preference for minimally managed successionally advanced grasslands do not differ from that of other mountain populations in Central and Western Europe. The transfer, initially motivated by fears for the donor population in the Türnitz Alps, Austria, established the butterfly in a previously unoccupied area, thus enhancing its total numbers in mountains of Central Europe, was a butterfly conservation success. The target area does not suffer the common problems encountered in insect conservation, such as intensive land use and resulting habitat homogenisation and landscape impenetrability. Ultimately, addressing these aspects in broad landscapes will be more decisive for butterfly biodiversity than single-species transfers. Encouragingly, the donor population was also still extant in 2023, and measures to sustain its habitats, including partial removal of the young spruce cultures from the former valley grasslands, have been adopted in the interim period.

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