



Has the currently warming climate affected populations of the mountain ringlet butterfly, *Erebia epiphron* (Lepidoptera: Nymphalidae), in low-elevation mountains?

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Abstract. Climate change scenarios predict losses of cold-adapted species from insular locations, such as middle high mountains at temperate latitudes, where alpine habitats extend for a few hundred meters above the timberline. However, there are very few studies following the fates of such species in the currently warming climate. We compared transect monitoring data on an alpine butterfly, *Erebia epiphron* (Nymphalidae: Satyrinae) from summit elevations of two such alpine islands (above 1300 m) in the Jeseník Mts and Krkonoše Mts, Czech Republic. We asked if population density, relative total population abundance and phenology recorded in the late 1990s (past) differs that recorded early in 2010s (present) and if the patterns are consistent in the two areas, which are separated by 150 km. We found that butterfly numbers recorded per transect walk decreased between the past and the present, but relative population abundances remained unchanged. This contradictory observation is due to an extension in the adult flight period, which currently begins ca 10 days earlier and lasts for longer, resulting in the same total abundances with less prominent peaks in abundance. We interpret this development as desynchronization of annual cohort development, which might be caused by milder winters with less predictable snow cover and more variable timing of larval diapause termination. Although both the Jeseník and Krkonoše populations of *E. epiphron* are abundant enough to withstand such desynchronization, decreased synchronicity of annual cohort development may be detrimental for innumerable small populations of relic species in mountains across the globe.

INTRODUCTION

Both poleward (Parmesan, 2006; Chen et al., 2011) and uphill (Konvicka et al., 2003; Lenoir et al., 2008; Roth et al., 2014) shifts in the distributions of species and shifts in their phenology (Altermatt, 2010; Diamond et al., 2011) are widely recognised as both evidence and major outcomes of the ongoing climate change, or global warming. In human-dominated landscapes, common taxa, including pests and pathogens, often perform better in tracking favourable thermal environments, whereas habitat specialists may lag behind, entrapped in climatically unsuitable areas (Warren et al., 2001; Oliver & Morecroft, 2014). These developments may imperil the very existence of numerous species, which are losing their habitats. It is predicted that as many as 15–35% of global biodiversity may be lost due to climate change in the foreseeable future (Thomas et al., 2004).

Rising temperatures may particularly imperil cold adapted species inhabiting islets of alpine habitats in mid-altitude mountains in temperate zones (Franco et al., 2006; Konvicka et al., 2014). Contrary to spacious high-altitude habitats found, e.g., in the Alps, the American Rockies or the Pyrenees, mountains at lower altitudes, such as the Hercynian system of Central Europe (Jeník, 1998), have only tiny treeless patches on their summits. Species restricted to such habitat islands, typically relics of a cooler past, may have nowhere to go if the climate warms up and the timberline ascends. In addition to the scientific and cultural value of these species and communities, such isolated relic populations are often genetically distinct as a result of their long isolation (Schmitt et al., 2006, 2014; Konvicka et al., 2014), sometimes forming endemic taxa at the specific or subspecific level.

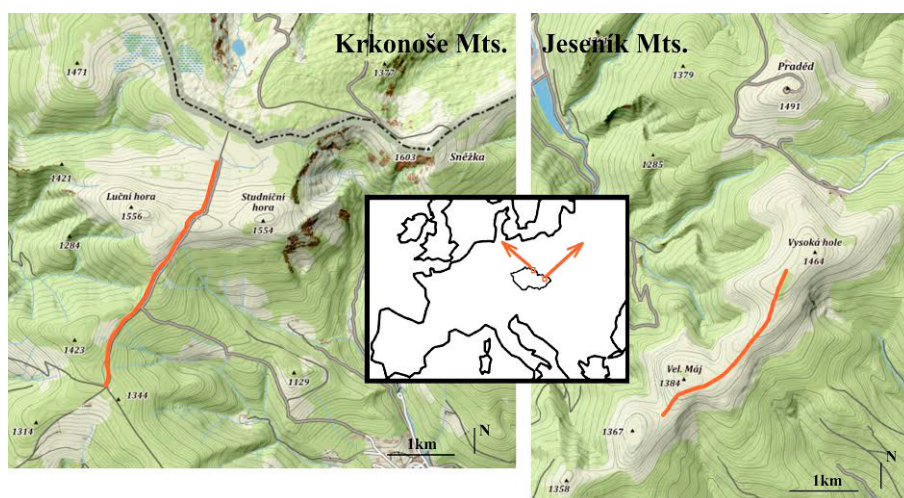


Fig. 1. Map showing the location of the Jeseník and Krkonoše Mts in Europe, and directions of the permanent transects established there to monitor the relative population abundance of *Erebia epiphron*. Note that the relief of the summit plateaux in these mountains is relatively flat. Although green in the maps indicates “forest”, the vegetation above ca. 1250 m consists of clumps of dwarf *Picea abies* (Jeseník Mts) and shrubby *Pinus mugo* interspersed among *Picea abies* (Krkonoše Mts).

Probably due to the logistic difficulties of collecting long-term data from mountain areas, there is still little knowledge of the responses of alpine animals to the current climatic warming, even for such model groups as butterflies. Perhaps the best long-term data available to date has targeted butterfly communities inhabiting the Sierra de Guadarrama mountains in Spain (maximum altitude: 2428 m), where upslope shifts in community composition attributable to climatic warming have been detected (e.g., Wilson et al., 2005, 2007). On the Kananaskis Ridge in Canada, the ascending timberline genetically isolates individual mountaintop populations (Keyghobadi et al., 2005) and desynchronizes their population dynamics (Roland & Matter, 2007; Matter et al., 2011). In Britain, Franco et al. (2006) report loss of low altitude colonies of the alpine species, *Erebia epiphron* (Knoch, 1783), whereas higher altitude populations seemed unaffected. These studies, however, targeted mountain ranges with plenty of space above the timberline, allowing the alpine species to move to a higher altitude. In contrast, very few researchers have targeted “middle high mountains” (cf. Boggs & Murphy, 1997), in which the alpine habitats currently extend above the timberline for just a few hundred metres, and hence can rapidly disappear due to shifts in altitudinal vegetation bands. One exception is the study by Scalercio et al. (2014), which compares the past and present distribution of *Erebia cassioides* (Reiner & Hohenwarth, 1792) on the Pollino Massif on the Apennines in Italy.

This paper reports the results of monitoring a high mountain butterfly, the Mountain Ringlet *Erebia epiphron* ssp. *silesiana* (Meyer et Dür, 1852) in the Jeseník Mts and Krkonoše Mts in the Czech Republic. These mountains have only narrow belts of alpine grassland and poor alpine zone faunas (cf. Liška & Skyva, 1997; Beneš et al., 2000). *E. epiphron*, the only true alpine butterfly occurring there and has been the subject of earlier population ecology and genetic studies (Cizek et al., 2003; Kuras et al., 2003; Schmitt et al., 2005). The monitoring, target-

ing its adult phenology and abundance, continued for two five-year periods (1995–1999 and 2009–2013), separated by a decade-long gap. This allowed the comparison of *E. epiphron* population parameters recorded in the late 1990s and early 2010s. During the interim decade, the mean annual temperature rose by 1°C in both areas (Halášová et al., 2007; Kliment et al., 2011), prompting us to ask the following questions: (1) Did the abundance of the target species change over time? (2) Were there detectable changes in the shape of the adult recruitment curve, such as higher or lower numbers recorded per transect walk, more or less prominent peak in adult emergence, etc.? (3) Was there a detectable change in adult phenology, such as an earlier adult flight in the later, i.e. warmer period?

METHODS

Species and locations studied

Erebia epiphron (Nymphalidae: Satyrinae), a member of the species-rich and mostly cold-adapted butterfly genus *Erebia* Dalman, 1816, is a mountain grasslands species distributed throughout most European mountains with areas above the timberline, except in Scandinavia and the mountains on the Iberian peninsula and in the southern Balkans, but including mountains in Britain and some low mountain ranges in Central Europe (details: Schmitt et al., 2005). Its adults occur during the short mountain summer, inhabiting alpine grasslands and reaching high densities there (e.g., Kuras et al., 2003; Polić et al., 2014). Females oviposit singly on thin-bladed grasses (e.g. *Nardus stricta*, *Festuca supina*, *Avenella flexuosa*); larvae feed both before and after overwintering and their development may span one or two seasons depending on weather conditions (Sonderegger, 2005).

Of the three Central European populations north of the Alps, one used to inhabit the Harz Mts, Germany (highest summit: Brocken Mt., 1141 m), but went extinct in the 1950s. The two remaining populations, both studied here, inhabit the Jeseník Mts, NE Czech Republic (highest summit: Praděd Mt., 1492 m, alpine zone area 1050 ha, timberline at ca 1300 m alt.), and the Krkonoše Mts, Czech-Polish border (highest summit: Sněžka Mt., 1653 m, alpine zone 5460 ha, timberline at ca 1250 m alt.). The Jeseník population is native, whereas the Krkonoše population was estab-

Table 1. Overview of the transect monitoring of the butterfly *Erebia epiphron* in the Jeseník and Krkonoše Mts, Czech Republic, together with properties of GAM functions fitted to the transect data for individual years, and population characteristics used for comparing the records obtained in the 1990s and 2010s (Jeseník Mts), and Jeseník vs. Krkonoše Mts (2010s). SRI – sight records index, is the density per transect walk; PAI – population abundance index, a relative measure of yearly recruitment estimated from the GAM curves; the phenology predictions 20%, 50%, 80% and Max are Julian days when the respective proportions of adults flew and the maximum yearly flight. See Methods for details.

Mountains	Year	Transect walks	Total records	Monitoring interval	Onset of flight season (Julian day)	Coefficients of fitted GAM function				SRI	PAI	Phenology predictions of GAM function				
						Deviance explained (%)	D.f.	F	P			20%	50%	80%	Max	Bulk flight period (days)
Jeseník	1995	13	993	8.vii.–5.viii.	189	90.6	2,867	18.2	0.000	28	885	200	205	210	206	10
Jeseník	1996	14	1025	15.vii.–12.viii.	197	90.5	2,260	8.3	0.003	27	658	209	213	218	213	8
Jeseník	1997	11	560	15.vii.–15.viii.	196	95.4	2,942	32.5	0.000	19	657	203	209	217	207	14
Jeseník	1998	14	460	18.vii.–31.vii.	199	84.4	2,488	12.8	0.000	12	174	202	204	206	203	4
Jeseník	1999	10	586	14.vii.–31.vii.	195	88.0	2,431	9.7	0.004	22	431	196	200	204	200	8
Jeseník	2009	7	117	13.vii.–23.vii.	194	33.1	1,672	0.8	0.505	6	200	193	202	217	197	24
Jeseník	2010	15	613	9.vii.–13.viii.	190	44.5	2,357	3.3	0.058	15	747	197	205	215	204	18
Jeseník	2011	12	329	6.vii.–11.viii.	187	86.0	2,717	12.1	0.001	10	435	196	203	209	203	14
Jeseník	2012	15	559	2.vii.–11.viii.	184	56.7	2,429	3.8	0.000	14	1314	190	201	211	202	21
Jeseník	2013	10	293	9.vii.–11.viii.	190	88.7	2,574	12.7	0.000	11	461	208	215	222	214	13
Krkonoše	1999	10	455	15.vii.–8.viii.	N.A.	82.5	2,624	6.9	0.015	12	470	194	201	208	200	13
Krkonoše	2009	7	15	16.vii.–23.vii.	197	N.E.	–	–	–	1	N.E.	–	–	–	–	–
Krkonoše	2010	13	247	11.vii.–5.viii.	192	29.5	1,826	1.1	0.379	5	148	194	201	208	201	14
Krkonoše	2011	21	525	5.vii.–12.viii.	186	64.4	2,713	8.3	0.001	7	337	173	180	193	170	20
Krkonoše	2012	18	334	1.vii.–5.viii.	183	33.2	2,225	2.3	0.117	5	244	192	199	213	195	21
Krkonoše	2013	19	753	4.vii.–10.viii.	185	67.1	2,424	7.7	0.002	11	378	202	207	211	207	9

N.A. – date not available due to late start of monitoring. N.E. – not possible to be estimate values due to the low number of days monitored.

lished by the artificial release of 50 females originally from the Jeseník Mts in the 1930s (Schmitt et al., 2005).

Both the Jeseník and Krkonoše mountains consist of gently rolling ridges on acidic rocks. They are isolated from each other (aerial distance ~100 km) and from similar high altitude regions in the Alps (~300 km) and Carpathians (~150 km). On both these mountains there are only narrow alpine zones, formed by short-turf alpine grasslands, an optimal habitat for *E. epiphron*.

Transect counts

To record changes in the relative abundance of *E. epiphron*, we established one permanent transect in each of the two mountain ranges (Fig. 1). Both transects crossed the central areas of the alpine grasslands on the main ridges in these two mountain ranges and both were walked daily, weather permitting, during the flight period of *E. epiphron*. During the walks, all individuals seen in a 5-metre cube in front of the recorder were counted. The entire Jeseník transect (length: 2.7 km, altitude 1325–1465 m, between 50°03'35.79"N, 17°13'52.23"E and 50°2'28.581"N, 17°12'26.860"E) crossed alpine grassland. It was walked in 1995–1999 (5 seasons), and again in 2009–2013 (5 seasons) (Table 1). The Krkonoše transect is longer (7 km) and ascends from the mountain taiga belt to the timberline (details: Kleckova et al., 2015). Here, we analyse only the records from the 3.7 km in the alpine zone (between 50°42'20.643"N, 15°40'27.286"E and 50°44'2.799"N, 15°41'50.145"E), which is at altitudes between 1345 and 1420 m, i.e. at similar altitudes to the Jeseník transect. It was walked in a single season in 1999, from 15 July to 11 August, and again in 2009–2013 (5 seasons), again on daily basis (Table 1). The entire flight period of *E. epiphron* was monitored in all years and on both mountains except in 2009, when the recording terminated at the end of July.

Analyses

We used two methods to compare the relative abundance of *E. epiphron* in the past (1995–1999) and present (2009–2013)

and currently on the two mountain ranges. First, we compared numbers recorded per day standardized per unit length of transect, obtained by summing all the daily records for a given year and dividing this annual sum by the number of walks in that year and transect length (in km). This sight record index [herein SRI], previously used by Kleckova et al. (2015) in a similar situation, allows the comparison of the average numbers of butterflies seen in the respective mountains per transect kilometre per day, but does not provide any information on phenology, total population size, etc.

Second, we used an annual abundance measure derived from the shapes of the population recruitment curves, defined as the trends in time (Julian dates) in daily abundance (e.g., Rothery & Roy, 2001). For fitting curves to the results, we used the generalised additive models (GAMs) in the library mgcv (Wood, 2011) in program R v. 2.15.2 (R Development Core Team, 2011). The curves (Fig. 1) were fitted using the quasi-Poisson distribution of errors and cubic splines ($k = 4$). For yearly datasets not containing initial or terminal visits with zero records (i.e., records for transect walks preceding and following the adult flight period: Jeseník 2010 and 2012, Krkonoše 2011 and 2012), we added zero records two weeks before and after the monitoring duration for the GAM computations. The areas under the GAM curves were computed using the rectangle method, which returns an approximation to definite integral. Specifically, the date interval (Julian date 170–240) was divided by subintervals (with step 0.01) representing the \bar{a} of all rectangles, b -bars of each rectangle agree with values predicted for each subinterval by the relevant GAM. The sum of the computed areas of all rectangles is the area under the curve. To obtain comparable values for the two transects, we divided the resulting values by the lengths of the transects to obtain the yearly population abundance index [herein PAI].

To compare the yearly SRIs and PAIs recorded in the past and recently in the Jeseník Mts, we used t-tests for independent samples. To compare these indices for the two mountain ranges re-

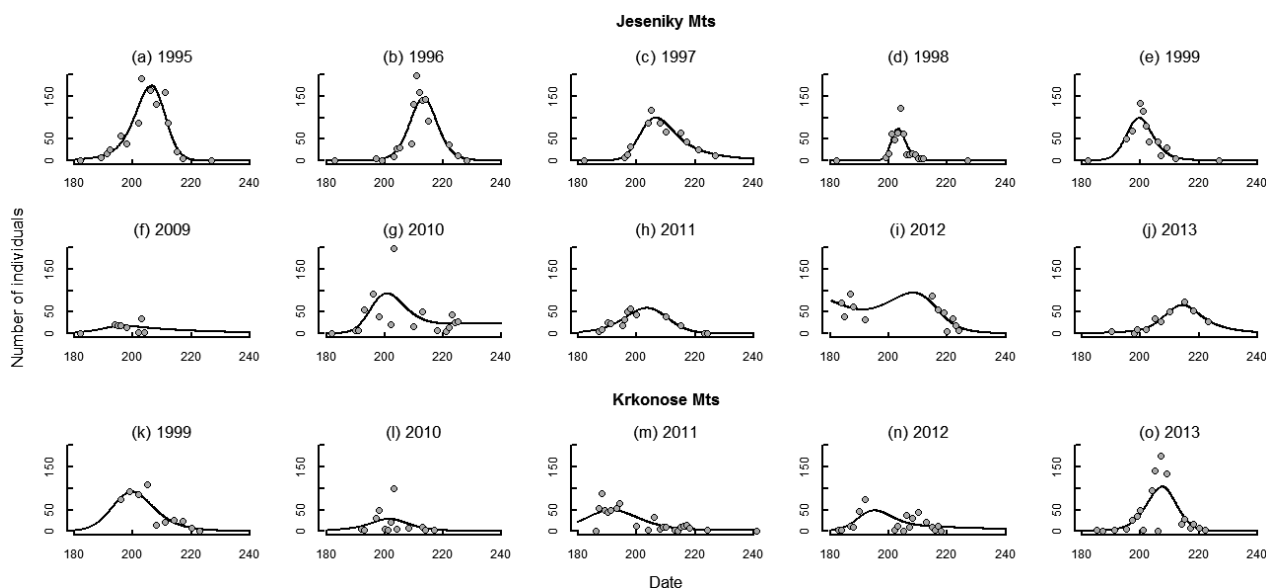


Fig. 2. Yearly population recruitment curves for *Erebia epiphron* based on monitoring along fixed transects in the Jeseník Mts (a–j) and Krkonoše Mts (k–o) and fitted using GAM functions. Points are the numbers of individuals recorded during individual transect walks. The panels (a–e), plus (k), are records recorded in the past, and (f–j) plus (l–o) those recorded recently. Dates are in Julian days.

corded recently, we used paired t-tests with samples represented by particular years (we compared PAI only in the 2010–2013 period, because the GAM function, and hence the relative abundance estimates, were not estimable for 2009). One-sample t-tests were used to compare the single (1999) Krkonoše past year with the Jeseník past period, and with the Krkonoše present period.

For comparing phenology, the earliest Julian date on which adults were recorded, the onset of annual flight. From the fitted GAM curves, we inferred the dates when 20%, 50%, 80% and the maximum number of individuals were recorded. The bulk flight period refers to the difference between the dates when 80% and 20% of the individuals were recorded. Then, t-tests were used to detect potential differences in the phenology in the past and present periods in the Jeseník Mts and currently in the two mountains, between the past period in the Jeseník Mts and the single past year (1999) in Krkonoše Mts and between the single past year (1999) and currently in Krkonoše Mts.

RESULTS

The weather on only about a third of the days during the annual monitoring periods was suitable for butterfly activity (Table 1, Fig. 2). The highest yearly sight record indices [SRI] were recorded in the Jeseník Mts in 1995 and 1996 and in the Krkonoše Mts in 2013; and the lowest values in 2009, a rainy year when monitoring terminated in late July in both mountain ranges. The highest values of the yearly population abundance index [PAI] were recorded in the Jeseník Mts in 2012 and 1995 and in the Krkonoše Mts in 2013. The fitted GAM models for annual counts explained more than 50% of the variability in annual counts (i.e., records of *E. epiphron* during a flight season) except for Jeseník 2009 and 2010, and Krkonoše 2010 and 2012. GAM was not computable for Krkonoše 2009, with only 7 recording days.

Comparing Jeseník SRIs recorded in the past (mean 21.6 ± 6.55 SD) and the present (mean 11.2 ± 3.48 SD) revealed those recorded in the past were higher ($t = 3.13$, d.f. = 8, $P = 0.014$). The single SRI for Krkonoše 1999 (Table 1)

is lower than the mean value recorded in the past in the Jeseník Mts ($t = 3.18$, d.f. = 4, $P = 0.033$), but higher than the current mean for the Krkonoše Mts ($t = -4.08$, d.f. = 4, $P = 0.015$). Comparing the present situation in the two mountain ranges revealed the SRI values recorded in the Jeseník are higher than those recorded in the Krkonoše Mts (mean 5.6 ± 3.65 SD) ($t = 3.12$, d.f. = 4, $P = 0.036$).

In contrast, the yearly PAIs recorded in the past (mean 561.0 ± 269.16) and present (mean 631.3 ± 428.29) in Jeseník Mts do not differ ($t = -0.31$, d.f. = 8, $P = 0.764$). The PAI recorded for the Krkonoše Mts (1999) is similar to that recorded in the past in the Jeseník Mts ($t = 0.76$, d.f. = 4, $P = 0.492$), but higher than the mean value recently recorded in the Krkonoše Mts ($t = -3.78$, d.f. = 3, $P = 0.032$). The present mean values recorded in the Jeseník and Krkonoše Mts do not differ (mean = 276.5 ± 102.49 SD) ($t = 1.97$, d.f. = 3, $P = 0.144$).

In the Jeseník Mts, the onset of the flight periods of *E. epiphron*, i.e. the dates on which the first adults were recorded, varied by over two weeks (Table 1, Fig. 1). The first records of flying *E. epiphron* were later in the past (mean Julian date 195.2 ± 3.77 SD, i.e. 14 July) than currently (mean date 189.0 ± 3.74 SD, i.e. 8 July) ($t = 2.61$, d.f. = 8, $P = 0.031$) and the bulk flight period was shorter in the past (mean 8.8 ± 3.28 SD) than currently (mean 18.1 ± 4.72 SD) ($t = 8.79$, d.f. = 8, $P = 0.007$). The remaining phenological characteristics did not differ (all t s > 0.15). Compared with the single Krkonoše past record (1999) (cf. Table 1, Fig. 1k), the bulk flight period was shorter (mean: 8.8 ± 3.28 SD) and the dates of 20%, 50% and maximum adult flight were latter in the past in the Jeseník Mts (20%: mean Julian date 202.0 ± 4.78 SD, $t = 3.59$, $P = 0.023$; 50% mean: 206.2 ± 5.10 , $t = 2.48$, $P = 0.07$; mean maximum date 205.8 ± 5.06 , $t = 2.72$, $P = 0.053$). Currently none of the phenological characteristics recorded in the Jeseník and Krkonoše Mts differ (all P s > 0.1) nor do those re-

corded in the past (1999) and currently in the Krkonoše Mts (all $P_s > 0.3$).

DISCUSSION

Transect counts in the late 1990s and early 2010s of *Erebia epiphron*, an alpine butterfly forming isolated relic populations in low altitude mountains in Central Europe, revealed that more individuals were observed in the past per unit transect length, but total yearly population abundances have not changed. There are fewer butterflies recorded together in recent years than a decade ago, but overall numbers occurring per season have not changed, at least in the Jeseník Mts, for which a rigorous comparison is possible. This can be attributed to changes in their phenology. At present, the annual adult flight begins about a week earlier than in the past, but it lasts longer, resulting in shallower adult recruitment curves. Because the current phenology does not differ on the well separated mountain ranges, Jeseník and Krkonoše, large scale climatic effects are the most likely cause.

For the vast majority of temperate zone butterflies with a single generation per year (e.g., Konvička et al., 2012) and those with multiple but temporally non overlapping generations (e.g., Soulsby & Thomas, 2012), annual adult recruitments curves are domed with a rather steep initial increase, distinct peaks and a subsequent gradual decline. This is a result of a rapid emergence of males and more gradual emergence of females (the “protandry” phenomenon, reflecting male competition for females, cf. Neve & Singer, 2008; Takeuchi & Honda, 2009). The adult numbers typically peak when there are still many males present and female numbers are just building up (Soulsby & Thomas, 2012), ensuring that the sexes meet in sufficient numbers. Such synchronisation is more prominent if there are some common triggers for pre-adult development, such as weather-controlled diapause termination and less prominent if disrupted by bouts of unfavourable weather (Junker et al., 2010).

Erebia epiphron is among the few alpine butterflies for which adult demography has been studied in some detail. In the 1990s, Kuras et al. (2003) used mark-recapture to study the Jeseník population, and Cizek et al. (2003) trapped Krkonoše adults using coloured dishes. These studies reported distinct protandry and prominent population peaks. In alpine conditions, adult flight is likely to be synchronized by diapause termination during snow melt. The earlier onset of the adult flight of *E. epiphron* in the 2010s is attributable to shorter winters, or more precisely to earlier snow melts (cf. Leingartner et al., 2014). On the other hand, the less distinct abundance peaks and prolonged adult flight duration in 2010s suggest a desynchronization of the annual development.

At present, very little is known about the ecology of the pre-adult stages of *E. epiphron*, or mountain butterflies in general. Investigations of the cold hardiness of diapausing larvae of four *Erebia* spp. and four *Colias* spp. revealed that lowland species of the two genera were more tolerant of severe frosts than those inhabiting alpine altitudes (Vrba

et al., 2012, 2014b), probably because the lowland species must survive occasional severe frosts not insulated by a covering of snow, whereas alpine species rely on the stable thermal conditions provided by a covering of snow. During recent years, winter snow has become less predictable in Central European Mountains (Räisänen & Eklund, 2012) and periods with no snow are occurring even on the summits in mid-winter. This may adversely affect overwintering butterfly larvae, despite their hiding in short grass tufts like those of *E. epiphron* (Sonderegger, 2005). In the Canadian Rockies, Matter et al. (2011) report that less reliable snow cover imperils populations of another mountain butterfly, *Parnassius smintheus*. Recording adult *Erebia cassioides* on the Pollino Massif, Italy, Scalercio et al. (2014), detected that an increase in snow cover at high altitudes and less reliable snow at low altitudes results in higher population densities of the species at alpine altitudes and lower population densities at the timberline, relative to the situation in the 1970s.

Focusing on adult butterflies, Cizek et al. (2003) present graphs depicting annual cohort development of *E. epiphron* and related *E. euryale* (Esper, 1805) at various altitudes between 1120 m and 1525 m in the Krkonoše Mts in the year 1999. They show that adult emergence peaks differed by about 2 weeks between the lowest and highest sampling points. However, the transect counts analyzed in this study covered only the upper parts of the species vertical range in the mountains. Possibly, the current milder and shorter winters with less reliable snow are enhancing the variation in the rate of development of *E. epiphron* at spatial scales that are much smaller than the four hundred altitudinal metre scale used by Cizek et al. (2003).

Despite its restricted distribution, *E. epiphron* is abundant in both the Jeseník and Krkonoše Mts, Kuras et al.'s (2003) estimate of the population size in the Jeseník Mts in 1996 is $\approx 10^5$ individuals. Based on the transects-based population abundance index, 1996 was rather average in terms of adult abundance (cf. Table 1), but even in years with the lowest PAI values (1998, 2009), there were probably tens of thousands of adults present. Thus, it is unlikely that desynchronized adult emergence with lower momentary densities would hamper the populations' prospects via, e.g., failure to locate mates (a possible cause of negative population growth under reduced densities: cf. Kadlec et al., 2010). The same processes, however, may be detrimental in smaller populations. Even in the Jeseník Mts in 1997, there was a smaller populations consisting ≈ 5000 individuals (Kuras et al., 2003), genetically isolated from the large central population (Schmitt et al., 2005). For this small population, and innumerable other small populations of relic insects entrapped on cold-climate islands in relatively low mountains, a desynchronized adult emergence may be the causative link between climatic warming and declines in abundance, eventually leading to population extinctions.

Declines in small populations of cold adapted insects near to their lower altitudinal limits, unlike in high altitude populations, have recently been reported for several European butterflies, including *Aporia crataegi* (Linnaeus,

1758) in Spain (Merrill et al., 2008), *Colias palaeno* (Linnaeus, 1761) in Central Europe (Vrba et al., 2014a) (both Pieridae), *E. epiphron* in Britain (Franco et al., 2006) and *E. cassioides* on the Pollino Massif, Italy (Scalercio et al., 2014). In the last case, however, the authors report an increase in momentary densities of *E. cassioides* at a high altitude, conceptually comparable to our sight record index rather than to our population abundance index. Increase in *E. cassioides* population density might reflect either a real increase in population size, or an apparent increase due to the shortened flight period, i.e. a reverse of what we recorded for *E. epiphron* in the Czech Republic. In any case, the mechanistic effects of a warming climate on relic cold-adapted insects may differ in different mountain systems and even closely related (congeneric) species may respond differently. It is also noteworthy that the data for *E. epiphron* in the Czech Republic do not indicate a decline in its abundance at the lower edge of its distribution (cf. Konvička et al., 2009), in contrast to the situation described by Franco et al. (2006) in Britain.

Consistent with global warming scenarios, uphill shifts in altitudinal vegetation belts are reported across the globe (Beckage et al., 2008; Holzinger et al., 2008), including in the Jeseník Mts and Krkonoše Mts, where the timberline of *Picea abies* has increased in altitude (Tremel & Banaš, 2000). In the Jeseník Mts, the situation is locally worsened by non-native *Pinus mugo* stands, locally expanding after cessation of grazing (Bila et al., 2013; Kasak et al., 2015). The ascending timberline may gradually fragment the currently extensive areas inhabited by *E. epiphron* in the two mountain ranges, making the resultant fragmented populations more vulnerable to demographic stochasticity (Roland & Matters, 2007). On the other hand, recent plant, bird and butterfly monitoring in mountainous Switzerland has revealed the remarkable resiliency of alpine communities, in terms of community composition, when compared to lowland communities (Roth et al., 2014). Allegedly, the higher microtopographic and microclimatic variation at high altitudes allows species to locate optimal niches at small scales. The importance of microtopography for alpine insects has also been shown by Klecková et al. (2014), who compare the behavioural thermoregulation of seven *Erebia* species. Further, Konvička et al. (2014) show that most of the regional genetic diversity of *Erebia sudetica*, another relic butterfly inhabiting the Jeseník Mts, occurs at locations at the highest-altitudes. Thus, the climate change prospects for high altitude species may not be as grim as might be expected from purely mechanistic predictions. This moderate optimism, however, requires that habitats of the cold-adapted species, such as the alpine grasslands targeted here, remain preserved, using active management if necessary.

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