



Uphill shifts in distribution of butterflies in the Czech Republic: effects of changing climate detected on a regional scale

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ABSTRACT

Aim To assess whether altitude changes in the distribution of butterflies during the second half of the 20th century are consistent with climate warming scenarios.

Location The Czech Republic.

Methods Distributional data were taken from a recent butterfly distribution atlas, which maps all Czech butterflies using a grid of 10' longitude to 6' latitude, equivalent to about 11.1 × 12 km. Cell altitude was used as an independent variable, and altitudinal ranges of individual species (less migrants, extinct species, recent arrivals and extremely rare species) in 1950–80 vs. 1995–2001 and in 1950–80, 1981–94, 1995–2001 were compared using *U*-tests and linear regressions.

Results Of 117 (*U*-tests) and 119 (regressions) species, we found significant uphill increases in 15 and 12 species, respectively. The two groups were nested; none (*U*-test) and one

(regression) species showed a significant altitudinal decrease. Binomial tests of frequencies of signs of the *U*-tests and regression coefficients, including nonsignificant ones, also showed that the increases prevailed. The mean and median of the significant shifts were 60 and 90 m, respectively, and the maximum shift per species was 148 m. The recording effort in individual time periods was not biased with respect to altitude.

Main conclusion Altitude shifts in the distribution of Czech butterflies are already detectable on the coarse scales of standard distribution maps. The increasing species do not show any consistent pattern in habitat affiliations, conservation status and mountain vs. nonmountain distribution, which renders climatic explanation as the most likely cause of the distributional shifts.

Key words altitudinal gradient, butterflies, Central Europe, climate change, Czech Republic, distribution atlas, global warming, mountain habitats.

INTRODUCTION

Consistent with the scenario of recent global warming (McCarty, 2001; Walther *et al.*, 2002), increasing evidence documents ongoing changes in the distribution of terrestrial species throughout the Earth (Parmesan & Yohe, 2003). The evidence includes phenology changes (Brown *et al.*, 1999; Fitter & Fitter, 2002; Sparks & Menzel, 2002; Tryjanowski *et al.*, 2002), poleward shifts in latitudinal distributions (Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Warren *et al.*, 2001; Kullman, 2002) and increases in altitudinal ranges (Grabherr *et al.*, 1994; Pounds *et al.*, 1999; Klanderud & Birks, 2003).

Whereas the poleward shifts have been reported for large collections of species across wide regions, the evidence for altitudinal shifts rely predominately on local data from permanent plots (Grabherr *et al.*, 1994), or on resampling of older snapshot data (Pounds *et al.*, 1999; Klanderud & Birks, 2003). It is easy to understand why there is relatively little evidence for altitudinal shifts affecting wider arrays of species across large regions. To observe latitudinal (or other 'planar') range changes, researchers can turn to rich historical and recent data in collections (Shaffer *et al.*, 1998) and distribution atlases (e.g. Kudrna, 2002; Palitzsch & Rahbek, 2002). On the other hand, vertical range changes are by definition too localized compared to the scales retrievable from old collection labels (typically a nearby settlement) and from standard distribution maps (typically in the orders of 100 km²).

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Only the highest-quality data on both historical and recent distribution can reveal spatially consistent altitudinal shifts in species ranges (e.g. Parmesan, 1996). As perhaps the best long-term distribution data are those for British butterflies (Asher *et al.*, 2001), analysing them revealed the only evidence so far available of changes in altitudinal distribution that covers multiple species across a large area (Hill *et al.*, 2002). The authors showed that both 'northern' and 'southern' species (relative to positions of their range margins in Britain) ascended to higher elevations during the 20th century. The apparent absence of shifts of southern range margins noticed by Parmesan *et al.* (1999) for some European butterflies could be due to the masking of the changes by vertical distribution shifts in southern regions. Building on those considerations, Hill *et al.* (2002) constructed climate-based models of future European ranges of the butterflies that occur on the British Isles.

There are several reasons for documenting altitudinal changes in butterfly distribution in areas outside Britain. First, Britain, as an island situated at the margin of the Palaearctic realm, has a naturally impoverished butterfly fauna with many species living on the extremes of their range. The general validity of the patterns found by Hill *et al.* (2002) would be strongly corroborated if congruent patterns were documented in biogeographically less aberrant areas. Second, warming-triggered altitudinal shifts pose a critical threat for narrowly distributed mountain species (Boggs & Murphy, 1997), which comprise a considerable portion of European butterfly diversity (Dennis *et al.*, 1998). Non-mountain species may in principle move back and forth latitudinally as the climate changes, provided that their habitats are not too fragmented (Warren *et al.*, 2001), whereas mountain species may have nowhere to go. Third, increases of altitudinal distribution, especially declines in lower-elevated areas, might be caused by habitat loss in densely populated lowlands rather than by a changing climate. Successful separation of the two factors would provide a critical test that the recent altitudinal range shifts are indeed climate-related.

Here we report 20th century altitudinal changes in the distribution of butterflies in the Czech Republic, Central Europe. This landlocked country hosts 161 species in an area of 79 000 km². Since it is situated near the geographical centre of Europe, the patterns detectable there may well represent the continent as a whole. We based our analysis on the database compiled for a recent comprehensive butterfly distribution atlas (Benes *et al.*, 2003b), which allows comparison of the situation across three periods during the second half of the 20th century. We also point to the conservation status of individual ascending species, and show that in the majority of them the changes were unlikely to be due to habitat loss in the lowlands.

MATERIALS AND METHODS

The Czech Republic (centroid coordinates 49°45'N, 15°30'E) is covered by a heterogeneous cultural landscape of arable

fields, broadleaf and evergreen forests and human settlements. Its western part is a basin filled by rolling plains, hills, and plateaux that is surrounded by densely forested Hercynian mountains, while its eastern part is the flat northernmost projection of the Panonnian basin surrounded by the western slopes of the Carpathians. The altitude ranges from Snezka Mt. (1602 m) to the Elbe river (115 m). Butterfly fauna are that of 'European mainland' (Dennis *et al.*, 1998) with some southern species reaching their northern limits in warmer areas and a few species with northern and/or alpine distribution forming insular populations in the mountains. The fauna exhibit prominent latitudinal, longitudinal and altitudinal gradients (Storch *et al.*, 2003).

The butterfly atlas by Benes *et al.* (2003b) maps individual species using the rectangular ('Central European', Ehrendorfer & Haman, 1965) grid, in which each grid cell spans 10' of longitude and 6' of latitude, i.e. 11.1 × 12 km in the country. The cells are thus approximately 30% larger than those used in the British atlas by Asher *et al.* (2001). There are 675 cells in the territory of the Czech Republic, 620 of which (91.8%) are covered in the atlas. The atlas database contains 151 451 species-distribution records on 161 resident, migrant, and extinct species, compiled by volunteer recorders or extracted from the literature and collections. It covers the entire 20th century (plus a few earlier records) divided into four time periods: pre 1950, 1951–80, 1981–94 and 1995–2001. We consider here only the latter three periods, since the pre 1950 data are disproportionately sparse (20 392 records) for its long time span.

We based the analysis on individual grid cells. Arithmetic means between maximum and minimum altitudes of each cell, as given in the LandSat database (Storch & Sizling, 2002), comprised the explanatory variable 'Altitude' (mean = 494 m, SD = 144 m, median = 475 m, min. = 115 m, max. = 1251 m). Since the altitude data were not available for borderline cells, we considered only the 624 cells that are entirely within the country. For this subset of cells, the data (records/cells, and mean altitude ± SD) were: 41984/479, and 494 ± 150.5 m for 1951–80 ('first period'); 58327/501, and 490 ± 148.9 m for 1981–94 ('second period'); and 30748/419, and 498 ± 157.6 m for 1995–2001 ('third period').

We restricted the analyses to resident (nonmigratory) butterflies, which were present in the country in each period tested in > 1 cell and were reported from a minimum of 20 (the U-tests) or 30 (the regressions) cells if summed across the periods. We thus excluded species with extremely narrow distribution, species that became extinct in the country, species that newly colonized the country, and the following long-distance migrants: *Aporia crataegi* (Linnaeus, 1758), *Colias crocea* (Fourcroy, 1785), *Pontia daplidice* (Linnaeus, 1758), *Vanessa atalanta* (Linnaeus, 1758), and *Vanessa cardui* (Linnaeus, 1758). In total, 117 (U-tests) and 119 (regressions) butterflies met the above criteria.

We used Mann–Whitney *U*-tests for all species to compare their present (1995–2001) altitudinal ranges with their ranges in the first period. Since uphill shifts could be caused either by a steady increase or by a U-shaped pattern (e.g. decrease in an interim period followed by increase at present), we also constructed linear regressions of altitudinal distributions of individual species against the three successive periods in order to assess whether at least some of the species had indeed increased steadily. We also used the regressions to compare frequencies of signs of regression coefficients, including the nonsignificant ones, to test whether increases prevailed over decreases.

A species may increase in altitude due to retractions of their lower range boundary accompanied by a stable upper boundary, expansion of the upper range boundary accompanied by a stable lower boundary, or a symmetrical increase. Since distinguishing the three patterns is complicated by outlying extreme values, we relied on the relative positions of lower and upper quartiles of past vs. recent distributions, taking the deliberate value of the quartile shift = 50 metres as ‘important’, and comparing how the positions of the quartiles changed.

In comparing habitat affiliations of individual species, we used the classification of habitats by Blab & Kudrna (1982) as modified by Benes *et al.* (2003b). It distinguishes xerophilous, mesophilous, hygrophilous, tyrophilous and ubiquitous butterflies. In referring to conservation status, we

distinguish ‘endangered’ vs. ‘safe’ species on the basis of percentage change in the number of occupied cells (the 2 periods after 1980 vs. all periods combined, endangered species were those that decreased by > 33.3% of cells). As to ‘mountain’ species, we refer to butterflies with a mean altitude of grid cells (computed across the three periods considered) > 600 m above sea level. The butterfly nomenclature follows Lastuvka (1998).

RESULTS

Between the periods 1951–80 and 1995–2001, increases in altitude prevailed over decreases among butterflies inhabiting the Czech Republic (binomial test of frequencies of signs of the *Z*-values of the Mann–Whitney *U*-tests, $n = 119$, 91 ascending, 26 descending, $P \ll 0.001$). Considering nominally significant *U*-tests, 15 species ascended and none descended in elevation (Table 1), which was highly unlikely to be due to chance (binomial test: $n = 117$; 15 ascending, 0 descending, $P \ll 0.001$). The mean and median of the significant shifts were 60 and 90 metres, respectively, with a maximum shift of 148 m in *Melitaea diamina*. To exclude the possibility that recording in the 2 periods was biased with respect to altitude, we tested altitudes of all cells containing records, taking cells as single data points. We did not find any significant bias (Mann–Whitney $U = 99847.0$, $Z = -0.13$, $P = 0.90$). Repeating the test with weighting the cells by integer-rounded \log_{10} of

Table 1 Mean altitudes, numbers of occupied grid cells per time period, and results of *U*-tests and linear regressions for all species of Czech butterflies that significantly increased in their altitude ranges in the second half of the 20th century

Species	Mean altitude (m)		Occupied cells in years			<i>U</i> -test <i>Z, P</i>	Linear regression (3 periods)			
	1951–80	1995–01	51–80	81–94	95–01		α	R^2	d.f.	<i>F, P</i>
<i>Heteropterus morpheus</i> (Pallas, 1771)	266	336	19	42	43	-2.18*	0.192	0.04	1101	3.9*
<i>Spialia sertorius</i> (Hoffmannsegg, 1804)	355	402	64	60	45	-1.95*	—	—	—	—
<i>Anthocharis cardamines</i> (Linnaeus, 1758)	458	497	238	366	238	-2.16*	0.074	0.01	1834	4.6*
<i>Gonepteryx rhamni</i> (Linnaeus, 1758)	479	510	270	387	274	-1.93*	—	—	—	—
<i>Limenitis camilla</i> (Linnaeus, 1764)	412	467	45	52	40	-2.28*	0.172	0.03	1135	4.1*
<i>Nymphalis antiopa</i> (Linnaeus, 1758)	485	525	247	345	213	-2.63*	0.071	0.01	1797	4.0*
<i>Araschnia levana</i> (Linnaeus, 1758)	455	485	259	373	256	-1.95*	—	—	—	—
<i>Melitaea diamina</i> (Lang, 1789)	597	745	76	59	33	-3.19**	0.258	0.07	1166	11.8***
<i>Erebia ligea</i> (Linnaeus, 1758)	663	735	102	109	33	-2.08*	0.136	0.02	1263	4.9*
<i>Arethusana arethusa</i> (Denn. & Schiff, 1775)	327	426	27	29	17	-2.23*	0.286	0.01	1,71	6.3*
<i>Lasiommata maera</i> (Linnaeus, 1758)	501	542	208	258	153	-2.57*	0.074	0.01	1834	4.6*
<i>Satyrium pruni</i> (Linnaeus, 1758)	357	404	97	125	78	-2.68**	0.132	0.02	1298	5.3*
<i>Lycaena hippothoe</i> (Linnaeus, 1761)	557	614	220	222	117	-2.71**	0.166	0.03	1552	15.6***
<i>Lycaena dispar</i> (Haworth, 1803)	320	376	47	77	70	-2.06*	0.153	0.02	1189	4.6*
<i>Cupido decoloratus</i> (Staudinger, 1886)	310	391	26	36	20	-2.16*	0.276	0.08	1,80	6.4*

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Table 2 Butterfly species that significantly increased towards higher altitudes in the Czech republic during the second half of the 20th century, according to patterns of the expansions and their conservation status and habitat association. The patterns were assessed on the basis of relative positions of lower/upper quartiles of their altitudinal ranges in the first (1950–80) vs. the third (1995–2001) period. Species that are underlined have recently expanded their ranges in terms of numbers of occupied grid squares

Pattern	'Safe' (= unlikely habitat loss)	'Endangered' (= likely habitat loss)	
Retracting lower, stable upper	<i>Nymphalis antiopa</i> <i>Gonepteryx rhamni</i> <i>Anthocharis cardamines</i>	M M M	
Stable lower, expanding upper	<i>Erebia ligea</i> <i>Lycaena hippothoe</i> <u><i>Lycaena dispar</i></u> <u><i>Heteropterus morpheus</i></u>	M, Mt M, Mt H X (H)*	<i>Limenitis camilla</i> M
Retracting lower, expanding upper	<i>Lasionympha maera</i> <i>Araschnia levana</i> <i>Satyrium pruni</i>	M, Mt M X	<i>Aretusana arethusa</i> <i>Cupido decoloratus</i> <i>Spialia sertorius</i> <i>Melitaea diamina</i> X, Mt

H, hygrophilous species; M, mesophilous species; X, xerophilous species; Mt, species with a mountain distribution. * Majority of populations inhabit xeric sites, but there are some hygrophilous populations in the western part of the country.

number of records per cell again gave a negative result ($U = 819258.5$, $Z = -0.52$, $P = 0.61$).

In the regressions of latitudes of occupied cells against the three periods (two as above plus the interim period 1980–95), positive slopes again prevailed over the negative ones ($N = 119$; 89 positive, 33 negative, $P << 0.001$). The regressions were nominally significant for 13 species, of which 12 increased significantly (Table 1) and one, *Coenonympha arcania* (Linnaeus, 1761), decreased ($\beta = -0.09$, d.f. = 1,539, $P < 0.01$). This was again unlikely to be due to chance ($n = 119$; 12 ascending, 1 descending, $P << 0.001$), and there was no significant signal of an elevational bias in recording (linear regression of altitudes of all cells against period, $F = 0.08$, d.f. = 1,1398, $P = 0.77$).

Since the 12 species that showed significant increases in the regressions formed a subset of the 15 species that showed increases in the U -tests (Table 1), the results were not in conflict. The species that showed significant increases in the U -tests were not straightforwardly associated with a particular habitat, with mountain or lowland distribution (Table 2), or with a conservation status (Fig. 1). All habitat affiliation categories except 'ubiquitous' were present among the ascending species (Table 2), and proportions of the categories among the ascending species did not differ from those among the nonascending

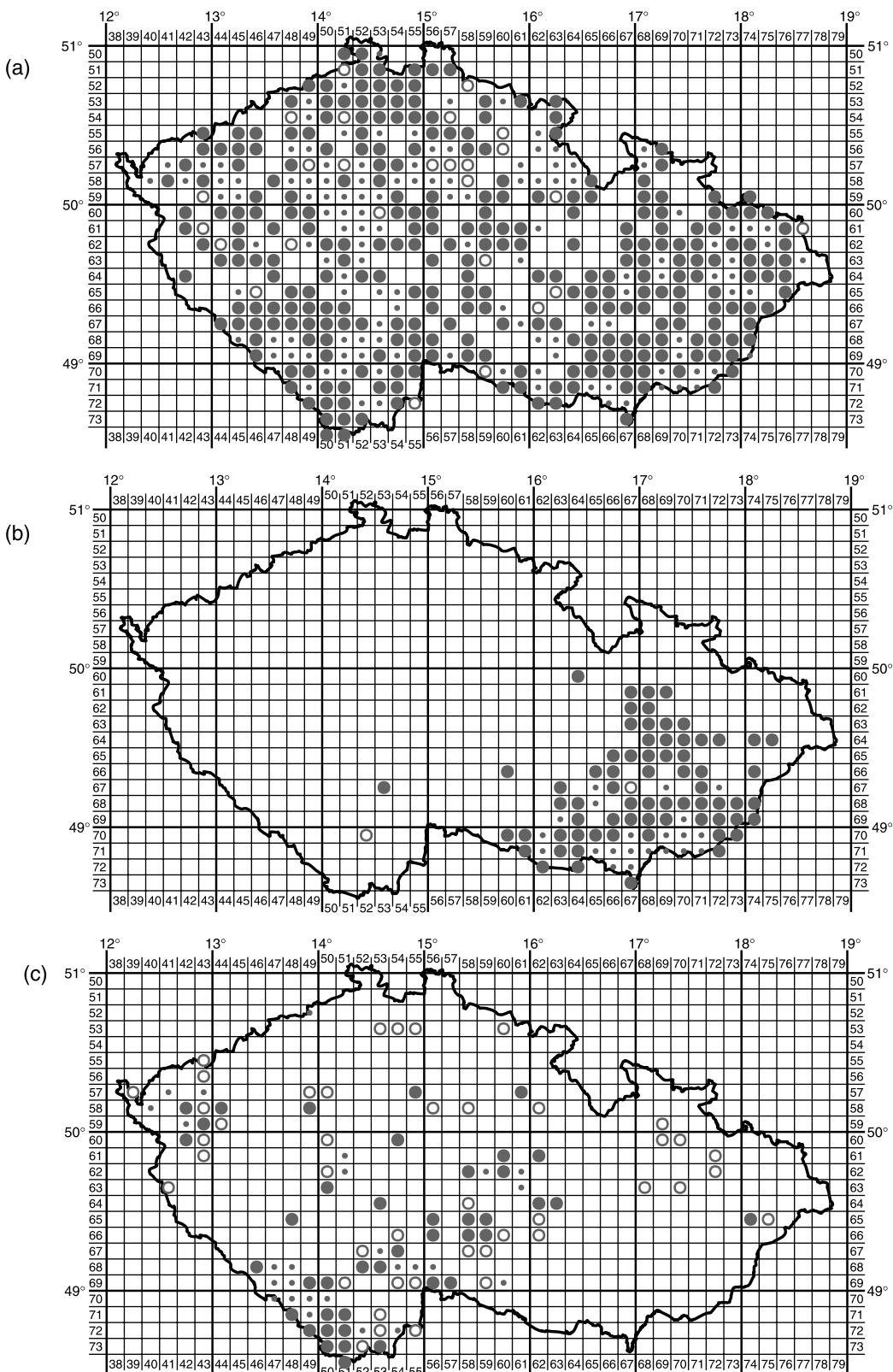
species ($\chi^2 = 5.54$, 3 d.f., $P = 0.14$). All of the three possible patterns of the increase in altitude (retraction from lowlands, expansion to highlands and symmetrical shift) were detected, but none of them prevailed. There was no obvious relationship between a habitat association and any of the three patterns, and even if xerophilous species prevailed among the butterflies showing a symmetrical shift, the difference was only marginally significant ($\chi^2 = 3.50$, 1 d.f., $P = 0.06$).

DISCUSSION

During the second half of the 20th century, 12–15 butterfly species (depending on method of analysis) ascended in elevation in the Czech Republic. The increases affected mountain and nonmountain species, endangered and safe species, and species associated with various habitats. To our knowledge, this is the first evidence that butterflies are ascending to higher elevations in mainland Europe and that the altitudinal pattern found by Hill *et al.* (2002) for Britain applies to other areas of the continent.

The analysis by Hill *et al.* (2002) compared altitudes of grid cells from which individual species disappeared with altitudes of cells where the situation remained unchanged and

Fig. 1 Examples of distribution maps for species that shifted their altitudinal distribution uphill in the Czech Republic during the second half of 20th century. Empty circles: species recorded in 1951–80 and not recorded after 1981. Full circles: species not recorded in 1951–80 and recorded after 1981. Small points: species recorded in both periods. (a) *Araschnia levana*. Mesophilous species that retracted at the lower boundary of its altitudinal range and expanded at the upper boundary. Not endangered. (b) *Lycaena dispar*. Hygrophilous species that has recently expanded northwards in the eastern part of the country. Stable lower and expanding upper altitudinal limits. Not endangered. (c) *Melitaea diamina*. Hygrophilous mountain species that retracted at the lower and expanded at the upper limits of its distribution. Endangered, likely due to habitat loss in lowlands. Note that mountain areas adjoin state borders in the Czech Republic, except for the south-east, which is flat and warm.



altitudes of cells that became colonized. We used a simpler approach based on comparison of mean altitudes per species and period, because the Czech data are less complete in terms of coverage of cells in individual periods. This precluded distinguishing between cells occupied in the past but not sampled in the present, and cells occupied in the past and vacant in the present. Our approach pointed to nominally significant increases in only a handful of species. Still, the increases overwhelmingly prevailed over the (almost none) descending species, suggesting that a considerable reassembly of the altitudinal distribution of the Czech butterfly fauna is underway.

The diverse habitat associations of the species that underwent nominally significant increases in altitude support the notion that the shifts were indeed caused by a warming climate. It is hard to postulate a causative factor other than climatic that would be so pervasive as to cause congruent altitudinal shifts in species of such diverse ecologies. The only alternative might be habitat loss, which is presumably more severe in densely populated and intensively farmed lowlands (Pysek *et al.*, 2002). This could have contributed to part of the pattern: for instance, the ascending butterflies *Arethusana arethusa*, *Cupido decoloratus*, *Sialia sertorius* are species of Mediterranean distribution inhabiting xeric barrens in Central Europe (Benes *et al.*, 2003a). For such species, one would expect that a warming climate should result in stable lower boundaries and increases of upper boundaries, rather than to the symmetrical shifts reported here. However, a symmetrical shift is exactly what could be expected if these species responded both to a warming climate, and at the same time suffered habitat loss in the lowlands.

The fact that two thirds of ascending butterflies are ‘safe’ from the conservation perspective actually excludes habitat loss as the *general* cause of the shifts in elevation. Even if habitat loss in the lowlands had caused some of the increases in endangered species, this was hardly so in such ‘safe’ species as *Nymphalis antiopa*, *Anthocharis cardamines* and *Gonepteryx rhamni*, which all inhabit mosaics of woods, meadows and fields, i.e. landscapes prevailing in the Czech Republic (Storch *et al.*, 2003).

We did not find any significant trend at all in a majority of the species tested. A conservative interpretation for these ‘stable’ species would be that of no changes occurring. However, there may be two other reasons behind the apparent lack of responses of species to a changing climate (Parmesan & Yohe, 2003). First, some species may indeed respond to climate, but not within the ranges of climatic variables considered. Second, the data may be too coarse, spatially or temporally, to reveal small responses. No changes within the range covered by the data likely apply to the ‘ubiquitous’ species, which invariably did not show any trends. Ubiquitous butterflies inhabit wide geographical ranges in Europe (Brandle *et al.*, 2002), which suggests broad tolerance to climatic conditions. Moreover, possible responses to climate could be masked by

relatively high mobility of these butterflies. Mobile species may respond instantaneously to any short-term (within years rather than within decades) climatic variation. Such responses were not detectable from our data, but there is an anecdotal observation (Kulfan *et al.*, 1997) that one such species, *Aglais urticae* (Linnaeus, 1758), had ‘disappeared’ from the lowlands of Central Europe for a brief period in the early 1990s only to ‘re-appear’ shortly thereafter. The butterfly remained common in mountainous regions for the entire period (Benes *et al.*, 2000), which agrees with a climatic cause of the event.

The coarse spatial scale of the data limited our ability to detect any trends in vertically diverse cells, i.e. those situated in mountains. For instance, the highest-altitude cell (maximum 1602 metres) has a minimum altitude of 900 metres and a vertical range 702 metres, whereas the mean range per cell was 250 ($SD = 127$) metres. Mountain butterflies are often restricted to a handful of cells in the Czech Republic, where they may inhabit narrower vertical ranges than those defined by ranges of the cells. Thus, the Mountain Ringlet *Erebia epiphron* (Knoch, 1783) inhabits 5 cells with mean = 1050 m, $SD = 118.9$ m and range 400–1602 m, but its actual lower limit is at 1050 m (Kuras *et al.*, 2001; Cizek *et al.*, 2003). We excluded this particular species from the analyses because it did not fulfil the condition of > 20 (30) cells in the 2 (3) periods combined, but its example points to the fact that our method was unsuitable for detecting shifts in vertically restricted alpine specialists. Hill *et al.* (2002) referred specifically to the Mountain Ringlet as a mountain species not occurring in Northern Europe, which is unlikely to colonize northern areas in the future, and thus is seriously threatened by the climate change.

It should be noted that some mountain butterflies may be restricted in distribution by closed canopy conditions in lower elevations rather than by climate itself (Roland *et al.*, 2000; Cizek *et al.*, 2003). Nevertheless, timberlines are already increasing in many regions (Sturm *et al.*, 2001; Grace *et al.*, 2002). On the other hand, a warmer period accompanied by an increasing mountain timberline occurred during the Atlantic period of the Holocene (e.g. Carcaillet & Brun, 2000; Ponel *et al.*, 2001). The alpine species occurring in ‘middle-high mountains’ of the temperate regions presumably survived the warm period at refuge sites where disturbances precluded canopy closure. It follows that the best available way to enhance their chances to survive the recent warming is discouraging afforestation above the recent timberline, and supporting the continuation of natural disturbance regimes instead.

Hill *et al.* (2002) observed that poleward and upward shifts were interrelated in Britain, where many butterflies reach their distribution limits in northern mountains. The Czech Republic has a more complicated geography (e.g. there are warm areas in the north-west) and such ‘planar’ patterns of distribution shifts may be less straightforward there. Still, northward shifts were recently observed in three of the vertically

ascending species — *Heteropterus morpheus*, *Lycaena dispar* and *Cupido decoloratus* (Benes *et al.*, 2003b). These butterflies reach local northern limits of their distribution in the Moravian Gate (Kudrna, 2002), a longitudinally orientated depression separating the Hercynian Mountains and the Carpathians. The area ascends uphill with increasing latitude, and the latitudinal shifts are thus inseparable from the altitudinal ones. The patterns of spread in these species notably agree with the spectacular northward expansion of the sulphur *Colias erate* (Esper, 1805), which underwent perhaps the most rapid recent distribution change of all European butterflies, colonizing most of Central Europe from the Balkans in less than 10 years (Stiova, 1991). The species arrived in the Czech Republic as late as the 1990s, and thus did not meet the criteria for our analysis. Still, congruent patterns of spread among all these species point to the importance of traditional areas of Holocene faunal migrations, such as the Moravian Gate, for movements of southern species under a warming climate. Restoration efforts aimed at counterbalancing habitat loss and facilitating movements to climatically favourable areas by the southern species that might decline in the south as the warming proceeds should focus on exactly such areas (Warren *et al.*, 2001).

To sum up, altitudinal changes in the distribution of Czech butterflies are already detectable at the coarse scales of standard distribution maps. Background knowledge of the ecology and conservation status of individual species allowed us to exclude habitat loss in lowlands as the main cause of the changes. On the other hand, the scale of the data did not allow detecting altitude changes in species that may be the most affected ones, be they mountain specialists, rapidly expanding southern species, or mobile species rapidly responding to short-term climatic variation.

ACKNOWLEDGMENTS

This study would not have been possible without hundreds of volunteers, who contributed their data for the Czech butterfly distribution atlas. We are obliged to V. Novotny and D. Storch for helpful discussions, and to two anonymous referees whose comments improved the quality of the manuscript. The work was funded by the Czech Ministry of Education (FRVS 1295/2002) and the Grant Agency of the Czech Academy of Sciences (B6007306/2003).

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