LETTER

Changes to the elevational limits and extent of species ranges associated with climate change

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Abstract

The first expected symptoms of a climate change-generated biodiversity crisis are range contractions and extinctions at lower elevational and latitudinal limits to species distributions. However, whilst range expansions at high elevations and latitudes have been widely documented, there has been surprisingly little evidence for contractions at warm margins. We show that lower elevational limits for 16 butterfly species in central Spain have risen on average by 212 m ($\pm$ SE 60) in 30 years, accompanying a 1.3 °C rise (equivalent to *c.* 225 m) in mean annual temperature. These elevational shifts signify an average reduction in habitable area by one-third, with losses of 50–80% projected for the coming century, given maintenance of the species thermal associations. The results suggest that many species have already suffered climate-mediated habitat losses that may threaten their long-term chances of survival.

Keywords

Conservation, elevational associations, extinction, Lepidoptera, range margins, range shifts, species distributions.

Ecology Letters (2005) **8**: 1138–1146

INTRODUCTION

Climate change is expected to force species distributions towards higher elevations and latitudes, leading to extinctions of species whose future habitable climate space becomes too small or too isolated from their current geographical ranges (Hill *et al.* 2002; Midgley *et al.* 2002; Williams *et al.* 2003; Thomas *et al.* 2004). However, whilst many species distributions have expanded at their cool, upper elevational and latitudinal margins in conjunction with recent warming (Grabherr *et al.* 1994; Parmesan 1996; Parmesan *et al.* 1999; Pounds *et al.* 1999; Thomas & Lennon 1999; Warren *et al.* 2001; Hill *et al.* 2002; Klanderud & Birks 2003; Konvicka *et al.* 2003; Parmesan & Yohe 2003), surprisingly few range contractions have been documented at warm, lower elevational and latitudinal limits (Parmesan *et al.* 1999; Thomas & Lennon 1999; Hill *et al.* 2002), perhaps because the locations of warm margins are determined by biotic interactions rather than climate *per se* (Davis *et al.* 1998; Loehle 1998; Pearson & Dawson 2003), or because the mechanisms that cause extinctions are not instantaneous (e.g. sporadic extreme climatic events; Pounds *et al.* 1999; Easterling *et al.* 2000; Parmesan *et al.* 2000; McLaughlin *et al.*

2002). Alternatively, spatial scales of recording or historical information may have been too imprecise to identify declines at lower latitudinal margins, particularly if species have shifted their regional distributions to higher elevations (Parmesan *et al.* 1999; Hill *et al.* 2002; Konvicka *et al.* 2003). Given that many taxa occupy spatially isolated mountainous regions at their warm margins (Stefanescu *et al.* 2004), such elevational shifts might have the capacity to mask range contractions, constraining species distributions to progressively smaller and less viable population networks until their entire regional persistence is threatened.

Here we document elevational shifts over the last 30 years in the butterfly fauna of the Sierra de Guadarrama (central Spain), a mountain range that represents the lower latitudinal or elevational boundary for many species of butterfly (Gómez de Aizpúrua 1987; Kudrna 2002; García-Barros *et al.* 2004). We propose that the elevational shifts are a response to regional warming, and quantify the effects of changing temperatures on the elevational associations and size of the species regional distributions. The results provide the clearest evidence for systematic, multi-species contractions at warm range margins in conjunction with recent climate change.
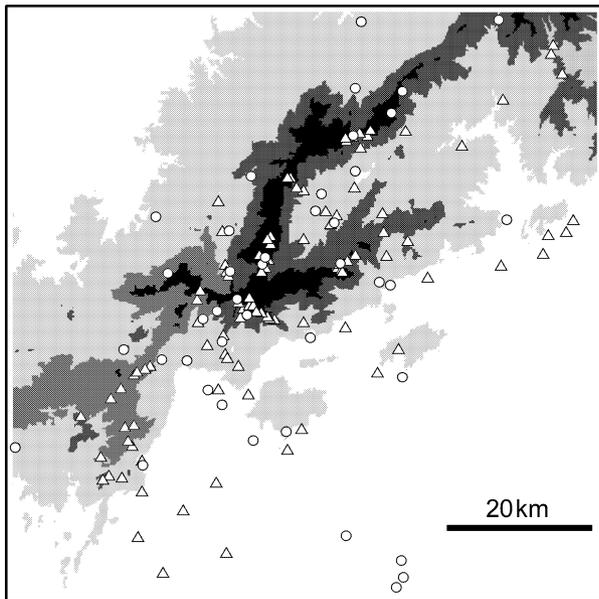
Figure 1 Map of the Sierra de Guadarrama, showing elevation and butterfly sample locations. Elevations (asl): white < 1000 m; pale grey 1000–1400 m; dark grey 1400–1800 m; black ≥ 1800 m. Sample locations: circles (1967–1973), triangles (2004).

MATERIALS AND METHODS

Study system

The Sierra de Guadarrama is a mountain range of *c.* 100 km, running from 40°30′N 4°20′W (UTM reference 30TUK8784) in the south-west to 41°10′N 3°30′W (UTM 30TVL5657) in the north-east. The range is bordered by plains with elevations of ≥ 535 m (to the south) and ≥ 700 m (to the north) (Fig. 1).

The elevational associations of butterfly populations were recorded in 1967–1973 and 2004. From 1967 to 1973, 66 sites with an elevational range of 620–2040 m above sea level were visited a total of 977 times (Monserrat 1976). In 2004, 100 locations (elevational range 640–2280 m) were visited 539 times in total. Survey sites were areas of grassland (pastures, woodland clearings and alpine meadows), stratified by elevation. In 1967–1973, all individuals of all species that were observed during each visit were recorded, but the number of visits to each site and the duration of visits varied. Study sites in 2004 were visited every 2 weeks between 16 May and 6 October (20 locations), or every 3 weeks between 25 May and 30 August (80 locations). In the 2004 survey, butterflies were counted on standardized 500 m transects (Pollard & Yates 1993) during suitable conditions for butterfly activity. Analysis includes all sites visited in 2004, and the 44 sites visited in 1967–1973 that contained no fewer than five species or

13 individuals, the minima recorded for individual sites visited in 2004. Mean distance between nearest neighbouring sites was 2.2 km ± SE 0.2 in 2004, compared with 6.2 ± 0.8 km for the 44 sites selected for 1967–1973.

Elevational associations were analysed for species with herbaceous or gramineous larval host plants (Tolman & Lewington 1997), and single annual flight periods with peak emergence between 27 May and 30 August 2004, determined by the 2-weekly transects. For 1967–1973 data, sites were only included in analysis if they were visited during the annual flight period for each species, in other words between the earliest and latest annual dates of observation for each species in 1967–1973. Species included were non-migratory (Pollard & Yates 1993; Cowley *et al.* 2001), but to avoid including vagrant individuals in analysis, species were considered 'present' only if two or more individuals were recorded at a site. Species were 'absent' if no individuals were recorded. Sites with one individual were excluded. Analysis was restricted to species that were present in ≥ 10% but ≤ 90% of locations.

Change in elevational associations

To determine elevational associations in each time period, binary logistic regressions (Norusis 1998) were carried out for presence/absence of each species against elevation (km) and elevation^2. Unimodal models that included a positive effect of elevation and a negative effect of elevation^2 were used to estimate an 'optimum altitude' with the highest probability of occupancy for each species.

To test the validity of results based on unimodal logistic regression models, species elevational distributions were also fitted to Huisman–Olff–Fresco (HOF) models (Huisman *et al.* 1993; Oksanen & Minchin 2002). HOF models allow testing of alternative responses to ecological gradients (skewed, symmetrical, plateau, monotone), using the model for probability of occupancy $(P) = 1/[1 + \exp (a + bx)] \{1/[1 + \exp (c-dx)]\}$, where the x variable was elevation, scaled between 0 (for the lowest elevation data point) and 1 (for the highest elevation data point). Potential HOF distribution models are: V) skewed, including parameters $a-d$; IV) symmetric, including parameters $a-c$, and parameter d = parameter b; III) plateau, including parameters $a-c$, parameter d = 0; II) monotone, including parameters $a-b$. Freely available software (Oksanen 1996) was used to fit HOF models for the probability of species occupancy against elevation. The software used a binomial error term and backwards-stepwise selection for the most parsimonious model for presence/absence that did not result in a significant change in deviance ($P < 0.05$).

To compare species lower and upper elevational limits between surveys, 2004 sampling locations were divided into 200 m elevational bands (600–799 and 800–999, etc.),

and 10 random sets of 44 locations were selected with the same number in each band as in 1967–1973. Change in minimum or maximum elevation for each species was the mean difference between 1967–1973 and the 10 random samples from 2004. Species that were recorded from the lowest elevation sites in 1967–1973 (620 m elevation) and the lowest elevation site in each random sample from 2004 (640 m elevation) were not considered to have increased their lower elevational limits.

Changes in elevational limits could be caused by changes in the status of species: expanding species might have colonized both higher and lower elevations than before; declining species might have disappeared from both high and low elevations (see Thomas & Lennon 1999; Hill *et al.* 2002). Thus, if most species were declining, lower elevational limits would be expected to increase irrespective of shifts in elevational associations. To control for these effects, we regressed change in minimum and maximum elevation against change in occupancy between surveys: the intercepts of these regressions indicate whether elevational limits have generally shifted, independent of changes in occupancy. Occupancy change was the proportion of locations occupied in 1967–1973, subtracted from the mean proportion occupied in the 10 random samples from 2004, divided by the proportion occupied in 1967–1973. For cross-species analyses of changes in elevational limits (or modelled habitable area, below) against occupancy change, we used the freely available software package COMPARE (Martins 2004) to run phylogenetic generalized least squares (GLS) regressions (Martins & Hansen 1997), with a butterfly phylogeny based on those presented in Harvey (1991) and Cowley *et al.* (2001).

Change in habitable area

A digital elevation model was obtained (NASA/JPL-Caltech 2004) for an 80×80 km square centred on the Sierra de Guadarrama (UTM co-ordinates SW corner 30TUK8575, NE corner 30TVL6555). The probability of occupancy for each species based on the elevation of each 100×100 m cell in the region was modelled in ArcView GIS (Environmental Systems Research Institute 1996) using the logistic regression or HOF models based on the species elevational associations in 1967–1973 and in 2004. Proportion change in area with modelled probability of occupancy ≥ 10, ≥ 20, and $\geq 50\%$ was calculated for each species as modelled area in 1967–1973, subtracted from area in 2004, divided by area in 1967–1973. In order to estimate the average change in habitable area between the two surveys, independent of changes in the proportion of locations where species were recorded (that could depend on changes in sampling intensity at different altitudes), change in modelled area was regressed against occupancy change between the surveys. Occupancy change was the proportion of locations occupied in 1967–1973,

subtracted from the proportion occupied in 2004, divided by the proportion occupied in 1967–1973.

Change in regional climate

We tested how climate had changed at meteorological stations in the Sierra de Guadarrama between the initial survey (1967–1973) and the same time period immediately preceding the 2004 survey (1997–2003). Meteorological stations were selected with complete records for 1967–1973 (13 temperature stations, 21 rainfall) or 1997–2003 (10 temperature stations, 11 rainfall). Mean annual temperature or rainfall were regressed against elevation (km).

Thermal associations of species ranges

The linear regressions of mean annual temperature against elevation for 1967–1973 and for 1997–2003 were used to model mean temperature at each butterfly sample location in each time period. Logistic regressions for presence/absence were repeated, substituting mean annual temperature for elevation. These logistic regression models were then used to predict the probability of occupancy of each butterfly at each sample site in each time period, based on the species' temperature associations in the other time period (i.e. thermal associations in 1967–1973 were used to predict distributions in 2004, and vice versa). For species whose temperature associations significantly predicted their distributions between the two time periods ($P < 0.05$ both predicting forwards from 1967–1973 and backwards from 2004), the regional area of climatically suitable habitat was then modelled, based on further increases in mean annual temperature of 1 °C (equivalent to mid-range projections for the mid-21st century, or minimum projections for the late 21st century) or 2 °C (equivalent to maximum projections for the mid-21st century, or mid-range projections for the late 21st century) (IPCC 2001). Habitable area was modelled in ArcView GIS as above, by converting elevation to modelled mean annual temperature using the equations: 2004 mean temperature $= 18.2$ °C $- 5.8 \times$ elevation (km); 2004 mean temperature $+1$ °C $= 19.2$ °C $- 5.8 \times$ elevation (km); 2004 mean temperature $+2$ °C $= 20.2$ °C $- 5.8 \times$ elevation (km) (see Results, Change in regional climate).

RESULTS

Abundance and species richness

The 1967–1973 survey recorded 16 698 individuals of 112 butterfly species, and the 2004 survey recorded 30 253 individuals of 98 species (in addition to three genera that were not identified to species level in 2004). The difference in species richness between the two surveys was partly related

to the absence of six spring-flying species from the 2004 survey, that have been observed in the study area during April/May of 2003 and 2005. Apart from these six springtime species, 10 species were observed in 1967–1973 but not in 2004, all of them very rare (29 individuals in total); two species were observed in 2004 but not in 1967–1973.

The median number of species observed per site in the first survey (30) was marginally greater than that in the second survey (25) (Mann–Whitney U-test, $n_1 = 44$, $n_2 = 100$, $U = 1714$, $P = 0.035$). However, for the 23 grassland species whose elevational associations are analysed in detail (see below), there was no change in site species richness between the two surveys (median 1967–1973 = 7, median 2004 = 8; $U = 2021$, $P = 0.44$).

Overall, relative rarity or commonness was consistent between the surveys. For species that were observed in two or more sample locations in both surveys the total number of sites occupied in 1967–1973 was significantly related to that in 2004 (Spearman's rank correlation, $n = 88$, $r_S = 0.38$, $P < 0.001$). Results were consistent using species abundance (total number of individuals observed), or dividing study sites into 400 m elevational intervals. Relative commonness of the 23 focal species in 1967–1973 was not significantly related to that in 2004 (for total number of sites occupied, $r_S = 19$, $P = 0.38$). However, the ranked correlation for all elevations for the 23 focal species masks significant correlations ($P < 0.05$) at every 400 m elevational interval apart from 1400 to 1800 m, where the relative number of sites occupied by species changed markedly between surveys ($r_S = -0.06$, $P = 0.79$).

Change in elevational associations

Twenty-five species satisfied the criteria for analysis, of which 23 had significant logistic regressions ($P < 0.05$) in both time periods for probability of occupancy against elevation and elevation[2] (see Table S1 in Supplementary Material). Seven of these species are widespread in central Spain and were found in the lowest 200 m elevational band (600–799 m), whereas 16 of the species have regional distributions that are restricted to higher elevations (Gómez de Aizpúrua 1987; García-Barros et al. 2004).

Of the 46 significant logistic regression models, 43 included a positive effect of elevation and a negative effect of elevation[2], producing unimodal curves for probability of occupancy against elevation, with an 'optimum elevation' where the species had the highest probability of occupancy (Fig. 2a,b). For the 19 species whose optima in both time periods fell within the available elevational range (> 600 and < 2400 m), mean change in optimum elevation from 1967–1973 to 2004 was +119 m (± SE 61), with a significantly larger number of species showing increases (14) than decreases (five) (Wilcoxon test, $Z = -1.97$, $P < 0.05$).

When the elevational distributions of the same 23 species were fitted to HOF models, 24 of the 46 best-fitting models were symmetric and unimodal, nine were skewed, four were

Figure 2 Probability of occupancy at different elevations for the butterfly *Satyrus actaea* Esper. (a and b) Histograms of probability of occupancy in 200 m intervals (bars), and probability of occupancy (P) modelled using logistic regression (curve) in (a) 1967–1973 [logit $P = -25.30 + 34.20$ elevation (km) $- 10.86$ (elevation)^2] and (b) 2004 [logit $P = -61.69 + 66.12$ elevation (km) $- 17.12$ (elevation)^2]. Crosses show 'optimum' elevations with highest modelled probability of occupancy. Number of samples per 200 m interval shown above each bar. In (a), dashed line denotes proportion of all four sites sampled above 1800 m. (c and d) Distributions of suitable elevations based on equations in (a) and (b) respectively, for (c) 1967–1973 and (d) 2004. Black ≥ 50% probability of occupancy; dark grey ≥ 20%; pale grey ≥ 10%; white < 10%. Sample locations: triangles (occupied), circles (vacant).
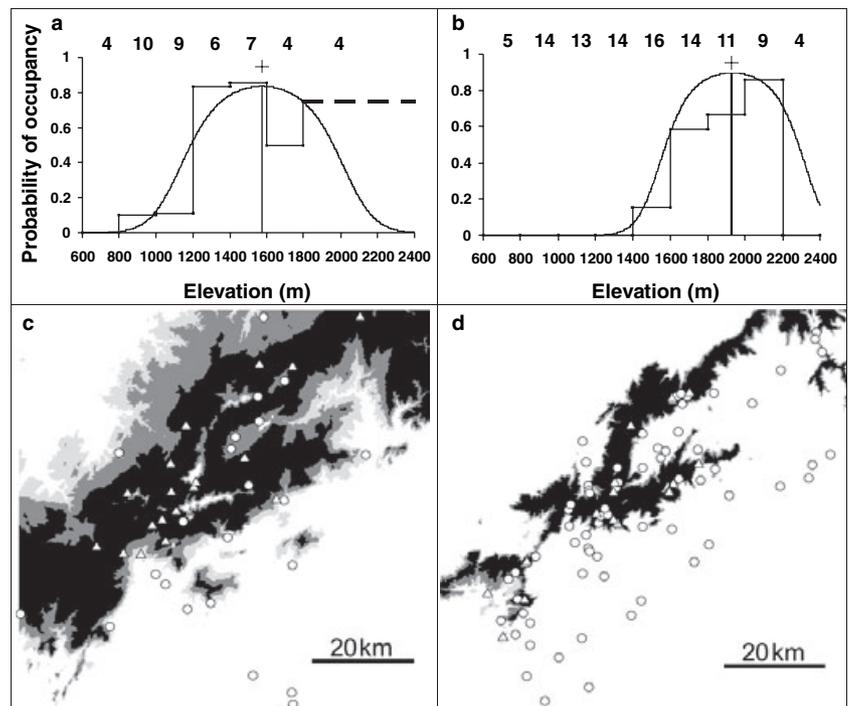
plateau and nine monotone (Table S2). For the 13 species whose HOF-modelled optima fell within the available range in both surveys, mean change was + 189 m ($\pm$ SE 57), with significantly more increases (nine) than decreases (four) ($Z = -2.48$, $P < 0.05$). Using the unimodal logistic regression models to calculate change in optimum elevation just for these 13 species (that had unimodal HOF models in both periods) gave a mean change of +203 m ($\pm$ SE 49).

Comparison of the 1967–1973 distributions with the randomly re-sampled 2004 data showed that the lower elevational limit had increased for 17 species and decreased for six (mean change +134 m $\pm$ SE 48; Wilcoxon test, $Z = -2.46$, $P < 0.05$). There was no significant change in upper elevational limit (12 increases, 11 decreases, mean change +64 m $\pm$ SE 59; $Z = -0.79$, $P = 0.43$). In general, species occupancy did not decline between the two surveys, with 11 species showing increases and 12 showing declines. Separating species into those found below 800 m and those that were restricted to higher elevations did not detect significant changes in occupancy in either group (Wilcoxon tests for occupancy in 1967–1973 versus re-sampled 2004 data: low elevation species, two declines, five increases, $Z = -1.18$, $P = 0.24$; high elevation species, 10 declines, six increases, $Z = -0.08$, $P = 0.94$). However, species varied widely in changes in their level of occupancy (maximum decline −0.84; maximum increase +2.49), potentially influencing the changes observed to elevational ranges.

For the 16 species that were restricted to high elevations in both surveys (> 800 m), the regression of change in lower elevational limits against change in occupancy between surveys was significant, with a significant intercept of 212 m [$R^2 = 0.39$, Ln likelihood = −89.86; $P = 0.013$; change (m) = 212 m ($\pm$ SE 60; $P = 0.003$) − 159 ($\pm$ SE 53; $P = 0.009$) × occupancy change] (Fig. 3a). Minimum elevations had not changed significantly for the seven species that occupied the lowest elevational band (600–799 m). Upper elevations had not changed significantly for either group of species (Fig. 3b; Table S3). These results remained consistent if one high-elevation species whose distribution size had increased greatly (*Hyponephele lycaon* Kühn) was removed from analysis (Fig. 3, Table S3).

Change in habitable area

The models relating species distributions to elevation were used to calculate the area of the landscape that exceeded 10, 20 and 50% probabilities of occupancy in each time period (Fig. 2c,d). Based on a 20% threshold probability of occupancy from logistic regression modelling, suitable area for 11 of the 16 high-elevation species had declined (mean proportional change = −0.22 $\pm$ SE 0.11; Wilcoxon test, $Z = -2.17$, $P < 0.05$). The regression of change in modelled suitable area against change in occupancy for the
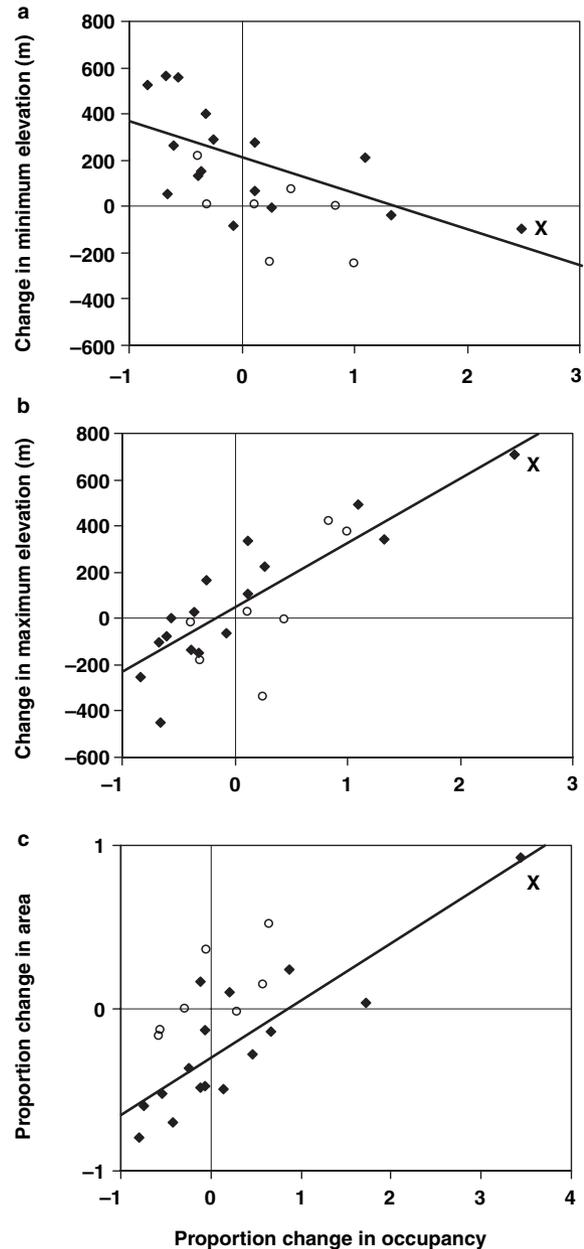

Figure 3 Changes in elevational associations and modelled habitat availability against occupancy change between 1967–1973 and 2004. (a) Change in lower elevational limit (m); (b) Change in upper elevational limit (m); (c) Proportion change in area with ≥ 20% modelled probability of occupancy. Species not found below 800 m: solid symbols, regression lines. Species found below 800 m: open symbols, regressions not significant. Full data set used to calculate occupancy change in (c), re-sampled data used in (a) and (b). X indicates one outlying species with a greatly increased distribution size.

16 high-elevation species had a significant intercept of −0.34 [Fig. 2c; $R^2 = 0.76$, Ln likelihood = 17.12, $P < 0.001$, Change in area = −0.34 ($\pm$ SE 0.09; $P = 0.002$) + 0.35

($\pm$ SE 0.05; $P < 0.001$) $\times$ occupancy change], signifying that species that still occupied the same proportion of sample locations had suffered a reduction of 34% in habitable area. Change in area with $\geq$ 10% probability of occupancy decreased by 32–37% (based on logistic regression and HOF models, respectively), while area with $\geq$ 50% probability of occupancy decreased by 46–50% (Table S3).

Change in regional climate

Annual mean temperature decreased by *c*. 6 °C per 1000 m elevational increase in each period, but annual mean temperatures in 1967–1973 were 1.3 °C cooler than 30 years later, based on the intercepts of linear regressions of temperature against elevation (Table 1a, Fig. 4). The increase of 1.3 °C indicated a *c*. 225 m rise in the locations of sites with comparable thermal microclimates (based on a decrease in temperature of 5.8 or 5.9 °C per 1000 m increase in elevation). Changes in temperature between the two periods remained consistent if data from the highest altitude station were excluded.

Mean annual rainfall increased with elevation, but did not change significantly between the two periods (Table 1b).

Thermal associations of species ranges

For the 16 high-elevation species, models predicting distributions either forwards (using 1967–1973 temperature associations to predict 2004 distributions) or backwards (using 2004 temperature associations to predict 1967–1973 distributions) were significant ($P < 0.05$) for 15 species (Table S4). Changes to the distribution of only one species (*Coenonympha arcania* Linnaeus) were unable to be predicted by temperature associations. Using the significant relationships of these 15 species ranges with mean annual

Figure 4 Annual mean temperature against elevation for 1967–1973 (open symbols, thick line) and 1997–2003 (solid symbols, thin line). Symbols represent meteorological stations in the Sierra de Guadarrama. Error bars show 1 standard deviation in annual mean.

temperature to model the extent of habitable area given a further increase of 1 °C in mean annual temperature (2.3 °C relative to 1967–1973) led to 50–70% declines relative to 1967–1973; an increase of 2 °C (3.3 °C relative to 1967–1973) led to 70–80% declines (Table 2).

DISCUSSION

Change in elevational associations

Over 30 years of regional warming there were pronounced upward shifts in the elevational ranges of the butterflies of the Sierra de Guadarrama. For most of the 23 species of grassland butterfly studied, the optimum elevation (with the highest modelled probability of occupancy) increased from 1967–1973 to 2004, with average increases of 120–200 m, depending on the type of model used to relate occupancy to elevation, and the number of species for which the models detected an elevation with a peak probability of occupancy. Increases in optimum elevation appeared to result from extinctions at low elevations rather than colonizations at high elevations. The lowest elevation at which species were observed increased between the surveys for 17 of the 23 species. For the 16 species that were restricted to high elevations in both surveys (i.e. species at their 'warm' range margins), the increase in lower elevational limits appeared to be independent of overall changes in occupancy: a regression of change in lower elevational limit against change in occupancy between the surveys suggested that lower elevational limits for these species had increased by 212 m (Fig. 3a). On the other hand, upper elevational limits only increased for 12 of the 23 species, and change in upper

Table 1 Linear regressions of (a) annual mean temperature (°C) and (b) annual rainfall (mm) against elevation (km) for 1967–1973 and 1997–2003

	R^2	N*	F	B_0†	$\pm$ SE	B_1‡	$\pm$ SE
(a) Temperature (°C)							
1967–1973	0.93	13	155.7***	16.9	0.5	−5.9	0.5
1997–2003	0.94	10	132.6***	18.2	0.5	−5.8	0.5
(b) Rainfall (mm)							
1967–1973	0.91	21	180.4***	−32.9	53.2	766.7	57.1
1997–2003	0.94	11	140.1***	16.3	53.5	683.2	57.7

*Number of meteorological stations.
†Units correspond to units of temperature or rainfall.
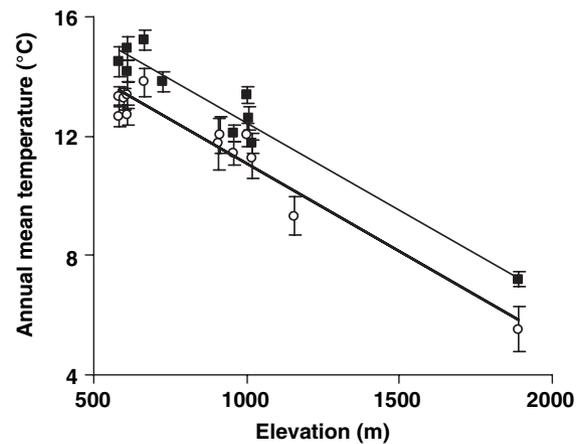‡Annual temperature or rainfall $= B_0 + B_1 \times$ elevation (km).
***$P < 0.001$.

Temperature increase (°C)	Temperature associations	Modelled proportion decline per habitat threshold (mean ± SE)		
		≥ 10%	≥ 20%	≥ 50%
1.3	1967–1973	0.45 (± 0.03)	0.46 (± 0.03)	0.50 (± 0.02)
1.3	2004*	0.23 (± 0.12)	0.25 (± 0.11)	0.29 (± 0.18)
2.3	1967–1973	0.65 (± 0.02)	0.66 (± 0.02)	0.71 (± 0.02)
2.3	2004	0.49 (± 0.09)	0.50 (± 0.09)	0.51 (± 0.13)
3.3	1967–1973	0.79 (± 0.02)	0.81 (± 0.02)	0.86 (± 0.02)
3.3	2004	0.69 (± 0.06)	0.70 (± 0.06)	0.72 (± 0.08)

Table 2 Projected declines in habitat availability relative to 1967–1973, based on the temperature associations of 15 high elevation species in 1967–1973 and 2004. Models use area of landscape with ≥ 10, ≥ 20 and ≥ 50% probability of occupancy for each species, given temperature increases of 1.3, 2.3 and 3.3 °C relative to 1967–1973

*For 2004 associations, values for 1.3 °C increase show observed mean decline in area.

elevational limit was not significant when controlling for the effects of changes in occupancy (Fig. 3b).

Two sources of evidence suggest that the patterns observed reflect genuine changes in distribution rather than inter-annual variation in abundance or temporary uphill dispersal associated with weather conditions. First, to test for changes in observed distributions between successive years, we calculated lower and upper elevational limits separately for 1970 and 1971, using the 18 sites which had distribution data from both years: the 23 study species showed minor and non-significant changes in elevational range limits [lower limits, mean change (± SE) = −17 ± 42 m; upper limits, mean change = −23 ± 32 m], even though temperature varied by 0.6 °C between the successive years (regressions of mean annual temperature against elevation had intercepts of 17.1 and 16.5 °C for 1970 and 1971, respectively). Second, the 120–200 m shifts in minimum and optimum elevations represent 3–5 km shifts in geographic location, based on an elevational gradient of *c.* 40 m per 1 km in the Sierra de Guadarrama. The non-migratory butterflies studied typically move less than a few hundred metres in their lifetime (Pollard & Yates 1993), so the changes almost certainly reflect genuine shifts in distributions to higher elevations, rather than temporary annual dispersal. Whilst making this point it is worth noting that the changes in distributional limits of 3–5 km would be unlikely to be detected at the kind of scales used for regional or national distribution mapping (e.g. 10 km, Warren *et al.* 2001; García-Barros *et al.* 2004).

Causes for elevational range shifts

The apparently systematic elevational range shifts suggest a wide-acting and consistent explanatory factor, such as climate. The magnitude of increase in lower elevational limits between the surveys (212 m for the 16 high-elevation species) was similar to that expected based on change in mean annual temperature (+1.3 °C *c.* 225 m increase). Furthermore, the thermal associations for 15 of the high-elevation species in 1967–1973 significantly predicted their distributions in 2004 (based on temperatures in 1997–2003), and vice versa.

Nevertheless, the close fit between changing temperatures and changing distributions is not sufficient to demonstrate causation. In some parts of their ranges, despite apparent climatic amelioration, species have declined because of habitat loss caused by land-use changes (Warren *et al.* 2001; Hill *et al.* 2002). In the Sierra de Guadarrama, direct anthropogenic influences on the landscape are likely to have been stronger at low elevations, making it difficult to disentangle the effects of land-use and climate on species distributions. But several sources of evidence point to climate being a more important explanatory factor. The elevational shifts were widespread among a sample of species with ubiquitous larval host plants (Tolman & Lewington 1997), for which large areas of otherwise suitable habitat remain at all elevations (Ministerio de Medio Ambiente 2003). Several of the species that are restricted to high elevations (e.g. *Argynnis adippe* Denis & Schiffermüller, *A. aglaja* Linnaeus, *A. paphia* Linnaeus, *Lycaena alciphron* Rottemburg, *L. virgaureae* Linnaeus) have congeneric species (*A. pandora* Denis & Schiffermüller, *L. phlaeas* Linnaeus) that use the same larval host plants and are common at all elevations, suggesting that the distribution patterns of the localized species are related to their own physiological tolerances or to interactions with the physiological condition of habitat or host plants. At a regional scale, mean annual temperature may capture sufficient variation in annual heat stress or moisture availability to be relatively closely related to the location of the 'warm' range margins of the species. In contrast, the lack of significant upward shifts in higher elevational limits may be related to more specific factors such as extreme winter temperatures (Bale *et al.* 2002; Sinclair *et al.* 2003).

Implications for species distributions and persistence

Even though levels of occupancy for the study species did not change significantly between 1967–1973 and 2004, the elevational shifts in species distributions signify a substantial

reduction in potentially suitable area for the 16 high-elevation species. When species elevational associations were used to model regional habitat availability in the two time periods, habitable area had declined on average by 22%. The intercept of −0.34 from the regression of change in habitable area against change in occupancy implied that species that still occupied the same proportion of sample locations had suffered a reduction of 34% in habitable area, simply because of the smaller area of the landscape at progressively higher elevations.

The significant relationships of 15 high-elevation species distributions with mean annual temperature allowed us to model their likely distribution sizes given projections of climatic warming for the coming century (IPCC 2001). Relatively conservative further increases of 1 °C and 2 °C respectively led to 50–70% and 70–80% declines in modelled habitable area relative to 1967–1973 (Table 2). The Sierra de Guadarrama is bordered to both north and south by lower elevation plains, preventing the northward migration of species range margins, so the projected habitat declines would almost certainly presage regional extinction for many of the species concerned, and for other montane fauna and flora.

Conclusion

Elevational shifts by species at their warm margins may prevent the identification of geographic-scale range contractions caused by climate change (Parmesan et al. 1999; Hill et al. 2002). Despite continuing high levels of occupancy by many species at their warm margins in the Sierra de Guadarrama, species distributions have shifted to higher elevations, implying a reduction in habitable area by one-third in only 30 years. These declines in habitable area might themselves be underestimates if there is a time-lag in extinctions from sites that are outside the long-term climatic tolerances of the species (Hill et al. 2002). The regional habitat losses of 50–80% predicted for the next century, given maintenance of the species climatic associations and continued regional warming, will probably be exacerbated by direct habitat loss through changes in land-use (Warren et al. 2001; Stefanescu et al. 2004). The magnitude of these declines in available habitat may be typical for species that are restricted to high elevations at their warm range margins (Stefanescu et al. 2004), or for endemic taxa that are entirely restricted to mountainous regions (Pounds et al. 1999; Williams et al. 2003). Given the spatial isolation of suitable high elevations for these taxa, and their consequent inability to colonize new areas as the climate warms (Grabherr et al. 1994; Pounds et al. 1999; Midgley et al. 2002; Klanderud & Birks 2003; Konvicka et al. 2003; Williams et al. 2003), the results forewarn of widespread extinctions unless climate change and habitat loss can be arrested.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article from http://www.Blackwell-Synergy.com:

Table S1 Logistic regression equations relating butterfly species occupancy to elevation.

Table S2 Huisman–Olff–Fresco models relating butterfly species occupancy to elevation.

Table S3 Phylogenetic regressions of change in elevational limits and modelled habitable area against occupancy change.

Table S4 Tests of models using temperature associations in 1967–1973 to predict distributions in 2004, and vice versa.