

Impacts of climate warming and habitat loss on extinctions at species' low-latitude range boundaries

ALDINA M. A. FRANCO*, JANE K. HILL*, CLAUDIA KITSCHKE*,
YVONNE C. COLLINGHAM†, DAVID B. ROY‡, RICHARD FOX§,
BRIAN HUNTLEY† and CHRIS D. THOMAS*

*Department of Biology (Area 18), University of York, PO Box 373, York YO10 5YW, UK, †School of Biological & Biomedical Sciences, Institute of Ecosystem Sciences, University of Durham, Durham DH1 3LE, UK, ‡NERC Centre for Ecology and Hydrology, Monks Wood, Abbots Ripton, Huntingdon, Cambridgeshire PE28 2LS, UK, §Butterfly Conservation, Manor Yard, East Lulworth, Dorset BH20 5QP, UK

Abstract

Polewards expansions of species' distributions have been attributed to climate warming, but evidence for climate-driven local extinctions at warm (low latitude/elevation) boundaries is equivocal. We surveyed the four species of butterflies that reach their southern limits in Britain. We visited 421 sites where the species had been recorded previously to determine whether recent extinctions were primarily due to climate or habitat changes. *Coenonympha tullia* had become extinct at 52% of study sites and all losses were associated with habitat degradation. *Aricia artaxerxes* was extinct from 50% of sites, with approximately one-third to half of extinctions associated with climate-related factors and the remainder with habitat loss. For *Erebia aethiops* (extinct from 24% of sites), approximately a quarter of the extinctions were associated with habitat and three-quarters with climate. For *Erebia epiphron*, extinctions (37% of sites) were attributed mainly to climate with almost no habitat effects. For the three species affected by climate, range boundaries retracted 70–100 km northwards (*A. artaxerxes*, *E. aethiops*) and 130–150 m uphill (*E. epiphron*) in the sample of sites analysed. These shifts are consistent with estimated latitudinal and elevational temperature shifts of 88 km northwards and 98 m uphill over the 19-year study period. These results suggest that the southern/warm range margins of some species are as sensitive to climate change as are northern/cool margins. Our data indicate that climate warming has been of comparable importance to habitat loss in driving local extinctions of northern species over the past few decades; future climate warming is likely to jeopardize the long-term survival of many northern and mountain species.

Keywords: butterfly, climate-change, extinctions, habitat loss, low-latitude, range boundary

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Introduction

Widespread evidence of polewards and uphill distribution shifts suggests that many species, from many taxonomic groups, are responding to climate change (Parmesan, 1996; Parmesan *et al.*, 1999; Thomas & Lennon, 1999; Hill *et al.*, 2002; Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2003; Hickling

et al., 2005, 2006; Perry *et al.*, 2005; Wilson *et al.*, 2005). The global mean temperature has risen 0.6 °C over the last 100 years (IPCC, 2001) and the 1990s was the warmest decade since records began in the 1600s (Hulme *et al.*, 2002). By the 2080s, average annual temperatures across the United Kingdom may rise by 3.5 °C (Hulme *et al.*, 2002), suggesting that future distribution changes are likely to dwarf those already seen.

While there is now considerable evidence that species are colonizing high latitudes and/or elevations in association with climate warming, there is far less evidence

Correspondence: Aldina M. A. Franco, tel. +44 1904 328643; fax +44 1904 328605, e-mail: amaf1@york.ac.uk

that they are retreating at their low latitude/elevation range margins (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Root *et al.*, 2005). If species are not going extinct at the low-latitude and/or low elevation margins of their distributions, where the climate would be predicted to be less suitable for their survival, then climate change may be not as great a threat to biodiversity as has been predicted (Thomas *et al.*, 2004). For example, the apparent discrepancy between responses of low- and high-latitude range boundaries could be due to low-latitude boundaries being limited by species interactions, rather than being limited directly by climate (Davis *et al.*, 1998). If, however, climate is important at low-latitude range margins (Parmesan, 1996; Hill *et al.*, 2002; Julliard *et al.*, 2004; Wilson *et al.*, 2005), then the lack of evidence for recent climate-driven extinctions may be due to scaling effects (colonizations may be easier to detect than extinctions at relatively coarse spatial scales), difficulty in recording absences (it is much easier to detect a new occurrence than to prove absence definitively) or to time lags between environmental deterioration and local extinction. In addition, good quality data sets describing distribution changes at low-latitude range margins are scarce, and studies in these regions are lacking (cf., Wilson *et al.*, 2005). There are difficulties, however, in distinguishing between extinctions due to climate change and those due to habitat change; a species that spreads northwards (in the northern hemisphere) across an otherwise deteriorating landscape is almost certain to be responding to climate warming, but a northern species that declines at its southern boundary could equally be responding to habitat loss or to climate change.

To tackle this issue, we surveyed the four northern species of butterfly that occur in Britain. We focused on butterflies because they have excellent long-term and fine-scale distribution data, because butterflies are known to be sensitive to climate changes (Warren *et al.*, 2001), and because information on species' habitat preferences are well understood. In 2004 and 2005, we revisited sites (1 km grid resolution) where the species had been recorded between 1970 and 1999, and examined habitat conditions, as well as climate-related variables that could be associated with species' distribution changes. We evaluated whether habitat loss or climate warming was likely to be responsible for patterns of extinction. In order to do this, (i) we examined whether extinctions were due to loss of breeding habitat; (ii) for the subset of sites where habitat remained, we investigated whether distribution changes were associated with latitude, elevation, climate suitability or habitat suitability (host-plant occupancy and abundance, and sward height), and (iii) we quantified southern range boundary shifts in relation to temperature changes.

Methods

Study species

We surveyed all four species of butterfly that have northern/montane distributions and reach a warm, southern and/or low elevation distributional limit in Britain. The four study species were three species of Satyrinae (large heath *Coenonympha tullia*; mountain ringlet *Erebia epiphron*; scotch argus *Erebia aethiops*) and one lycaenid species (northern brown argus *Aricia artaxerxes*). The taxonomy of *A. artaxerxes* is under debate making it difficult to designate populations in northern England as either *A. artaxerxes* or *A. agestis* (Asher *et al.*, 2001), so we consider that all univoltine *Aricia* populations in Britain were *A. artaxerxes*. The host-plants surveyed were *Eriophorum vaginatum*, *Nardus stricta* and *Helianthemum nummularium* for *C. tullia*, *E. epiphron* and *A. artaxerxes*, respectively. *E. aethiops* has two main host-plants; populations in Scotland are known to use *Molinia caerulea* and populations in Northern England (Cumbria) use *Sesleria caerulea* (Asher *et al.*, 2001) so we surveyed these two main host-plants.

Field surveys

The study sites for new field surveys were selected from butterfly data collated by Butterfly Conservation (a UK nongovernmental organization) and the UK Biological Records Centre. These data comprise two comprehensive surveys of butterfly distributions in Britain, corresponding with the publication of two atlases (Heath *et al.*, 1984; Asher *et al.*, 2001). For each northern butterfly species, we selected 120 sites to resurvey from northern England or Scotland that had been recorded in either of these two time periods. Distribution data for northern species are not as extensive as for other butterflies and so, in order to survey a sufficient number of sites across all species, half of the sites selected for each species had records only from the first atlas survey (1970–1982) and the other half were sites from the second atlas survey (1995–1999). Sites were included only if the earlier record was at a fine spatial resolution (1 km grid resolution or better). In order to ensure equal sampling of sites from a wide range of climatic conditions, a logistic regression was carried out to fit each species' distribution (including records from the two atlases) to elevation (at 1 km resolution) and climate variables (at 10 km resolution). We included in the regression model mean temperature of coldest month, day degrees accumulated above 5 °C, and moisture availability for the period 1970–1999, using mean values for each 10-km grid square (interpolated surface for the United Kingdom obtained from Hulme *et al.*, 1995).

The sites we surveyed for each species spanned the full range of species' probability of occurrence from the regression model.

Sites were surveyed during the butterflies' flight periods between June and August 2004 and 2005. The surveys were carried out during each species' flight period only in good weather and when the temperature was above 13 °C, following recommendations for Butterfly Monitoring Scheme surveys (Pollard & Yates, 1993). In order to maximize the number of sites visited during the flight period, only sites at <4 km from a road were surveyed in 2004. However, this greatly limited the number of sites visited for *E. epiphron* and so, in 2005, the remaining sites for this species were surveyed, regardless of distance from a road. Each 1 km study site was surveyed once for the presence of butterflies and suitable habitat/host-plants for one person-hour. In order to determine the reliability of our methods for recording absences, we resampled a subset of sites ($N = 30$) more intensively (based on an exhaustive survey, with no time limitation) where butterflies had not been recorded in our first visit. In only four of these sites were the butterflies found on the second visit, indicating that our sampling protocol was robust (see Discussion). At all sites, the number of 100 m grid squares visited within each site during the survey was recorded (using a GPS), and the presence of butterflies and host-plants within each 100 m square was recorded. At each site where host-plants were recorded, we selected two nonadjacent 100 m squares where the species was recorded and measured host-plant presence and sward height at 40 points every 5 m along a zigzag transect through each square (80 points in total per site). Although study sites were selected only if the earlier record had been at a grid resolution of 1 km or better, in approximately 70% of sites, the species had been recorded previously at a finer spatial resolution (usually 100 m). In order not to bias results in favour of grid squares with better-quality information, the recorder was not aware of the exact 100 m location of butterfly records (when they existed) at the start of the survey. In the event that the target species was not found during the one hour survey, the recorder checked if the 100 m grid cell with the species' record had been visited (when this information was available), if not, this location was surveyed for an additional 15 min.

Distribution data from the second atlas (Asher *et al.*, 2001) also include information on butterfly abundance at study sites. Information is coded into five abundance categories; 1, 2–9, 10–29, 30–99 and >100 individuals counted on a single visit. We used this information to evaluate if recorded absences in 2004/2005 were more likely to be from sites where small numbers of individuals had been recorded previously (e.g. sites that held

only small populations or where single vagrant individuals had been recorded).

Analysis of patterns/causes of extinction

We investigated distribution changes in relation to habitat and climate. All sites resurveyed in 2004/2005 had at least one previous record of the study species, so we assumed that suitable breeding habitat had been present previously. For each site, we determined whether or not there were currently any host-plants present. If no host-plant was found, the absence of butterflies was attributed to complete loss of habitat. For each butterfly species, we estimated the number of extinctions due to complete habitat loss as the percentage of former sites that lacked host-plants during 2004/2005.

We then focussed on those sites with host-plants present in 2004/2005, and used stepwise logistic regressions to determine the presence or absence of each of the four butterfly species in relation to three habitat and three climate factors: (i) occupancy of host-plant(s) in each 1 km site (measured as the proportion of 100 m cells with host-plants, subsequently termed 'occupancy'), (ii) average abundance of host-plant(s) (based on percentage of cover obtained from a transect sample of 80 points in two 100 m squares), (iii) mean height of the vegetation (from the 80 transect points), (iv) elevation (data from Countryside Information System, 1 km resolution), (v) latitude (1 km resolution) and (vi) probability of occurrence of each species according to climate response surface (CRS) models (10 km resolution data). Details for fitting CRS models have been explained more fully elsewhere (Hill *et al.*, 1999), here, we will focus on the modifications we made. We fitted European distribution data for each species (Kudrna, 2002) to four bioclimate variables (0.5° resolution grid) calculated for the period 1961–1990 (New *et al.*, 1999), corresponding to the period when the European distribution records were collected. The bioclimatic variables used were: (i) mean temperature of the coldest month (MTCO; a correlate of over-wintering survival), (ii) day degrees accumulated above 5 °C (GDD5; a measure of the period for larval development), (iii) moisture availability as measured by the ratio of actual and potential evapotranspiration (AET/PET; predominantly an index of larval host-plant quality) and (iv) total sunshine hours between 7 and 17 °C (PSUN; a measure of the potential for butterfly activity at low temperatures, Bryant *et al.*, 2002). For three species where CRS models were good fits to species distributions in both continental Europe and Britain ($AUC > 0.7$), we used the models to predict climate suitability in Britain at a 10 km grid resolution. Because

of the poor fit of the CRS model for *E. epiphron* in Britain (AUC = 0.37), measures of climate suitability were not included in analyses of this species. Vegetation height was log transformed and all proportion values were arcsine transformed before analysis. We investigated both forward and backward stepwise logistic regressions: all variables with $P < 0.05$ according to the log-likelihood ratio test were retained/included in the regressions (Hosmer & Lemeshow, 2000) and we included all significant interaction terms into the regression models.

Rates of range shift

Shifts in each species' southern range boundary and lower elevation limit between 1970–1999 and 2004–2005 were quantified for those sites where host-plants were present in 2004/2005, for the species for which climate factors affected distribution changes (see Results). For each species, we compared (i) the difference in latitude and elevation of sites where butterflies were recorded present in 2004/2005 vs. those sites where the butterfly went extinct, and (ii) the difference in the mean elevation and latitude of the 10 most southerly/lowest elevation sites between the two time periods. Distribution shifts were analysed using Mann–Whitney *U*-tests. To estimate how the temperature changed from 1970 to 2004, we determined the slope of the regression line fitted to temperature data from seven weather stations that covered the distributions of the four species, from Northern England and Scotland. We looked at changes in the mean yearly maximum and minimum temperatures during March to September (months when the immature stages and adult butterflies are active/developing). The slope of the regression line which fitted temperature data to year was used to determine the annual temperature change from 1970 to 2004.

Results

Extinctions due to habitat loss

We visited 421 sites where the species had been recorded previously (111 sites for *A. artaxerxes*, 85 for *C. tullia*, 89 for *E. epiphron* and 136 for *E. aethiops*). Our estimates of rates of extinction over the 30-year study period were high and ranged from 24% of study sites extinct for *E. aethiops* to 52% for *C. tullia* (Table 1). Habitat loss was apparently responsible for just over half of all local extinctions of *A. artaxerxes* and *C. tullia*, for which 25% and 28% of their previous sites, respectively, no longer had host-plants present. Loss of the habitat was less important for *E. epiphron* where only one site no longer had its host-plant (Table 1). For

E. aethiops, we estimated that 7% of populations were likely to have become extinct associated with the loss of host-plants (Table 1). However, this estimate should be interpreted with caution because we only surveyed the two main host-plants, *Molinia caerulea* and *Sesleria caerulea*, and there is evidence that other grasses may also be used, particularly towards the core of its range (Asher *et al.*, 2001; Kirkland, 2005). This was confirmed by our study, during which we recorded *E. aethiops* present in 19 sites (18% of sites where the species was recorded) where neither of the two main host-plants was present. This meant that if *E. aethiops* was absent from a square that lacked *Molinia caerulea* and *Sesleria caerulea*, it was not possible to attribute extinction unambiguously to habitat loss, because an alternative host-plant might still be present.

We used abundance from Asher *et al.* (2001) to test whether extinctions were more likely from sites that historically had the lowest butterfly abundance. There was no significant difference in past population size between extinct and occupied sites for any species (*A. artaxerxes* $\chi^2 = 2.24$, $df = 3$, $P = 0.52$; *C. tullia* $\chi^2 = 2.50$, $df = 3$, $P = 0.47$; *E. aethiops* $\chi^2 = 2.63$, $df = 3$, $P = 0.45$; *E. epiphron* $\chi^2 = 2.33$, $df = 3$, $P = 0.51$), indicating that extinctions occurred in sites containing large as well as small populations.

Patterns of extinction in sites with breeding habitat

Hereafter, we consider only those sites where the main host-plants were still present in 2004–2005 and investigated extinction patterns in locations where at least some breeding habitat remained. This analysis included 83 sites for *A. artaxerxes*, 61 for *C. tullia*, 88 for *E. epiphron* and 102 for *E. aethiops* (Table 1). In these sites, *E. epiphron* had disappeared from 36% of sites, *A. artaxerxes* and *C. tullia* from approximately 24% of sites, and *E. aethiops* was no longer found in 18% of the sites that still contained *Molinia caerulea* and/or *Sesleria caerulea* (Table 1).

Stepwise logistic regression correctly predicted the presence or absence of *C. tullia* at 70.1% of sites, and indicated that this species was more likely to have survived in sites where the host-plant was widespread (Table 2). Note that host-plant occupancy was the only significant variable in the stepwise multivariate analyses ($g(x) = -0.178 + 1.883 \times \text{host-plant occupancy}$; $G = 5.261$, $P = 0.022$; where $g(x)$ is the logit of survival, no other variables were included in the model at $P < 0.05$). This model fits the data quite well according to the Hosmer–Lemeshow goodness-of-fit statistic ($\chi^2 = 3.720$, $df = 8$, $P = 0.882$). Larval host-plant occupancy was not related to survival in the other three species.

Table 1 Total sites surveyed per species, presences recorded, overall extinction and extinctions associated with complete habitat loss

Species	1 km sites surveyed (host-plants present)*	Butterfly presences*	Overall extinction (%)	Extinctions due to host-plant extirpation (%)
<i>Aricia artaxerxes</i>	111 (83)	56	49.5	25.2
<i>Erebia aethiops</i>	136 (102)	103	24.3	6.6 [†]
<i>Erebia epiphron</i>	89 (88)	56	37.1	1.1
<i>Coenonympha tullia</i>	85 (61)	41	51.8	28.2

*Number of sites.

[†]For *E. aethiops*, the estimate of extinction due to host-plant loss assumes that the percentage extinction associated with climate change is the same in sites with and without the two main host-plants present: i.e. climate-driven extinction = 17.6% (Table 2) \Rightarrow 24 out of 33 extinctions due to climate, leaving nine due to habitat loss = 6.6%.

Table 2 Patterns of butterfly extinction/survival in sites where host-plants were present

Species	N	Percentage of extinctions	Habitat variables			Climate-related variables		
			Host-plant(s) occupancy (1 km)	Host-plant(s) abundance (100 m)	Vegetation height (cm)	Elevation (m)	Latitude (km)	CRS (1970–1999)
<i>Aricia artaxerxes</i>	83	24.3	0.927 (0.295)	−0.977 (0.527)	5.866 (0.001)	−0.002 (0.245)	0.005 (0.004)	5.378 (0.022)
<i>Erebia aethiops</i>	102	17.6	0.427 (0.535)	−0.353 (0.645)	3.292 (0.063)	0.004 (0.060)	0.008 (0.001)	1.730 (0.260)
<i>Erebia epiphron</i>	88	35.9	1.203 (0.060)	3.614 (0.010)	−0.123 (0.950)	0.007 (0.001)	−0.001 (0.799)	na
<i>Coenonympha tullia</i>	61	23.5	1.883 (0.035)	1.266 (0.192)	−2.697 (0.171)	−0.003 (0.083)	−0.002 (0.219)	2.537 (0.117)

Values are the coefficients of the slopes of the relationship between butterfly survival and each variable, based on univariate analyses (with the associated probability value in brackets). Butterfly absences were coded as 0 and presences as 1, such that positive coefficients indicate higher probability of survival in relation to the independent variable. Significant relationships retained in stepwise logistic regressions are shown in bold. CRS, index of climate suitability for the species based on output from climate response surface models. No useful CRS model was developed for *E. epiphron*, so this variable was not included in analyses.

A. artaxerxes was more likely to have survived in areas where the vegetation was taller, at high latitude sites, and also in areas of high climate suitability (Table 2; $g(x) = -7.269 + 4.852 \times \text{vegetation height} + 0.006 \times \text{latitude} + 7.959 \times \text{CRS}$ model; $G = 10.775$, $P = 0.001$; $G = 9.176$, $P = 0.002$ and $G = 8.016$, $P = 0.005$, respectively). This model classified 81% of the sites correctly and fitted the data well ($\chi^2 = 6.608$, $df = 8$, $P = 0.579$).

The multiple regression model correctly predicted the presence and absence of *E. aethiops* at 85.3% of sites, indicating that this species was more likely to have survived at high latitudes ($g(x) = -4.317 + 0.008 \times \text{latitude}$; $G = 11.683$, $P = 0.001$). The model fits the data well ($\chi^2 = 9.452$, $df = 8$, $P = 0.306$).

E. epiphron was more likely to survive at high elevations ($g(x) = -2.962 + 0.006 \times \text{elevation}$; $G = 15.025$, $P < 0.001$); the model classified 77.2% of sites correctly and had a good fit ($\chi^2 = 12.355$, $df = 8$, $P = 0.206$).

No significant interaction terms were retained in the final multivariate models for any of the four species.

For *A. artaxerxes*, the multivariate model included both habitat (vegetation height; itself related to microclimate) and climate-related factors; the relative importance of each variable included in the model was estimated using the results of the G test, indicating that habitat was potentially responsible for 37% of the effects explained by the multiple logistic model (i.e., of the 24.3% of extinctions observed in Table 2, we regard 9.0% as associated with vegetation height, and the remainder 15.3% with climate-related variables). Figure 1 illustrates the patterns of extinctions in relation to latitude and elevation, for those three species that showed a significant response to climate-related variables.

Extent of range shifts

We considered only those sites that contained host-plants in 2004/2005 to estimate the distance over which ranges had shifted between the original distribution and our 2004/2005 survey. Our estimates were broadly

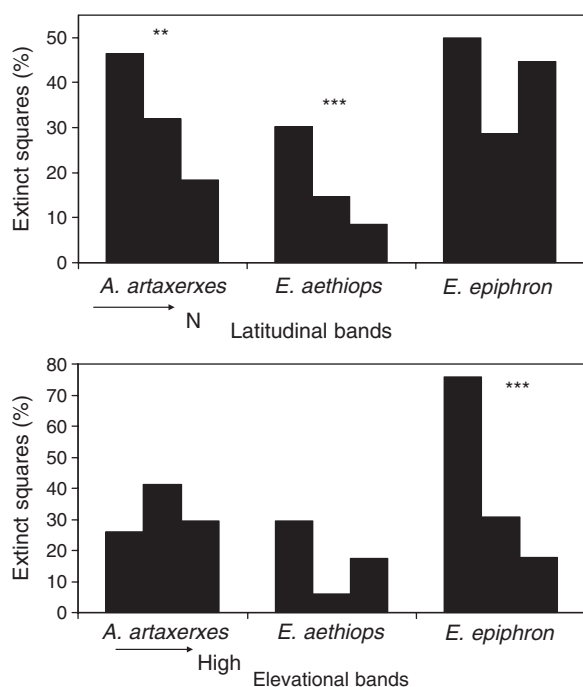


Fig. 1 Percentages of extinct sites, at different latitudes and elevations, for the three northern species of butterflies whose distribution changes were associated with climate-related variables. Each latitudinal band corresponds to one third of the latitude and elevation data for each species. Species marked with ** $P < 0.01$ and *** $P < 0.001$ showed significant shifts in relation to latitude or elevation (see Table 2).

similar regardless of whether we calculated the shift in mean elevation/latitude over time, or the shift in the 10 lowest elevation/latitudinal sites over time (Table 3). We excluded *C. tullia* from these calculations as we had no evidence that climate factors were responsible for any distribution changes. Depending on the method of calculation, we estimated that *E. aethiops* moved 80–92 km northwards, *A. artaxerxes* moved 73–106 km northwards, and *E. epiphron* shifted approximately 132–149 m uphill during the study period. There was some suggestion that *E. aethiops* also shifted uphill but this requires confirmation as elevation shifts were significant for only one of the estimation methods (analysing the 10 marginal squares; Table 3) and elevation was not significant in the logistic regression analysis (Table 2).

Over the study period, the average temperature increased by $0.031^{\circ}\text{C}/\text{yr}^{-1}$ (Fig. 2). In Europe, an increase of 0.8°C corresponds to a northwards shift in isotherms of approximately 120 km (Watson *et al.*, 1998). Thus, an increase in temperature of $0.031^{\circ}\text{C}/\text{yr}^{-1}$ corresponds to a predicted average range shift of $4.7\text{ km}/\text{yr}^{-1}$ (i.e. 88.4 km in 19 years the mean time period between the mid-points of the two earlier time periods, 1970–1982

Table 3 Range shifts in latitude (km) and elevation (m) from 1970–1999 to 2004–2005 for the three species whose distribution changes were related to climate factors

	Extinct vs. occupied sites	10 squares at the distribution edge
Latitude shift (km)		
<i>Aricia artaxerxes</i>	106.4 (0.002)	73.4 (0.001)
<i>Erebia aethiops</i>	95.3 (0.023)	80.3 (<0.001)
<i>Erebia epiphron</i>	6.3 (ns)	2.7 (ns)
Elevation shift (m)		
<i>A. artaxerxes</i>	−35.2 (ns)	1.8 (ns)
<i>E. aethiops</i>	57.8 (ns)	26.9 (0.001)
<i>E. epiphron</i>	132.2 (<0.001)	149.3 (<0.001)

Results are based on two methods: (i) comparison of mean value of extinct vs. occupied sites, (ii) comparison of the 10 lowest elevation/latitude sites. Values in brackets show the significance of range shifts from Mann–Whitney *U*-tests. Only sites where host-plants were present in 2004/2005 were included in analyses.

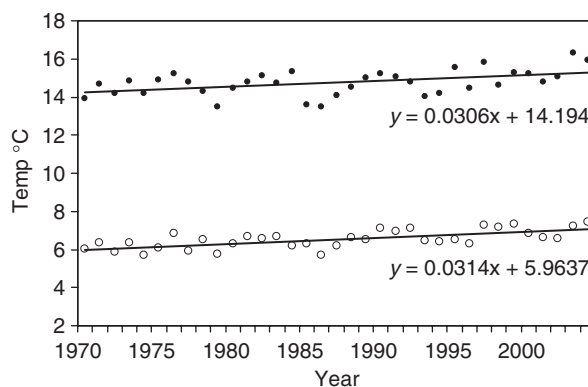


Fig. 2 Time trend of average annual maximum (solid circles) and minimum (open circles) temperature from March to September during the study period from 1970 to 2004. Data were obtained from seven weather stations across Northern England and Scotland.

and 1995–1999, and 2004/2005). Similar calculations were made for shifts in elevation; in this case we considered a lapse rate (rate of change in temperature with elevation) of $0.6^{\circ}\text{C}/100\text{ m}^{-1}$ increase in elevation (Pepin *et al.*, 1999; Metoffice, 2005). Using this figure, we would expect species to move uphill by an average of $5.17\text{ m}/\text{yr}^{-1}$, corresponding to 98.2 m in 19 years.

Discussion

Extinction in relation to habitat loss

Habitat loss was implicated in most (*C. tullia*) and some (*A. artaxerxes*, *E. aethiops*) local extinctions for three of

the four northern butterfly species. In 25–28% of the sites surveyed for *A. artaxerxes* and *C. tullia*, there was no suitable habitat remaining. After excluding sites with no host-plants, *C. tullia* was also more likely to have gone extinct in sites with low occupancy of host-plants (Table 2), confirming the over-riding importance of habitat availability for this species. For *A. artaxerxes*, half of the extinctions were associated with complete habitat loss (Table 1), and further extinctions could be attributed to vegetation height on sites where the host-plant survived (Table 2). However, this component of the extinction is difficult to interpret, in part because we do not know whether the vegetation height has changed at these sites. High maximum temperatures are associated with short vegetation (Thomas, 1983; Thomas *et al.*, 1999), so the species might have gone extinct from sites with short vegetation because it has become too hot, or alternatively because some other factor associated with vegetation height affected population survival.

For *E. aethiops*, it was difficult to quantify habitat loss because this species is polyphagous and was occasionally found in sites where neither of the main host-plants was present. Recent observations of nocturnal larvae (Kirkland, 2005) revealed that they feed on a variety of grasses and sedges, not just the two main grass species listed in field guides; in 18% ($N = 19$) of sites where *E. aethiops* was present in our surveys, none of the main host-plants was found. Assuming that sites without the main host-plants are no more or less susceptible to climate-related extinction than are sites containing the two major host-plants, we estimated that approximately 7% of sites may have gone extinct due to habitat loss (Table 1). To derive this value, we first calculated that 17.6% of extinctions were associated with climate; (i.e. the percentage extinction at sites where the main host-plants remained present) (Table 2). We then assumed that this 17.6% figure can be applied to all sites, such that 24 sites would have been expected to become extinct due to climate-related factors, leaving 9 sites (7% of sites) where the species is likely to have become extinct due to habitat loss. Further work is required to identify the degree to which extinctions can be attributed to habitat loss in this species. In only one species (*E. epiphron*) did we find little evidence for any habitat-driven local extinction, and the host-plant was found in all but one of the sites visited for this species.

The main causes of habitat loss at study sites were related to intensification of agriculture, particularly the improvement of pastures (for *A. artaxerxes*) and land drainage (for *C. tullia*). Our surveys indicated that the loss of host-plants occurred predominantly at lower latitudes and elevations where agricultural intensification has been greatest (Wilson *et al.*, 1991; Pain *et al.*,

1997; Pain & Pienkowski, 1997), and where climate change effects on upland species might be expected to be discernable first.

Evidence for climate-driven extinctions

Once we had taken account of the presence and abundance of host-plants, butterfly distribution changes were still found to be related to climate factors for three of the four species. Our data show that *A. artaxerxes* went extinct from sites at low latitudes and from less climatically-suitable sites (according to the CRS model). *E. aethiops* was also less likely to have survived at low latitudes and possibly also at low elevation sites. *E. epiphron*, the only true montane butterfly in Britain, went extinct disproportionately from low elevation sites. The distribution changes in these three species are consistent with climate change predictions. For *C. tullia*, in contrast, extinctions were associated with habitat availability alone; this butterfly might decline in the longer term if its wetland habitats are eventually altered by climate change, but, after excluding the effect of habitat loss, we did not detect any direct effect of climate change on its British distribution.

These extinction patterns are consistent with a response to climate change, but other processes could potentially generate the patterns we observed without there being any systematic distribution shift. For example, extinctions are more likely to be recorded where vagrant individuals have been recorded historically, and metapopulation theory predicts that small populations are more likely to go extinct (Hanski & Thomas, 1994). In addition, small populations are more likely to be located in relatively unfavourable areas at the edge of the range, and may thereby be more extinction-prone. However, we found no tendency for extinctions to have been restricted to sites where only small populations had been recorded in the past, suggesting that we have detected genuine distribution shifts and not simply the consequences of local population dynamics. In addition, an independent landscape survey carried out for *E. epiphron* in Cumbria in 2005 indicated that some populations have gone extinct at a landscape scale (Clarke, 2005), corroborating the results we obtained based on 1 km sample sites.

Our survey represented a standardized census, rather than an exhaustive search, so it is likely that some of the absences recorded would not have been true local extinctions. This source of error was assessed by re-visiting 30 sites that had previously been visited for 1 h and where the host-plants were present but the species was not detected. The data from the second survey indicated that our 'standard' surveys failed to detect species that were actually present in four of these sites.

Assuming that there was no error in our recording of extinctions in sites which no longer supported any host-plants (presences are also correctly determined), this suggests an overall error rate of approximately 2% (or about two errors per species). Thus, we believe that our overall conclusions are robust. Results from our study, carried out at a fine spatial-scale resolution and allowing for habitat effects, provide evidence of recent climate-driven range retraction for three out of four northern species.

In this study, we deliberately attempted to distinguish habitat loss and/or deterioration from climate change effects, and we conclude that the two have been of comparable importance over the past 35 years (averaged across all four species). However, these two effects can be linked. Climate change could be responsible for habitat deterioration, for example, if increased drought were to cause a decline in host-plant quality or abundance. Similarly, any form of habitat degradation that reduces population size might be expected to make populations more susceptible to extinction from new climatic extremes. Disentangling further the relative contributions of different pressures will require more detailed study. Extinctions will often be driven by climate change and other threats acting in concert (Pounds *et al.*, 2006).

Quantifying range shifts

Spring–summer temperatures increased by 1–1.5 °C from 1976 to 1998 according to the Central England Temperature records (Roy & Sparks, 2000). Following a similar approach, we determined that the average temperature increase for Northern England and Scotland was 0.031 °C yr⁻¹ from 1970 to 2004 (Fig. 2). This translates into predicted northwards range shifts of approximately 4.7 km yr⁻¹, and uphill shifts of 5.2 m yr⁻¹. Our data suggest that *A. artaxerxes* shifted northwards by 73–106 km (Table 2) in 19 years, corresponding with a shift of 3.8–5.6 km yr⁻¹. *E. aethiops* moved on average 80–90 km northwards, corresponding with shifts of 4.2–4.7 km yr⁻¹. The observed range shifts are comparable with those expected if these species were shifting their distributions at the same rate as climate change. *E. epiphron*, the mountain ringlet, moved approximately 130–150 m uphill in 19 years, a value slightly higher than that expected (98.2 m). Of course, the conversion of temperature change to distance moved is an approximation. For example, we used a lapse rate of 0.6 °C 100 m⁻¹ as a mean value, but lapse rates can vary between 0.5 and 0.98 °C 100 m⁻¹ in wet or dry conditions, respectively (Metoffice, 2005). Using this range of values would have given expected distribution shifts of

81.8 to 160.4 m uphill, which incorporates the observed shift of *E. epiphron*.

Conservation implications

Our data indicate that both specialist (*A. artaxerxes* and *E. epiphron*) and generalist (*E. aethiops*) species are retreating at approximately the rate that would be expected, given the 0.6 °C rise in temperature that occurred between field surveys. Similar findings have also been recorded for other montane species; the lower elevation limits of 16 species of butterflies in Spain have also retreated uphill in parallel with temperature increases (Wilson *et al.*, 2005). Recent studies have shown that climate-driven range expansions at high-latitude northern range boundaries are confined to generalist species and that specialists are failing to expand northwards because of the loss and fragmentation of their breeding habitats (Warren *et al.*, 2001). This study shows that climate-driven range retractions are affecting specialist, as well as generalist northern species, and thus recent climate warming may be beginning to cause systematic reductions in the range sizes of specialist species.

For the four northern species we studied, climate change already seems to have caused as much extinction as habitat loss. As impacts of climate change are expected to accelerate in future, but habitat loss decline in Britain, we would expect climate change to become the dominant cause of extinction for many northern and/or montane species in the future.

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