between 270 and 4,000 ms after target onset) and to ignore changes in the distractor. Failure to respond within a reaction-time window, responding to a change in the distractor or deviating the gaze (monitored with a scleral search coil) by more than 1° from the fixation point caused the trial to be aborted without reward. The change in the target and distractors was selected so as to be challenging for the animal. In experiments 1 and 2 the animal correctly completed, on average, 79% of the trials, broke fixation in 11%, might have responded to the distractor stimulus in 6% and responded too early or not at all in 5% of the trials. In Experiment 3 the corresponding values are 78, 13%, 8% and 2%. In none of the three experiments was there a difference between the performances for the two possible targets. Differences between average eye positions during trials where one or the other stimulus was the target were very small, with only an average shift of 0.02° in the direction of the shift of position between the stimuli. Only correctly completed trials were considered. Firing rates were determined by computing the average neuronal response across trials for 1,000 ms starting 200 ms after the beginning of the target stimulus movement.

Tuning curves. Tuning curves were derived by fitting the responses to the 12 directions presented with gaussian functions: $r_{null} + dirGain \times \exp^{(-0.5*(dir - prefdir)^2/width^2)}$. The four parameters of a gaussian curve capture the four features of a direction-selective cell: preferred direction ($prefdir$), response to the anti-preferred direction (r_{null}), the directional gain ($dirGain$; the maximal response modulation) and the selectivity or tuning width ($width$; the range of directions the neuron responds to).

1. Moran, J. & Desimone, R. Selective attention gates visual processing in the extrastriate cortex. *Science* **229,** 782–784 (1985).
2. Motter, B. C. Focal attention produces spatially selective processing in visual cortical areas V1, V2, and V4 in the presence of competing stimuli. *J. Neurophysiol.* **70,** 909–919 (1993).
3. Treue, S. & Maunsell, J. H. R. Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature* **382,** 539–541 (1996).
4. Luck, S. J., Chelazzi, L., Hillyard, S. A. & Desimone, R. Neural mechanisms of spatial selective attention in areas V1, V2, and V4 of macaque visual cortex. *J. Neurophysiol.* **77,** 24–42 (1997).
5. Newsome, W. T., Wurtz, R. H., Dürsteler, M. R. & Mikami, A. Deficits in visual motion processing following ibotenic acid lesions of the middle temporal visual area of the macaque monkey. *J. Neurosci.* **5,** 825–840 (1985).
6. Newsome, W. T. & Paré, E. B. A selective impairment of motion perception following lesions of the middle temporal visual area (MT). *J. Neurosci.* **8,** 2201–2211 (1988).
7. Britten, K. H., Newsome, W. T., Shadlen, M. N., Celebrini, S. & Movshon, J. A. A relationship between behavioral choice and the visual responses of neurons in macaque MT. *Vis. Neurosci.* **13,** 87–100 (1996).
8. Snowden, R. J., Treue, S. & Andersen, R. A. The response of neurons in areas V1 and MT of the alert rhesus monkey to moving random dot patterns. *Exp. Brain Res.* **88,** 389–400 (1992).
9. McAdams, C. J. & Maunsell, J. H. R. Effects of attention on orientation tuning functions of single neurons in macaque cortical area V4. *J. Neurosci.* **19,** 431–441 (1999).
10. Spitzer, H., Desimone, R. & Moran, J. Increased attention enhances both behavioral and neuronal performance. *Science* **240,** 338–340 (1988).
11. Lankheet, M. J. M. & Verstraten, F. A. J. Attentional modulation of adaptation to two-component transparent motion. *Vision Res.* **35,** 1401–1412 (1995).
12. Duncan, J. & Nimmo-Smith, I. Objects and attributes in divided attention: Surface and boundary systems. *Percept. Psychophys.* **58,** 1076–1084 (1996).
13. Valdes-Sosa, M., Bobes, M. A., Rodriguez, V. & Pinilla, T. Switching attention without shifting the spotlight: Object-based attentional modulation of brain potentials. *J. Cogn. Neurosci.* **10,** 137–151 (1998).
14. Reynolds, J. H. & Desimone, R. Attention and contrast have similar effects on competitive interactions in macaque area V4. *Soc. Neurosci. Abstr.* **23,** 302 (1997).
15. Treue, S. & Martinez, J. C. Attentional modulation of direction-selective responses in MT/MST resembles the effect of reducing contrast of unattended stimuli. *Soc. Neurosci. Abstr.* **24,** 1249 (1998).
16. O'Craven, K. M., Rosen, B. R., Kwong, K. K., Treisman, A. & Savoy, R. L. Voluntary attention modulates fMRI activity in human MT-MST. *Neuron* **18,** 591–598 (1997).
17. Beauchamp, M. S., Cox, R. W. & DeYoe, E. A. Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *J. Neurophysiol.* **78,** 516–520 (1997).
18. Motter, B. C. Neural correlates of attentive selection for color or luminance in extrastriate area V4. *J. Neurosci.* **14,** 2178–2189 (1994).
19. Chelazzi, L., Miller, E. K., Duncan, J. & Desimone, R. A neural basis for visual search in inferior temporal cortex. *Nature* **363,** 345–347 (1993).
20. Itti, L., Braun, J., Lee, D. K. & Koch, C. Attentional modulation of human pattern discrimination psychophysics reproduced by a quantitative model. *Neural Information Processing Systems* (in press).
21. McAdams, C. J. & Maunsell, J. H. R. Attention enhances neuronal responses without altering orientation selectivity in macaque area V4. *Neurosci. Abstr.* **22,** 1197 (1996).
22. Martinez, J. & Treue, S. Attention does not sharpen direction-tuning curves in macaque monkey MT/ MST neurons. *Soc. Neurosci. Abstr.* **24,** 649 (1998).
23. Desimone, R. & Duncan, J. Neural mechanisms of selective visual attention. *Annu. Rev. Neurosci.* **18,** 193–222 (1995).
24. Reynolds, J. H., Chelazzi, L. & Desimone, R. Competitive mechanisms subserve attention in macaque areas V2 and V4. *J. Neurosci.* **19,** 1730–1753 (1999).
25. Treue, S. & Maunsell, J. H. R. Effects of attention on the processing of motion in macaque visual cortical areas MT and MST. *J. Neurosci.* submitted.

Poleward shifts in geographical ranges of butterfly species associated with regional warming

Camille Parmesan[*†], **Nils Ryrholm**[‡], **Constantí Stefanescu**[§], **Jane K. Hill**[‖], **Chris D. Thomas**[¶], **Henri Descimon**[#], **Brian Huntley**[‖], **Lauri Kaila**[☆], **Jaakko Kullberg**[☆], **Toomas Tammaru**[**], **W. John Tennent**[††], **Jeremy A. Thomas**[‡‡] & **Martin Warren**[§§]

* *National Center for Ecological Analysis and Synthesis, 735 State Street, Suite 300, Santa Barbara, California 93101, USA*
‡ *Evolutionary Biology Centre, Section of Zoological Ecology, Uppsala University, Norbyvägen 18 D, S-752 36 Uppsala, Sweden*
§ *Butterfly Monitoring Scheme, Can Liro, 08458 Sant Pere de Vilamajor, Barcelona, Spain*
‖ *Environmental Research Centre, Department of Biological Sciences, University of Durham, Durham DH1 3LE, UK*
¶ *Centre for Biodiversity and Conservation, School of Biology, University of Leeds, Leeds LS2 9JT, UK*
# *Laboratoire de Systématique Évolutive, Université de Provence, 3 place Victor Hugo, 13331 Marseille, Cedex 3, France*
☆ *Finnish Museum of Natural History, Division of Entomology, University of Helsinki, P.O. Box 17, Helsinki FIN-00014, Finland*
** *Institute of Zoology and Botany, Estonian Agricultural University, Riia 181, EE-51014 Tartu, Estonia*
†† *Biogeography and Conservation Laboratory, The Natural History Museum (BMNH), London SW7 5BD, UK*
‡‡ *Furzebrook Research Station, Institute of Terrestrial Ecology, Wareham, Dorset BH20 5AS, UK*
§§ *Butterfly Conservation, P.O. Box 444, Wareham, Dorset BH20 5YA, UK*

....

Mean global temperatures have risen this century, and further warming is predicted to continue for the next 50–100 years[1–3]**. Some migratory species can respond rapidly to yearly climate variation by altering the timing or destination of migration**[4]**, but most wildlife is sedentary and so is incapable of such a rapid response. For these species, responses to the warming trend should be slower, reflected in poleward shifts of the range. Such changes in distribution would occur at the level of the population, stemming not from changes in the pattern of individuals' movements, but from changes in the ratios of extinctions to colonizations at the northern and southern boundaries of the range. A northward range shift therefore occurs when there is net extinction at the southern boundary or net colonization at the northern boundary. However, previous evidence has been limited to a single species**[5]** or to only a portion of the species' range**[6,7]**. Here we provide the first large-scale evidence of poleward shifts in entire species' ranges. In a sample of 35 non-migratory European butterflies, 63% have ranges that have shifted to the north by 35–240 km during this century, and only 3% have shifted to the south.**

We analysed distributional changes broadly spread over the past century for non-migratory species of butterfly whose northern boundaries were in northern Europe and whose southern boundaries were in southern Europe or northern Africa. We excluded some data where circumstances suggested that range boundaries were controlled or altered by non-climatic factors. This yielded a subset of sufficient quality for us to detect distributional changes predicted by models of global warming, yet is unbiased with respect to such changes. However, because data for some species were excluded at either their northern or southern boundaries, we

....

† Present address: Integrative Biology, Patterson Laboratories, University of Texas, Austin, Texas 78712, USA.

present three analyses: (1) northern boundary analysis, including all species with suitable data for the northern boundary; (2) southern boundary analysis, including all species with suitable data for the southern boundary; (3) whole-range analysis, encompassing species with suitable data for both boundaries, covering the intersection of datasets 1 and 2.

The northern boundary analysis used data for 52 species, of which the northern boundaries have extended northwards in the past 30–100 years for 65%, been stable for 34%, and retracted southwards for 2% (Table 1; binomial test, 34 extended north, 1 retracted south, $P \ll 0.001$). There is a high level of agreement among countries. Of the 34 species extending northwards, 24 have data from more than one country; for 71% of these, data from two or more countries indicate northward extension. Disagreements occur where one country classifies a species as stable while another country classifies it as extending its range. In no case did a species show conflicting trends, being classified as extending in one country and retracting in another. A detailed history of range extension in Great Britain since 1915 is shown for *Pararge aegeria* in Fig. 1.

The southern boundary analysis used data for 40 species, of which the southern boundaries have retracted northwards in the past 30–100 years for 22%, remained stable for 72%, and extended southwards for 5% (Table 2, binomial test, 9 retracting north, 2 extending south, $P < 0.04$). The proportion of stable boundaries is significantly higher along southern than along northern boundaries (Fisher's exact test, 72% versus 34%, $P < 0.001$). This could be because southern boundaries may be determined by factors other than temperature, such as moisture, or by non-climatic factors, such as competition[8]. Alternatively, the difference may be because southern study regions are more mountainous, and populations may have shifted elevation or slope aspect, rather than latitude. Finally, southern study areas may have experienced less climatic change than northern areas. Further data are required to test the relative merits of these hypotheses.

The whole-range analysis encompassed 35 species with data at both northern and southern boundaries, of which 63% shifted northwards, 29% were stable at both boundaries, 6% shifted southwards, and 3% extended at both boundaries (Table 3, Figs 2–4; binomial test, 22 moving north, 2 moving south, $P \ll 0.001$). These patterns do not exhibit any obvious phylogenetic component. All four families or subfamilies that are represented in the analysis by at least three species include both shifting and non-shifting species.

We conducted analyses only on boundary changes, not on distributional changes in non-boundary regions. For example, although *Carterocephalus palaemon* has become extinct in the southern parts of both Great Britain and Finland (possibly as a result of habitat alterations), its northern boundary in each of those countries is stable, as is its southern boundary in the Pyrenees (Catalonia), so it is categorized as non-shifting (Fig. 1).

Nearly all northward shifts involved extensions at the northern boundary with the southern boundary remaining stable (about two-thirds of 22 species; see Fig. 3), or retracting northwards (about one-third of 22 species). Thus, most species effectively expanded the size of their range when shifting northwards. The remaining species shifted their entire distribution northwards, more or less without altering the range size. For example, *Heodes tityrus* has completely disappeared from the Montseny region of Catalonia, where it was easily seen early this century. At the northern limit of the same species, there were only three isolated records in Estonia before 1998, when several breeding populations were found (Fig. 4).

The magnitudes of these range shifts (35–240 km along a single boundary) are on the order of 5–50 times the colonization distances achieved by comparable butterflies in single colonization events[9,10]. Northward extensions therefore seem to have been a consequence of sequential establishment of new populations, each giving rise to further colonizations. In *P. aegeria*, at least one (and usually several) new population has been established in each of the 10-km grid squares to the north of its historical distribution (Fig. 1).

Table 1 Northern boundary assessment

Family/subfamily*	Extended northwards	Stable	Retracted southwards
Papilionidae	*Parnassius apollo*		
	Parnassius mnemosyne		
Pieridae	*Anthocaris cardamines*	*Gonepteryx rhamni*	
	Aporia crataegi		
Lycaenidae	*Agrodiaetus amanda*	*Celastrina argiolus*	
	Everes argiades†	*Cyaniris semiargus*	
	Glaucopsyche alexis	*Heodes alciphron*	
	Heodes tityrus	*Heodes virgaureae*	
	Quercusia quercus	*Plebejus argus*	
	Strymonidia pruni	*Strymonidia w-album*	
	Hamearis lucina (Riodininae)	*Thecla betulae*	
Nymphalinae	*Apatura iris*	*Argynnis adippe*	*Apatura ilia*
	Araschnia levana	*Brenthis ino*	
	Argynnis paphia	*Clossiana selene*	
	Argynnis niobe	*Melitaea cinxia*	
	Clossiana dia		
	Brenthis daphne		
	Inachis io†		
	Limenitis camilla		
	Limenitis populi		
	Polygonum c-album		
Satyrinae	*Aphantopus hyperantus*	*Coenonympha arcania*	
	Coenonympha glycerion	*Erebia aethiops*	
	Hipparchia semele	*Lasiommata maera*	
	Lasiommata megera		
	Lopinga achine		
	Maniola jurtina		
	Melanargia galathea		
	Pararge aegeria		
	Pyronia tithonus		
Hesperiidae	*Erynnis tages*	*Carterocephalus palaemon*	
	Ochlodes venatus	*Thymelicus acteon*	
	Thymelicus lineola		
	Thymelicus sylvestris		

Data are from one or more countries: Great Britain, Sweden, Finland and Estonia.
* Taxonomy for all species are from ref. 19.
† Highly mobile species included because the distance of boundary change is much greater than individual dispersal distances.
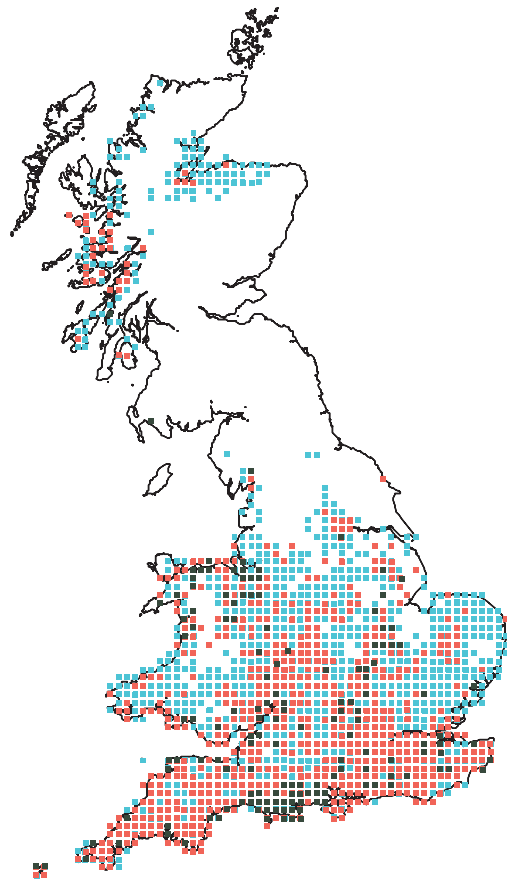
Figure 1 Twentieth-century changes in the range of *Pararge aegeria* in Great Britain, plotted by presence in Ordnance Survey 10 × 10 km grid squares. A coloured grid cell indicates more than one population in 1915–1939 (black), 1940–1969 (red) or 1970–1997 (blue).
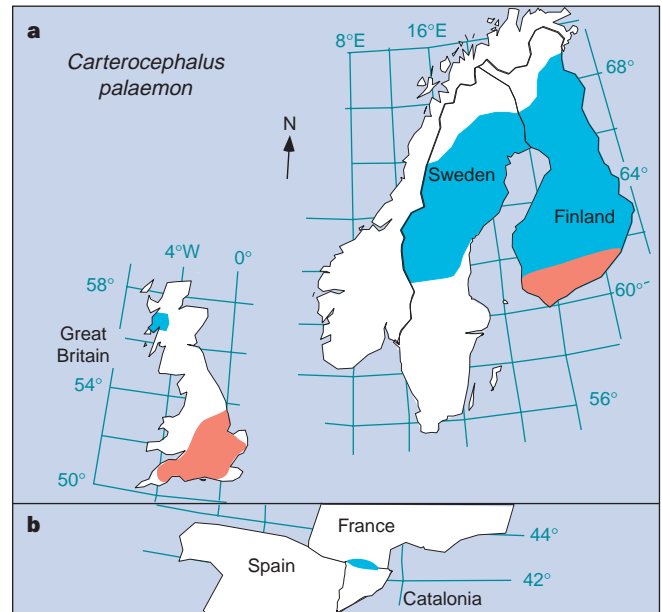

Figure 2 Distribution of a non-shifting species, *Carterocephalus palaemon*. Orange indicates areas of retraction, where all historical populations are extinct. Blue indicates stable areas, with no change. **a**, Northern boundary; **b**, southern boundary.

Changing land use is unlikely to account for these boundary changes. We selected species least likely to have been affected by modern habitat alterations. For Great Britain, we tested whether this selection might have biased our conclusion. We reanalysed the data to incorporate all 38 non-migratory species that have northern boundaries within Great Britain, including those known to be severely habitat-restricted or to have suffered severe habitat loss. We still found 47% with northward extension and only 8% with

Table 2 Southern boundary assessment

Family/subfamily	Retracted northwards	Stable	Extended southwards
Papilionidae	*Parnassius apollo* *Parnassius mnemosyne*		
Pieridae		*Aporia crataegi*	
Lycaenidae	*Everes argiades* *Glaucopsyche alexis* *Heodes tityrus* *Hamearis lucina* (Riodininae)	*Agrodiaetus amanda* *Celastrina argiolus* *Cupido minimus* *Heodes alciphron* *Heodes virgaureae* *Quercusia quercus* *Strymonidia w-album* *Thecla betulae*	
Nymphalinae	*Clossiana dia* *Clossiana selene*	*Apatura ilia* *Apatura iris* *Argynnis adippe* *Argynnis paphia* *Brenthis daphne* *Clossiana euphrosyne* *Limenitis camilla* *Limenitis populi* *Limenitis reducta* *Polygonum c-album**	*Brenthis ino* *Araschnia levana*
Satyrinae	*Aphantopus hyperantus* *Minois dryas*	*Coenonympha arcania* *Lasiommata maera* *Maniola jurtina* *Melanargia galathea* *Neohipparchia statilinus* *Pyronia tithonus*	
Hesperiidae		*Carterocephalus palaemon* *Thymelicus acteon*† *Thymelicus sylvestris*	

Data are from one or more countries: France, Catalonia (Spain), Morocco, Algeria and Tunisia.
* Disappeared from 6 out of 11 historically recorded sites in Africa, but the southernmost site is still present; the conservative assessment is to call this 'stable'.
† Disappeared from 3 out of 6 historically recorded sites in Africa, but the southernmost site is still present; the conservative assessment is to call this 'stable'.
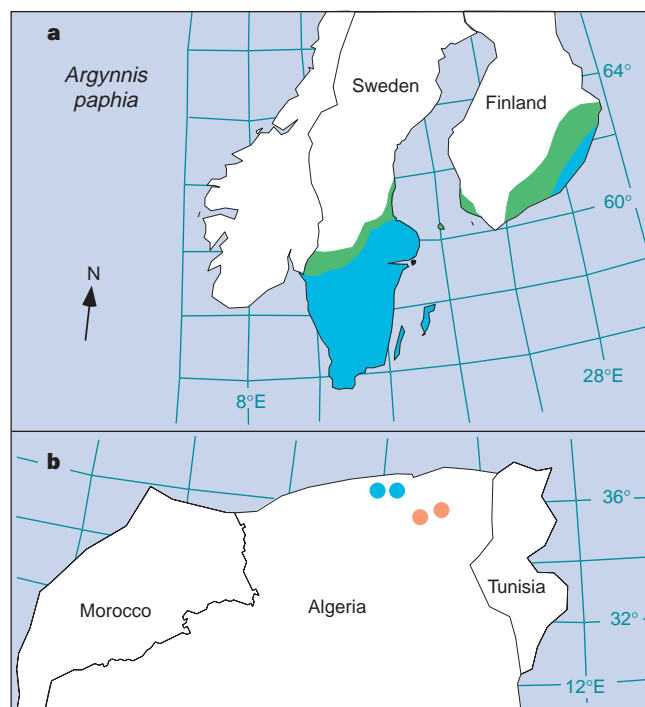
Figure 3 A northward-shifting species, *Argynnis paphia*, stable at its southern boundary and extending at its northern edge. **a**, Northern boundary; for Fennoscandia, blue represents the distribution in 1970, green in 1997. *A. paphia* is present in Great Britain but this is excluded from the analysis because of habitat loss with recent woodland management changes. **b**, Southern boundary; for northern Africa, each historical site (recorded from 1906 to 1912) is shown as a separate circle. Blue indicates that the species is present in the current census; orange indicates absence in the current census.

Figure 4 A northward-shifting species, *Heodes tityrus*, retracting at its southern boundary and extending at its northern boundary. **a** Northern boundary. Blue indicates the distribution for most of this century, taken from published maps[20], green indicates the distribution in 1998. There are also three other records in Estonia, once each in 1942, 1994 and 1996. **b**, Southern boundary. Orange indicates multiple populations recorded in the first half of this century, all now extinct.

southward retraction in the past 30 years (binomial test, 18 extended north, 3 retracted south, $P < 0.001$). Several of these species have extended northwards across heavily cultivated landscapes that are clearly less suitable for those species than they were a hundred years ago. In our study area as a whole, habitat loss has been greater in the northern countries than in the southern ones[11]. Although habitat loss has been severe in northern Africa, we controlled for this effect by only including sites where the habitat was still suitable for butterflies, regardless of whether the species of
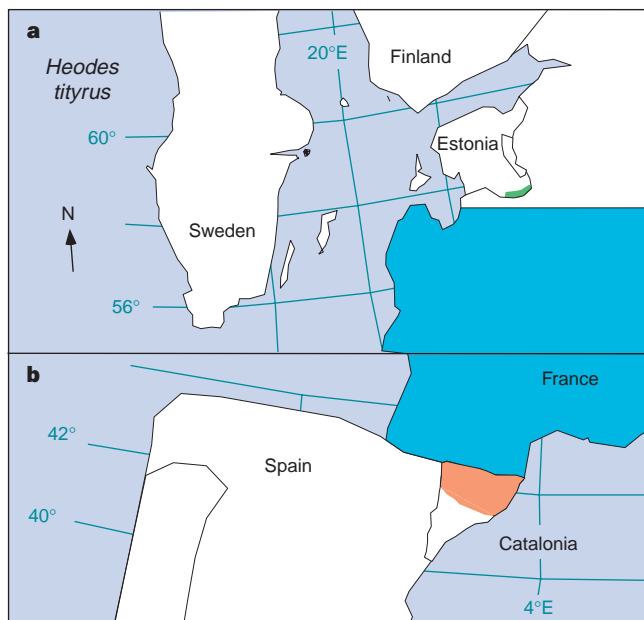
interest was present in the recent census. Thus, the influence of human land-use changes on our data set should tend to generate southward range shifts. Our conclusions are therefore conservative with respect to these effects.

Europe has warmed by about 0.8 °C this century, shifting the climatic isotherms northwards by an average of 120 km (ref. 3), on the same order of magnitude as the detected range shifts. In western North America, isotherms have shifted north by 105 km (ref. 12), while the mean location of populations of the butterfly *Euphydryas*

Table 3 Whole-range assessment

	No shift			Southward shift			Northward shift		
Northern limit: Southern limit:	Stable Stable	Retraction Retraction	Extension Extension	Stable Extension	Retraction Stable	Retraction Extension	Extension Stable	Stable Retraction	Extension Retraction
Papilionidae									P. apollo P. mnemosyne
Pieridae							A. crataegi		
Lycaenidae	C. argiolus H. alciphron H. virgaureae S. w-album T. betulae						A. amanda Q. quercus H. lucina		E. argiades G. alexis H. tityrus
Nymphalinae	A. adippe	A. levana	B. ino	A. ilia			A. iris A. paphia B. daphne L. camilla L. populi P. c-album*	C. selene	C. dia
Satyrinae	C. arcania L. maera						M. galathea M. jurtina P. tithonus		A. hyperantus
Hesperiidae	C. palaemon T. acteon*						T. sylvestris		

* Large density decreases in south: *T. acteon* extinct at 3 of 6 sites; *P. c-album* extinct at 6 of 11 sites.

editha shifted north by 92 km (ref. 5). Consistency across taxa and continents indicates that butterfly species in the northern hemisphere are shifting generally northwards in response to a common environmental change.

Nearly all population-dynamic studies have concluded that butterflies, and insects in general, are sensitive to temperature[13–16]. Although the correlational nature of our study limits our ability to determine causal factors, the summed knowledge of butterfly biology, including numerous experimental studies, implies that the northward shifts represent responses to increased temperatures. If this is correct, it has implications for climate-sensitive organisms with similar population structures characterized by discrete populations and limited dispersal, such as many beetles, grasshoppers, rodents and frogs.

Given the relatively slight warming in this century compared with predicted increases of 2.1 to 4.6 °C for the next century[2], our data indicate that future climate warming could become a major force in shifting species' distributions. But it remains to be seen how many species will be able to extend their northern range margins substantially across the highly fragmented landscapes of northern Europe. This could prove difficult for all but the most efficient colonizers. □

Methods

Assembling data sets. Data were assembled and analysed for non-migratory butterflies with northern boundaries in Great Britain, Sweden, Finland or Estonia, and southern boundaries in southeastern France, Catalonia (in Spain), Algeria, Tunisia or Morocco. A species was excluded if: (1) it is extremely habitat-restricted, requiring for example such a narrow combination of microclimate, plant phenology and other characteristics that it is highly localized, even within habitats containing its host; or (2) it cannot tolerate even a modest level of human-mediated habitat modification. A particular country's data for a species were excluded if, within that country: (1) the species' range is limited by host-plant distribution; (2) the range boundary lies in an area with so little potential habitat that it could have changed because of habitat alteration; or (3) the species suffered severe habitat loss. In some northern regions, specialists on dry meadows, calcareous grasslands and marshes were excluded owing to severe declines in these habitats in recent decades. In northern Africa, data from sites that no longer provided good butterfly habitat during the period of late censuses were excluded; if good habitat was still available, irrespective of the presence or absence of the target species, the data were included. (Species lists for each country are available on request from C.P.)

Data quality. The data are not of consistent resolution or temporal span within or among countries. Data for northern Africa are from historically famous collection sites (mainly from 1901 to 1932) that were re-censused by W.J.T. in the 1990s. Catalonia had a period of extensive collecting from 1900 to 1930, with moderate records since 1950. Distributions for the past 20 years are well documented by C.S. and a network of modern recorders; high-quality data collection began five years ago through a systematic, government-funded monitoring scheme. For France and Estonia, H.D. and T.T. had carried out field research and worked with naturalist societies. Final assessments incorporated literature records and combined data from amateur recorders. For most species, the changes analysed represent the past 20 years for Estonia and 40 years for southeastern France; a few species could be tracked from the 1920s and 1930s. In the northern third of Finland, Sweden and Great Britain (north Scotland and Lapland), collecting and recording activity was relatively poor for the first half of the century, so, except for the most conspicuous species, we focused on changes since the 1950s. However, in the southern two-thirds of those countries, observations have been detailed throughout the century, yielding data on a decadal scale. For detailed descriptions of data sets for each country, see Supplementary Information.

Assessment within a country. A species' boundary was defined as stable where census data show that populations recorded from earlier in this century are still present; it was defined as extended where recent censuses found new populations in areas outside the known historical distribution that had been visited by earlier collectors or recorders; and it was defined as retracted where historically recorded populations that defined a boundary are absent in recent censuses whose sampling effort was sufficient for absence of a record to indicate true absence of the species. Where population changes at a range boundary were small, we conservatively assessed that species as stable at that boundary. Thus, extended or retracted distributions involved boundary changes of at least several individual dispersal distances and could not be the result of a few ephemeral populations or be an artefact of stochastic sampling.

Assessment among countries, along a boundary. A single status for each boundary (northern or southern) was determined by the following: a boundary is deemed stable if it shows no changes in any country along the same boundary; a boundary is retracting if it has moved towards the centre of the distribution within one or more countries and is stable in other countries along the same boundary; a boundary is extending if it has moved away from the centre of the distribution within one or more countries and is stable in other countries along the same boundary.

Assessment of range status. Where the status of both northern and southern boundaries has been determined for a species, a northward shift is defined as either both boundaries moving north, or one moving north and the other remaining stable; a southern shift is similarly defined.

Analysis of fluctuations. This methodology leaves unclear how to classify species whose boundaries have fluctuated over time, with periods of both extension and retraction. For the southern boundaries, such information is not available; the same is true for most of the northern boundaries. However, for some species in northern regions, we have sufficient data to show northward extensions in the 1930s and 1940s and southward retractions in the 1950s and 1960s[16–18]. These fluctuations coincide with decadal temperature fluctuations in northern Europe[3] that are overlaid on the background temperature rise over the century. Species showing these fluctuations have all re-extended their northern boundaries concurrent with the recent warming trend (starting in 1970)[18], and all have current distributions that are further north than they were at the beginning of the century. Therefore, we have recorded them as 'extended'.

1. Easterling, D. R. *et al*. Maximum and minimum temperature trends for the globe. *Science* **277,** 364–367 (1997).
2. Intergovernmental Panel on Climate Change. *Climate Change 1995. Report of Working Group I* (eds Houghton, J. T. *et al.*) (Cambridge Univ. Press, 1996).
3. Beniston, M. *et al.* in *The Regional Impacts of Climate Change. Intergovernmental Panel on Climate Change Working Group II* (eds Watson, R. T., Zinyowera, M. C. & Moss, R. H.) 149–185 (Cambridge Univ. Press, 1998).
4. Root, T. L. in *Elements of Change 1996* (eds Hassol, S. J. & Katzenberger, J.) 203–206 (Aspen Global Change Institute, Aspen, Colorado, 1997).
5. Parmesan, C. Climate and species' range. *Nature* **382,** 765–766 (1996).
6. Barry, J. P., Baxtern, C. H. K., Sagarin, R. D. & Gilman, S. E. Climate-related long-term faunal changes in a California rocky intertidal community. *Science* **267,** 672–675 (1995).
7. Grabherr, G., Gottfried, M. & Pauli, H. Climate effects on mountain plants. *Nature* **369,** 448 (1994).
8. Davis, A. J., Jenkinson, L. S., Lawton, J. H., Shorrocks, B. & Wood, S. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391,** 783–786 (1998).
9. Thomas, C. D. & Hanski, I. in *Metapopulation Biology: Ecology, Genetics and Evolution* (eds Hanski, I. & Gilpin, M. E.) 359–386 (Academic, London, 1997).
10. Thomas, C. D., Thomas, J. A. & Warren, M. S. Distributions of occupied and vacant butterfly habitats in fragmented landscapes. *Oecologia* **92,** 563–567 (1992).
11. Baldock, D. Agriculture and habitat loss in Europe (CAP Discussion paper No 3, Gland, Switzerland, 1990).
12. Karl, T. R., Knight, R. W., Easterling, D. R. & Quayle, R. G. Indices of climate change for the United States. *Bull. Am. Meteorol. Soc.* **77,** 279–292 (1996).
13. Dennis, R. L. H. *Butterflies and Climate Change* (Manchester Univ. Press, 1993).
14. Coope, G. R. in *Extinction Rates* (eds Lawton, J. & May, R.) 55–74 (Oxford Univ. Press, 1995).
15. Uvarov, B. P. Insects and climate. *Trans. Entomol. Soc. Lond.* **79,** 174–186 (1931).
16. Ford, E. B. *Butterflies* (Collins, London, 1945).
17. Kaisila, J. *Immigration und Expansion der Lepidopteren in Finnland in den Jahren 1869–1960* (ACTA Entomologica Fennica, Helsinki, 1962).
18. Pollard, E. & Eversham, B. C. in *Ecology and Conservation of Butterflies* (ed. Pullin, A. S.) 23–36 (Chapman & Hall, London, 1995).
19. Ackery, P. R. Systematic and faunistic studies on butterflies. In *Biology of Butterflies* (eds Vane-Wright, R. I. & Ackery, P. R.) 9–21 (Academic, London, 1984).
20. Tolman, T. *Butterflies of Britain and Europe* (HarperCollins, London, 1997).