Climate and habitat availability determine 20th century changes in a butterfly's range margin

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Evidence of anthropogenic global climate change is accumulating, but its potential consequences for insect distributions have received little attention. We use a 'climate response surface' model to investigate distribution changes at the northern margin of the speckled wood butterfly, *Pararge aegeria*. We relate its current European distribution to a combination of three bioclimatic variables. We document that *P. aegeria* has expanded its northern margin substantially since 1940, that changes in this species' distribution over the past 100 years are likely to have been due to climate change, and that *P. aegeria* will have the potential to shift its range margin substantially northwards under predicted future climate change. At current rates of expansion, this species could potentially colonize all newly available climatically suitable habitat in the UK over the next 50 years or more. However, fragmentation of habitats can affect colonization, and we show that availability of habitat may be constraining range expansion of this species at its northern margin in the UK. These lag effects may be even more pronounced in less-mobile species inhabiting more fragmented landscapes, and highlight how habitat distribution will be crucial in predicting species' responses to future climate change.

Keywords: climate change; habitat fragmentation; metapopulation; *Pararge aegeria*

1. INTRODUCTION

Evidence of a discernible human impact on global climates is accumulating (Houghton *et al.* 1996) and this has generated an urgent need to be able to predict the effects of climate change on species' abundances and distributions. Insects are likely to be particularly responsive to climate change, and available data indicate that the most likely response is for species' distributions to shift polewards and to higher elevations (Coope 1978; Parmesan 1996; Parmesan *et al.* 1999). However, the spatial distribution of habitats is likely to have a great impact on the capacity of insects to respond to climate change. Recent anthropogenic habitat destruction may mean that new climatically suitable habitats are beyond the reach of migrants, preventing species from tracking climate change. Thus, although they have received little attention, the interacting effects of climate and habitat availability may be crucial in determining insect distributions both now and in the future (Lawton 1995; Yonow & Sutherst 1998; Thomas *et al.* 1999).

Many butterfly species have distributions that appear directly constrained by climate (Pollard 1979; Turner *et al.* 1987; Dennis & Shreeve 1991), yet it is not clear whether species will be able to track changing climates. Many species conform to a metapopulation structure (e.g. Thomas & Hanski 1997), where the spatial and temporal availability of habitat is crucial for the persistence of

populations even within areas of suitable climate. The presence of apparently suitable habitat that is unoccupied, together with low colonization rates in fragmented landscapes, have highlighted the difficulties butterflies have in reaching isolated habitats (Thomas *et al.* 1992). Thus, butterfly distributions will be unable to shift in response to climate change if new habitats are fragmented and too isolated to be colonized.

The relationship between a species' geographical distribution and present climate can be modelled by a surface representing the probability of encountering that species under a given combination of climate conditions. This 'climate response surface' may then be used to predict potential future distributions of the species in response to forecast climate scenarios (Beerling *et al.* 1995; Huntley 1995; Huntley *et al.* 1995). Here we use this approach with a model species of UK butterfly, the speckled wood, *Pararge aegeria* (L.). This species, along with other UK species, has undergone marked changes in its distribution over the past 150 years that may have been related to past climate change (Emmet & Heath 1990). After contraction of its distribution at the end of the 19th century, *P. aegeria* has subsequently re-expanded its distribution, but has not yet recolonized all areas formerly occupied (figure 1*a,b*). We use a climate response surface to investigate the importance of climate in determining European distributions of *P. aegeria*. Towards the northern and eastern margins of its range, the species is restricted to woodland; we focus on the UK at a finer resolution to investigate whether incorporation of habitat availability,
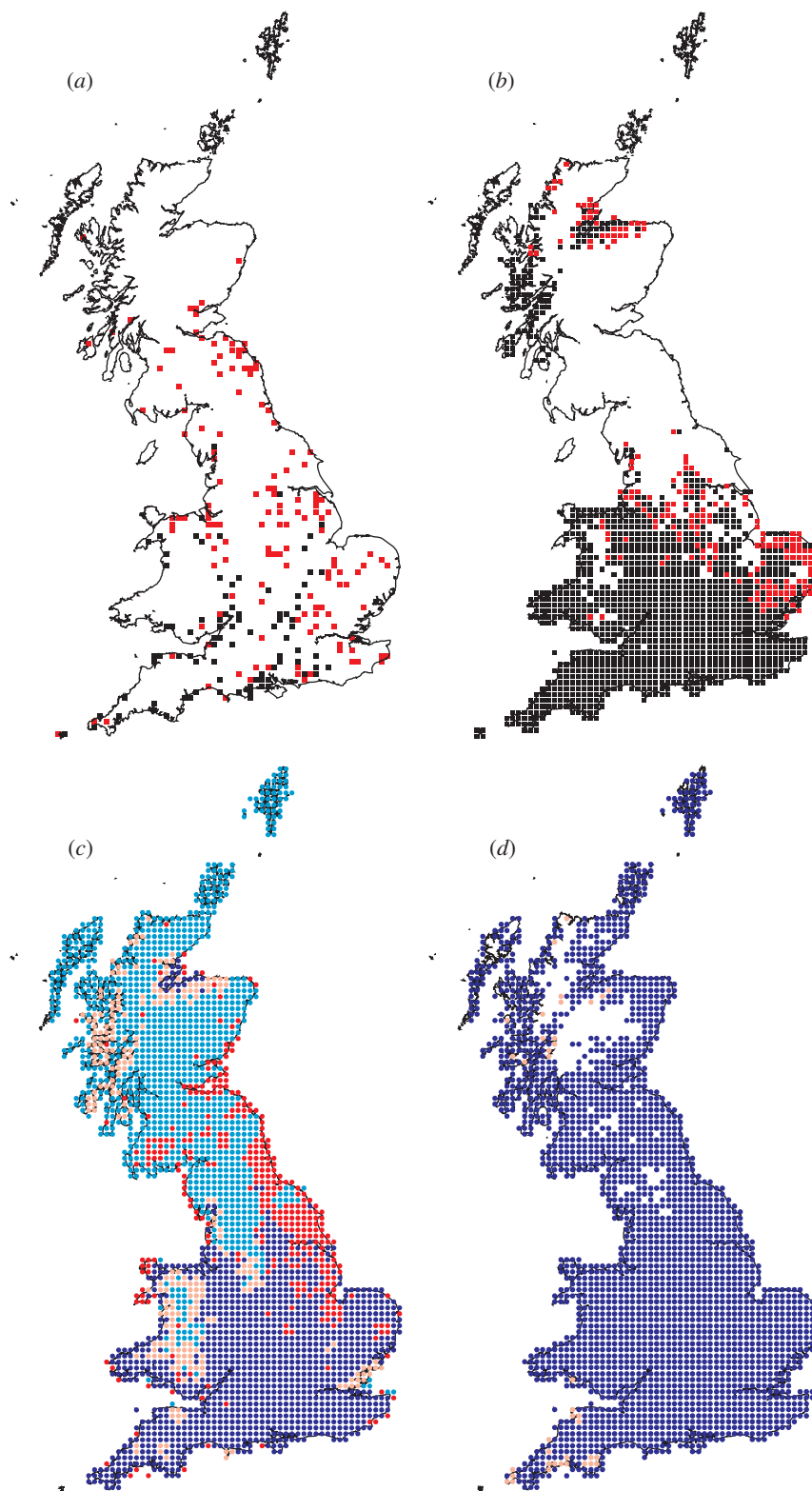
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Figure 1. Distribution of *P. aegeria* in the UK at a grid resolution of 10 km. (*a*) Historical distribution: red squares, pre-1915 distribution; black squares, most restricted distribution (1915–1939). (*b*) Current recorded distribution: black squares, species recorded 1940–1989; red squares, first recent record 1990–1997. (*c*) Simulated current distribution from the logistic regression model incorporating climate suitability and woodland availability (threshold probability of occurrence $p \geqslant 0.5$): blue dots, simulated occurrence coinciding with recorded presence; turquoise dots, simulated absence coinciding with recorded absence; red dots, simulated occurrence coinciding with recorded absence; pink dots, simulated absence coinciding with recorded presence. (*d*) Simulated future distribution for 2070–2099 from the logistic regression model incorporating climate suitability and current woodland availability ($p \geqslant 0.5$; blue circles). Pink circles indicate sites where *P. aegeria* is currently recorded but not predicted by 2070–2099. (Woodland data were not available for the Isle of Man and so it is excluded from *c* and *d*.)

as well as climate, significantly improves the fit of the model to current distributions. We test the performance of the model with historical climate data, for which we can test model predictions against available distribution data for that period. We then use the model to predict potential future European distribution under a climate change scenario for the end of the 21st century, and we also predict potential future UK distribution incorporating current availability of habitat.

2. MATERIAL AND METHODS

(a) *Generating the model at a European scale for current climate and distribution*

Current European records were collated from a number of sources (e.g. Aagaard & Gulbrandsen 1976; Marttila & Saarinen 1996; Tolman 1997; local butterfly recorders, unpublished data) and converted to presence or absence on a 50 km Universal Transverse Mercator (UTM) grid (figure 2*a*). The
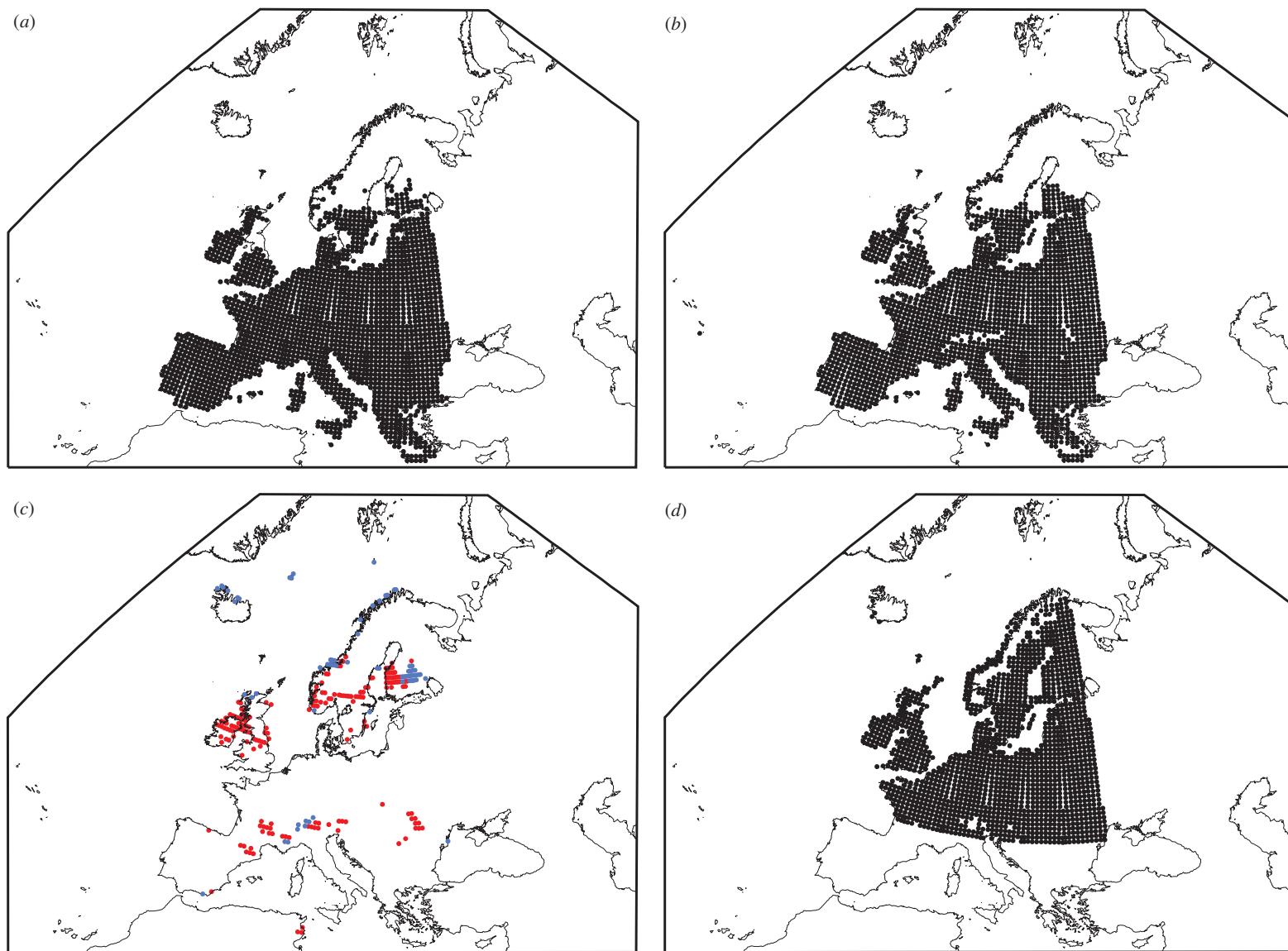
Figure 2. *P. aegeria* distributions for areas west of longitude 30° E (see text) on a 50 km UTM grid (*a*,*b*,*d*) and 0.5° latitude–longitude grid (*c*). (*a*) Current records. (*b*) Simulated current distribution (probability of occurrence $p \geqslant 0.45$). (*c*) Changes in climate suitability between 1901–1910 and 1986–1995. Only grid cells with probability values within or crossing the range 0.40–0.60 are plotted. Red circles, increased climate suitability during this century; blue circles, decreased climate suitability. (*d*) Simulated future distribution for the period 2070–2099 ($p \geqslant 0.45$) for areas north of latitude 45° N.

grid extended from the Azores east to longitude 30° E (reliable records could not be obtained for areas further east), and from the Mediterranean Sea (reliable records could not be obtained for North Africa) north to Svalbard (a total of 2648 grid squares). Particular efforts were made to define accurately the species' northern range limit on the basis of data obtained from recorders in the relevant countries. Any inaccuracies in the mapped distribution are likely to arise only from small areas in the central or southern parts of the species' range where it may be locally absent but be recorded as present in our data. We used mean monthly temperature, precipitation and cloudiness from a meteorological station data set relating to the climate normal period of 1931–1960 (Leemans & Cramer 1991) to interpolate values for locations at the midpoint and mean elevation of each 50 km cell (Huntley *et al.* 1995). We computed a number of derived climatic and bioclimatic variables, and evaluated several possible combinations of these variables as predictors of the species' distribution. We fitted climate response surfaces describing the species' European distribution in terms of each combination of variables (Huntley *et al.* 1995). We then used each response surface to simulate *P. aegeria* distribution for the current climate. The goodness-of-fit between simulated and observed butterfly distributions was used as a test of the response surface, and was assessed by using the κ-statistic (Monserud & Leemans 1992). The best performing model used three bioclimatic variables reflecting principal limitations on growth and survival of *P. aegeria*: annual temperature sum above 5 °C (GDD5; the developmental threshold for larvae) (Lees 1962; Blakeley 1997), coldest month mean temperature (MTCO; related to overwintering survival); and moisture availability (AET/PET; related to host-plant quality and expressed as an estimate of the ratio of actual to potential evapotranspiration) (Huntley *et al.* 1995).

(b) *Refining the model to take account of habitat availability*

Current *P. aegeria* records at a 10 km resolution were obtained for the UK from the Biological Records Centre (ITE Monks Wood) and Butterfly Conservation. Values for the three bioclimate variables used to fit the response surface were derived for locations at the midpoint and mean elevation of each 10 km cell (total of 2805 cells) using the same data sets and techniques as before. The climate response surface generated from the data at 50 km resolution was then applied to these finer-scale climate data to simulate the probability of occurrence of *P. aegeria* in the UK. Distribution of potential *P. aegeria* habitat was measured by using data from the ITE landcover data set, derived from satellite remote-sensed data (Fuller *et al.* 1994), for the percentage cover of woodland landcover types (combining deciduous and coniferous woodlands). Availability of woodland in each 10 km cell was expressed as the maximum percentage cover of woodland in any 1 km square within each 10 km square. This measure was chosen, after testing a variety of alternative measures, because it identified grid squares within which there are extensive woodlands, as opposed to others with numerous small patches classified as woodland (the pixel size of the land cover data set is 25 m), and performed better as a predictor of the species' distribution than did the alternative measures.

We used logistical regression to model the species' observed UK distribution in relation to climate suitability (represented by the probability of occurrence predicted by the response surface) and woodland cover; both variables were arcsine transformed before analysis. The probability of butterfly occurrence from the logistical-regression model was then compared with observed *P. aegeria* distribution in the UK at a resolution of 10 km.

(c) *Testing the modelling approach by using historical data*

We obtained annual climate data for the period 1901–1996 from the Climate Research Unit 0.5° gridded monthly climate data set (CRU05) (New *et al.* 1999a,b). These data are derived from long-term meteorological station records and are interpolated to a global 0.5° latitude–longitude grid. Because these climate data are at a resolution different from those used previously to fit the response surface, we generated another climate response surface with 0.5° data; this was then used to predict historical distributions. For the relevant subset of the 0.5° grid (a total of 4169 grid squares) we computed the same three bioclimate variables as before (GDD5, MTCO, AET/PET) for the decades 1901–1910 (when *P. aegeria* had a very restricted distribution in the UK) and 1986–1995. We remapped the present European distribution of *P. aegeria* to this grid and fitted a climate response surface based on climate data for the decade 1986–1995. From this response surface and the bioclimate variable values for the two decades, distributions were simulated for both decades and compared with observed current and historical *P. aegeria* distributions for the two decades.

(d) *Predicting potential future distributions*

We obtained output from a transient climate change simulation made by means of the HADCM2 general circulation model for the period 2070–2099. The simulation chosen combined the negative forcing of sulphate aerosols with the positive forcing of greenhouse gases (Mitchell *et al.* 1995) and can be viewed as a conservative simulation of the likely magnitude of climate change over the next century. Mean anomalies between the periods 1931–1960 and 2070–2099 in the transient simulation were computed for the model grid cells for 36 meteorological variables (monthly mean temperature, precipitation and cloudiness). These anomalies were then interpolated to the 50 km UTM grid across Europe, and added to the previously interpolated observed climate values for the period 1931–1960. The new values were then used, as before, to compute values for the three bioclimate variables (GDD5, MTCO and AET/PET) for the climate scenario for 2070–2099. These predicted future values were then used with the climate response surface fitted to the 50 km grid data to generate a simulated potential distribution for *P. aegeria* for the period 2070–2099.

To simulate potential *P. aegeria* distribution in the UK, the anomalies from the HADCM2 simulation were applied to the meteorological data for the 10 km grid, and values for the three bioclimate variables computed for the period 2070–2099 as before. The climate response surface for *P. aegeria* generated from the 50 km grid European data sets was then used to predict the butterfly's probability of occurrence in the UK under the changed climate scenario. These values for probability of occurrence were then used in the logistic regression (see above) to predict *P. aegeria*'s potential distribution in the UK, taking into account habitat availability. The habitat availability values were those for the present as there was no obvious basis on which we could predict how this might change over the next century.

(e) *Rates of range expansion*

To estimate the time required for *P. aegeria* to colonize newly available climatically suitable habitats in the UK, we used the

Table 1. *Mean values for three bioclimate variables for the 50 km grid*

(Data for the climate-normal period 1931–1960 are from Leemans & Cramer (1991); values for the period 2070–2099 are derived from the HADCM2 scenario. GDD5, annual temperature sum $> 5\,°C$; MTCO, mean temperature of the coldest month; AET/PET, actual/potential evapotranspiration. Values in parentheses are standard deviations.)

	GDD5 (degree days)	MTCO (°C)	AET/PET
1931–1960	1915.5 (1079.0)	−1.36 (6.21)	0.842 (0.288)
2070–2099	2788.6 (1354.4)	3.41 (5.17)	0.837 (0.201)
change	+873.1 (320.5)	+4.77 (1.32)	−0.006 (0.255)

area method (Van den Bosch *et al.* 1990) to calculate the rate of expansion of the area that the species has occupied in the UK this century. We plotted the area occupied each decade (square root of the area of number of 10 km squares with butterfly records) against year, and calculated the marginal velocity of range expansion (E) from the slope (C) of this line ($E = C/\sqrt{\pi}$) (Lensink 1997).

3. RESULTS

(a) *Current European distribution*

Table 1 shows mean values for the three bioclimate variables for the period 1931–1960. There was a good fit between currently observed (figure 2*a*) and simulated (figure 2*b*) butterfly distributions based on the 50 km UTM grid data sets ($\kappa = 0.803$ at a threshold probability of butterfly occurrence of 0.45; 2096 simulated occurrences compared with 2064 observed occurrences). Given, however, that *P. aegeria* currently occurs in more than 77% of squares, a more valuable test of the response surface is its ability to simulate accurately the species' northern range margin; visual inspection showed that this was also good overall (figure 2*a,b*). However, the model predicted occurrence in a few areas in the UK beyond the species' current limits. These areas included the Isle of Man and the Western Isles, and also localities along the east and west coasts of England where the species was historically present before its 19th century range contraction (figure 1*a*). The model was also good at predicting range margins in Fennoscandia, although it predicted occurrence in part of south-west Sweden in an area where *P. aegeria* has never been recorded. The model also predicted absence in the core of the Alps in grid cells where *P. aegeria* is restricted to specific habitats (e.g. south-facing slopes and valley bottoms) below the mean elevation of the grid cell; such predicted absences are to be expected given that the model was fitted to bioclimate values for the mean elevation of the grid squares. An alternative response surface model, fitted to the climate interpolated for the minimum elevation of each grid cell, successfully simulated occurrence in these Alpine grid squares when run with the climate for the minimum elevation; however, this model was less successful at simulating distributions at the northern range margins, and therefore we present data only for models fitted to mean elevation climate data.

(b) *Current UK distribution and habitat availability*

The current UK distribution of *P. aegeria* at a 10 km grid resolution is shown in figure 1*b*. The logistical regression model incorporating climate suitability (simulated probability of butterfly occurrence) and woodland availability predicted 78% of *P. aegeria* presence or absence in grid cells correctly ($\chi^2 = 1236.1$, 2 d.f., $p < 0.0001$; $\kappa = 0.569$) (figure 1*c*). Both variables were significantly and positively related to butterfly presence, and the probability (p) of *P. aegeria* occurrence is described by the equation

$$\ln\left(\frac{p}{1-p}\right) = 2.88 \times C + 1.98 \times W - 3.84,$$

where p is the species' probability of occurrence, C is the species' probability of occurrence, as predicted for the 10 km grid cell using the climate response surface, and W is the availability of woodland habitat, expressed as the maximum percentage of woodland land cover types in any 1 km square within the 10 km grid cell. Standard errors for coefficients are, respectively: 2.88 ± 0.10; 1.98 ± 0.15; 3.84 ± 0.16.

As at the European scale, the majority of the grid cells where *P. aegeria* occurs, but was not simulated, are grid cells of high relief (such as the Welsh mountains and Western Highlands of Scotland) where the bioclimate variables used reflect the mean elevation whereas the species occurs in specific habitats at low elevation. As before, *P. aegeria* was predicted to occur in areas currently beyond its northern range margin in England, but which it occupied in the 19th century (figure 1*a*).

(c) *Predicted historical European distribution*

At a latitude–longitude grid resolution of $0.5°$ there was also a good fit between the observed distribution of *P. aegeria* and its simulated distribution from the response surface using climate data for 1986–1995 ($\kappa = 0.844$ at a threshold probability of occurrence of 0.46; 2716 observed occurrences, 2725 simulated occurrences). As for the 50 km grid, the response surface performed well at the species' range margins, although once again it predicted occurrences in south-west Sweden where *P. aegeria* has never been recorded, and further north in England than the species is currently found. As before, it did not predict distributions in the core of the Alps or mountainous regions in Scotland where *P. aegeria* is recorded from unusually warm microclimates.

Table 2 shows mean differences in the three bioclimate variables between historical (1901–1910) and current (1986–1995) climates. Values of the three variables were weighted by the cosine of the latitude of each cell when calculating mean values to take account of decreasing cell area and increasing the number of cells with increasing latitude. These data show that during this century climates in the study area have on average become warmer and drier. Simulated historical distributions were slightly more restricted than simulated current distributions (2670 simulated historical occurrences compared with 2725 simulated current occurrences; threshold probability of occurrence = 0.46). We compared differences between the two simulations by calculating changes in the species' probability of occurrence for each grid cell.

Table 2. *Mean values for three bioclimate variables for the 0.5° latitude–longitude grid*

(Values are means weighted by cell area; see text. Standard deviations in parentheses. Data are from the CRU05 1901–1996 data set. Abbreviations as in table 1.)

	GDD5 (degree days)	MTCO (°C)	AET/PET
1901–1910	1876.2 (1160.5)	−1.52 (7.50)	0.853 (0.199)
1986–1995	2086.2 (1248.4)	−0.32 (7.65)	0.842 (0.206)
change	+210.0 (204.6)	+1.19 (0.93)	−0.011 (0.031)

We focused on grid cells with current or historical values for probability of occurrences within the range 0.40–0.60, or where the change in probability values between the two decades crossed this range. This range was chosen to highlight grid cells for which changes in climate would be most likely to affect butterfly occurrence.

Figure 2c illustrates these changes and shows that substantial areas along the species' northern range margin in both the UK and Fennoscandia have become more climatically suitable for the species in the course of the 20th century. We then focused on Britain (a total of 196 grid cells) (figure 3), for which there are reasonable historical butterfly records (figures 1a and 3a). Figure 3b illustrates changes in GDD5 in Britain between 1901–1910 and 1985–1996, and shows that most of Britain has become warmer during this period. There are 30 cells with values lying within the specified range of probability values (0.40 0.60) and which have improved in climate suitability this century (figure 3a). Of these 30 cells, ten have been recolonized since the 1940s and the remainder were either occupied (four cells) or unoccupied (16 cells) throughout this period. Only three cells with probability values lying within the specified range have declined in climatic suitability in the UK during this century; all three are on the west coast of Scotland. One cell has been unoccupied in both periods, and the two other cells have been recolonized since the 1940s (and have simulated probabilities of current occurrence of 0.34 and 0.46; see figure 3c).

(d) *Predicted future European distributions*

Table 1 shows mean differences for the three bioclimate variables between the climate-normal period of 1931–1960 and future predicted climates. These data indicate that climates within the study area will on average become warmer and drier by the end of the 21st century. The simulated potential future distribution of *P. aegeria* for the period 2070–2099 is shown in figure 2d (using the probability threshold of occurrence of 0.45 derived from the current climate simulation). The model predicts considerable northward extension of the potential distribution of *P. aegeria*, and indicates that *P. aegeria* would have the potential to extend its range throughout the UK, with only the highest mountains in Scotland being excluded. In Fennoscandia the species' potential range extends almost to the Arctic coast, reaching southern Finnmark, and extends along the west coast of Norway as far as the Lofoten Islands. The southern range margin of *P. aegeria* (in North Africa) was not included in the response surface,

making it impossible to predict future changes at the southern margin; areas south of latitude 45° N have therefore been excluded from the simulated future distribution.

In the UK, predictions from the logistical-regression model are for *P. aegeria* to occur throughout the UK, with the exception of the high mountain areas in central Scotland (figure 1d). At a resolution of 10 km, a sufficient extent of woodland is present almost everywhere that the climate is suitable for the butterfly, so that habitat availability at a 10 km resolution does not generally constrain the species' potential future range.

(e) *Expansion rates*

Extrapolation of the rate of increase of the area occupied suggests that *P. aegeria* could colonize all currently suitable habitat in the UK within the next three years (figure 4), although, because it does not take into account the relative locations of empty and occupied habitats, this estimate is probably unrealistic. Expressing the expansion rate of *P. aegeria* in the UK this century as the marginal velocity of expansion (E) of the area occupied, which we estimate as $2.7 \, \text{km yr}^{-1}$ (without correcting for geometrical distribution of potential new areas for colonization) (Lensink 1997; see figure 4), emphasizes this point and suggests that colonization of more isolated areas of suitable habitat may take much longer than three years. Furthermore, there is some indication from figure 4 that expansion rate has already declined over the past 30 years; recalculating the marginal velocity of expansion for the period since 1970 results in a reduced estimate of $1.6 \, \text{km yr}^{-1}$. Nonetheless, the rate of areal increase for this recent expansion predicts *P. aegeria* to have colonized all currently suitable habitats in the UK within the next seven years, and, furthermore, to be able to colonize within the next 50 years all areas of the UK predicted to be suitable during the late 21st century (figure 4). Once again, however, these estimates are likely to be unrealistic because they take no account of the location of suitable empty habitat, much of which is remote from currently occupied areas and would take much longer to be colonized if the marginal velocity of the recent expansion, rather than the rate of areal increase, is taken as an indication of the likely rate of future range expansion.

4. DISCUSSION

(a) *Performance of models*

The high values for the κ-statistic for the response surfaces fitted to both the 50 km and 0.5° latitude–longitude grids indicate that climate is important in determining *P. aegeria* distribution at a European scale, and that butterfly distributions can be modelled very successfully by using three appropriate bioclimate variables. A test of the model with historical data indicated that recent range expansions are consistent with a response to the changing climate, confirming the robustness of this approach (Beerling *et al.* 1995). It is likely that this modelling approach will also be successful for other butterfly species, although different combinations of bioclimate variables may be more appropriate; for example, distributions of species with thermoregulating larvae may be more responsive to a combination of variables that includes hours of sunshine (Bryant *et al.* 1997).
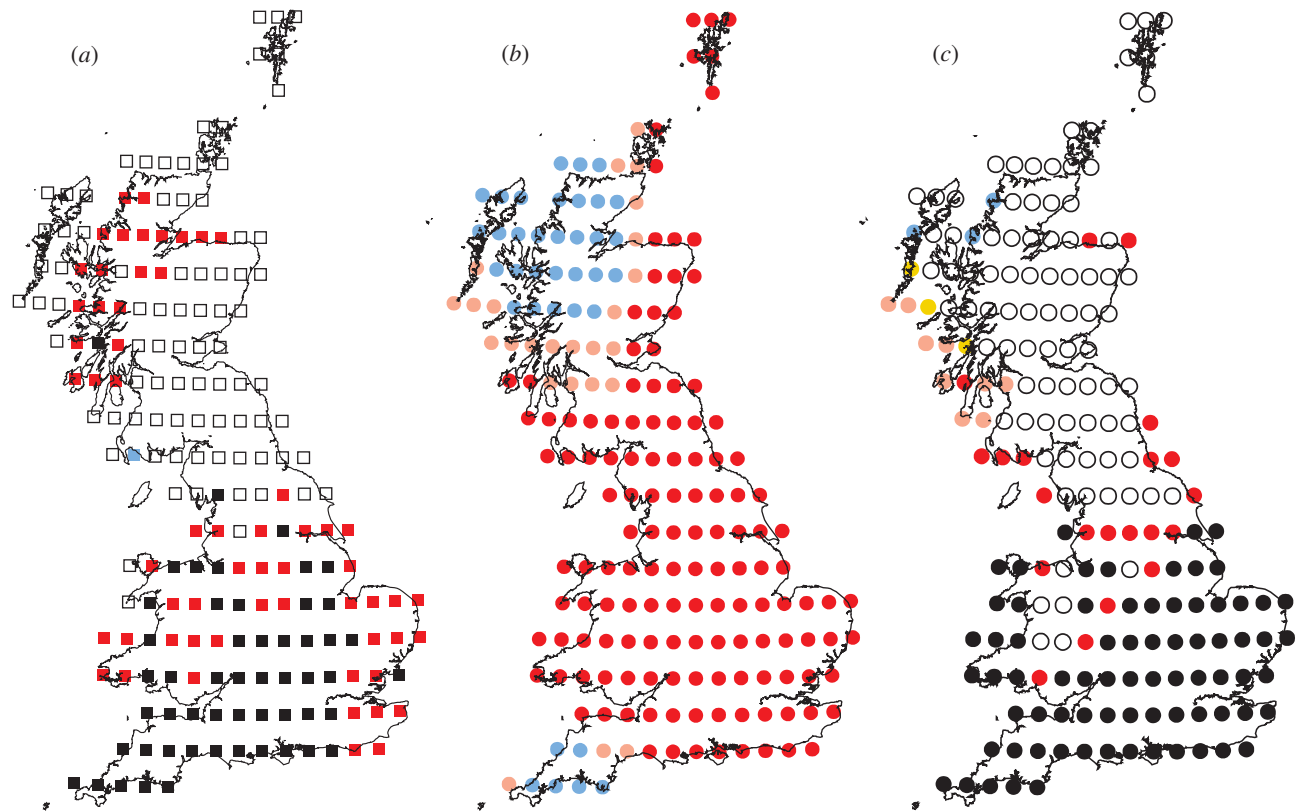
Figure 3. Changes in *P. aegeria* distribution and climate in the UK from 1901–1910 to 1985–1996 on a 0.5° latitude–longitude grid. (*a*) Recorded *P. aegeria* distribution: hollow squares, not recorded in either time period; black squares, present in both periods; blue square, only recorded historically; red squares, only recorded currently. (*b*) Changes in GDD5 this century: blue circles, decrease (fewer than 60 degree days); red circles, increase of 50 degree days or more; pink circles, increase of fewer than 50 degree days. (*c*) Changes in simulated occurrence this century: black circles, simulated presence in both periods; open circles, simulated absence in both periods. Other circles show grid cells with probability values within or crossing the range 0.40–0.60: red and pink, increased probability of occurrence (red ⩾ 10%, pink < 10%); yellow, no change; blue, decreased probability of occurrence.

At the European scale, although there was a good fit between the observed and simulated northern range margin, there was some indication that *P. aegeria* distributions are currently lagging behind changing climates. In some regions of Europe this may be partly an artefact of recording effort. However, this is unlikely to be an explanation in the UK, where recording coverage is good and a substantial difference in its UK distribution from that shown in figure 1*b* is very unlikely. There is considerable geographic variation among *P. aegeria* populations, which has a substantial genetic component (Nylin *et al.* 1993; Gotthard *et al.* 1994), and differences among populations in adult morphology and larval growth rates indicate local thermal adaptation of populations. These factors may also contribute to some of the mismatches between observed and simulated occurrences at northern range margins.

At the scale of Britain, climate alone was insufficient to explain the distribution of *P. aegeria* at the 10 km grid scale, whereas a combination of climate suitability and woodland availability was more successful. However, as at the European scale, the logistical-regression model predicted butterfly occurrence in several regions beyond the current range limit of *P. aegeria*. Some of these areas were occupied historically (e.g. northern England and lowland Scotland), but have not yet been recolonized, although other areas with simulated occurrence have

never been occupied (e.g. the Western Isles of Scotland and the Isle of Man) and are probably too isolated currently to be colonized (Dennis & Shreeve 1997). Thus, at both European and UK scales, the models indicate that *P. aegeria* has failed to keep up with the changing climates of the 20th century.

(*b*) ***Historical distributions***

Comparison of historical and current simulated distributions shows that substantial areas along the species' northern range margin have become more climatically suitable for the species during the course of the 20th century, as have a number of grid cells around the flanks of major mountain areas. In the UK, where good historical records of distributions exist, the species' range expansion is consistent with a general warming of the climate during this time. However, the response to changing climate is not as pronounced in some areas as that indicated by historical records. For example, *P. aegeria* was absent from most of Denmark and disappeared from large areas of eastern England at the beginning of the 20th century (Chalmers-Hunt & Owen 1952), areas that the model predicts to be climatically suitable during that time (figure 2*d*). However, the historical results do not take account of habitat availability; areas in south and west England and Wales where the butterfly occurred at that time currently appear from the landcover data to
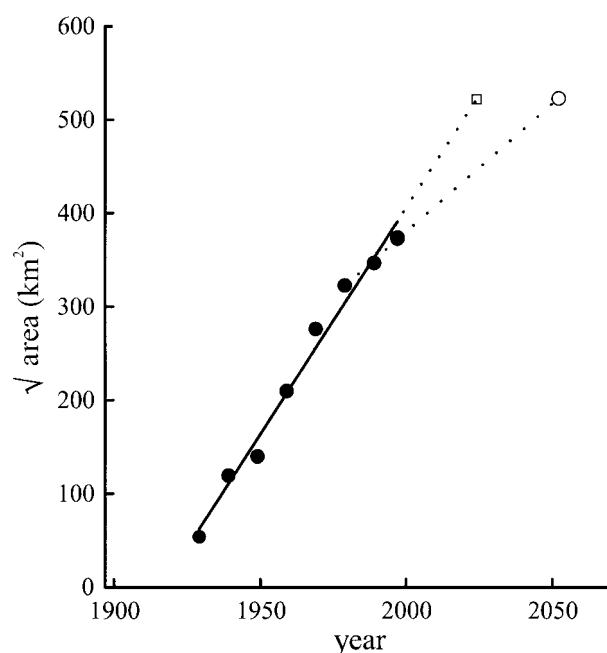
Figure 4. Expansion of *P. aegeria* in the UK from 1900 to the present (filled circles) and predicted extent of climatically suitable habitat for the period 2070–2099 (cf. figure 1*d*) (open symbols). Extrapolations predict time to colonize new areas and are based upon rates of areal increase since 1900 (open square) and since 1970 (open circle), respectively.

have extensive areas of woodland, suggesting that historical distribution of habitat, in addition to climate, may have been important in determining distributions.

The response-surface model is generated by using mean monthly climate values; these cannot reflect short-lived climatic events or extreme conditions that may have an important influence upon population dynamics (for example, a period of particularly wet or cold summer weather during the flight period will affect oviposition and survival rates). These events may depress local populations to levels where they are vulnerable to extinction by other processes, and in fragmented landscapes these may result in the collapse of population networks (Hanski *et al.* 1995) even in areas that appear climatically suitable from the perspective of mean conditions. Such interactive effects may explain why *P. aegeria* appears more sensitive to climate change than the model predicts.

A number of grid cells with probability values within the specified range were simulated to have become less suitable for *P. aegeria* during this century. Many of these cells lie beyond the species' current and known historical distribution in areas of Fennoscandia and Iceland. This anomaly appears to result from the current presence of *P. aegeria* in mountainous grid cells in other areas of its range, the climate of which, at their mean elevation, is similar to the historical climate of these northern cells. As a result of 20th century warming, these northern grid cells now have climates more similar to northern boreal areas where the species is absent, and thus they have apparently become less suitable for the species.

(c) *Habitat fragmentation*

P. aegeria is essentially a woodland species in the UK, although it is much less restricted to these habitats in the south and west of its UK distribution. The logistical-

regression model, however, was generated for the UK distribution as a whole and, as a consequence, predicts *P. aegeria* to occur in areas beyond its range margin that have very little woodland according to the landcover data (e.g. areas around the Wash and the Vale of York). The model also assumes that all woodland is suitable, although this is unlikely to be the case; age and density of woodland, and size of woodland patches, are likely to be important (Thomas *et al.* 1992). The logistical model may therefore be predicting *P. aegeria* in areas at its range margin with less woodland than it actually requires, and may be overestimating its current range limit. However, given that many areas where the logistical model predicts it to occur do appear to have large areas of woodland (e.g. southern Scotland), at least some of these lag effects are likely to be real. The spatial distribution of woodland within grid cells, as well as the area of woodland *per se*, will affect the species' distribution (Thomas & Jones 1993) and these lag effects indicate that finer-scale habitat fragmentation is likely to be affecting colonization rates in *P. aegeria*.

(d) *Rates of expansion*

Expansion rates in the UK over the past 30 years, expressed in terms of rate of areal increase, suggest that *P. aegeria* could colonize all currently available habitat within the next seven years. This is almost certainly unrealistic given the distribution of suitable but unoccupied habitat (figure 1*c*). The estimated marginal velocity of expansion (E) suggests a dispersal rate of approximately 1 km per generation, and although there are currently no direct estimates of dispersal for this species, data for other species of intermediate mobility (Hill *et al.* 1996) indicate that this rate is probably realistic for *P. aegeria*. These data indicate that, in the past, *P. aegeria* distribution has expanded at a rate that is consistent with the likely dispersal rate, and that long-range dispersal events have not been a major influence on its expansion. Although there have been a number of introductions of *P. aegeria* during its recent range expansion (see, for example, Rimmington 1986), these introductions have generally been into areas just beyond the range margin at the time and are unlikely to have greatly influenced expansion rates; some introductions may only have been successful because populations were supplemented by colonists (Rimmington 1986). Given such dispersal rates, and given the location of newly available habitat beyond presently occupied areas in the UK for the future climate scenario, it is possible that the species will reach equilibrium in the UK by the end of the next century.

In contrast to the UK, the potential range expansions of over 500 km that the model predicts in Fennoscandia in the 20th century are far greater than the range expansions that the species is likely to achieve in that time. Thus *P. aegeria*'s realized European range is likely to lag well behind its potential range if climate changes of the rate and magnitude forecast do indeed occur.

(e) *Future climate change*

Maps of simulated potential future distributions, such as that for *P. aegeria* (figure 2*d*) do not represent forecasts of future distributions but do provide an indication of the magnitude of the potential impact of climate change

upon species' distributions. Species are likely to respond individually to future climate change, and new associations among species are likely to arise as climate changes (Huntley *et al.* 1995; Huntley 1991, 1996; Davis *et al.* 1998*b*). Newly suitable habitats may also contain new predators and competitors, making the actual outcomes of any change difficult to predict precisely (Davis *et al.* 1998*a*). However, the results presented here are in agreement with current empirical data showing a general poleward shift of species distributions over the past century (Parmesan 1996; Parmesan *et al.* 1999). Our results reveal that even moderately mobile species such as *P. aegeria* appear to be lagging behind current climates. Such lags are likely to be even greater in less mobile species in fragmented landscapes, and in species with more restricted habitat requirements. The consequences of lags for these species will be of particular concern because these species are likely to be of high conservation value. Further research is needed to investigate whether such lags are common and the degree to which species will be unable to keep track of climate changes in landscapes that are becoming increasingly fragmented.

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