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## Predicting microscale shifts in the distribution of the butterfly *Plebejus argus* at the northern edge of its range

Jenny A. Hodgson, Jonathan J. Bennie, Gemma Dale, Natalie Longley, Robert J. Wilson and Chris D. Thomas

J. A. Hodgson ([jenny.hodgson@liverpool.ac.uk](mailto:jenny.hodgson@liverpool.ac.uk)), Dept of Evolution, Ecology and Behaviour, Biosciences Building, Crown Street, Univ. of Liverpool, Liverpool, L69 7ZB, UK. – J. J. Bennie, G. Dale and R. J. Wilson, Centre for Ecology and Conservation, Univ. of Exeter, Cornwall Campus, Penryn, TR10 9EZ, UK. – N. Longley and C. D. Thomas, Dept of Biology, Wentworth Way, Univ. of York, York, YO10 5DD, UK.

Species are often observed to occur in restricted patches of particularly warm microclimate at their high latitude/altitude geographic range margin. In these areas, global warming is expected to cause small-scale expansion of the occupied area, but most previous studies of range expansion have used very coarse scale data. Using high resolution microclimate models together with detailed field surveys, we tested whether the butterfly *Plebejus argus*, occurring on limestone grassland in north Wales, was responding as might be expected due to climate change in the last 30–40 yr. The abundance of adult *Plebejus argus* at 100 m resolution in 2011 was strongly affected by elevation and near-ground temperatures in May. A statistical model including microclimate, fitted to 2011 data, was successful (67% correct) at hindcasting the occurrence of *Plebejus argus* in 1983 when the average May air temperature was 1.4°C cooler. However, the model was less accurate at hindcasting occurrences in 1972 (50% correct). Given the distribution of micro-sites in this landscape, we predict that further warming of approximately 1°C would make the majority of sites highly microclimatically suitable for this species. There are a growing number of long-term studies of range change, and investigations into the mechanisms driving them, but still surprisingly few that explicitly make and test predictions with independent data. Our tests are a valuable example of how accurate predictions of distribution change can be, but also of the inevitable uncertainties. Improved understanding of how well models predict will be very important to plan robust climate change adaptation measures.

Under climate change, many species are expected (Engler et al. 2011) and have been observed (Chen et al. 2011) to shift their geographic ranges. Most observational studies have measured latitudinal and altitudinal shifts at fairly coarse spatial resolution, and these give compelling evidence of a widespread response to climate warming. However, there are significant numbers of species that do not seem to be shifting in the direction expected by climate change, if at all (Lenoir et al. 2010, Angert et al. 2011, Chen et al. 2011, Tingley et al. 2012, Zhu et al. 2012). Reasons for the lack of expansion at cool range margins could be that suitable habitat around the range margin is not available or is excessively fragmented (Warren et al. 2001, McNerny et al. 2007, Melles et al. 2011, Hodgson et al. 2012), or that additional constraints are imposed by interactions with other species (Gutiérrez and Thomas 2000, Merrill et al. 2008). A small but growing number of studies have focused on the issue of predictive power, or ‘transferability’ of correlative spe-

cies distribution models (SDMs), and the reasons why they may have limited success in predicting range shifts under climate change (Pearman et al. 2008, Dobrowski et al. 2011, Rapacciuolo et al. 2012, Blois et al. 2013, Smith et al. 2013). Quantifying transferability is important because SDMs are already being used to guide conservation policy.

Some apparent inconsistencies between predicted and observed range shifts could be resolved by examining both the environment and species’ responses at a finer spatial resolution (Randin et al. 2009, Engler et al. 2011, Suggitt et al. 2011). In particular, populations near their high latitude/altitude geographic range margin often inhabit a very small proportion of the landscape (Cowley et al. 2001), partly because of habitat specialization (Oliver et al. 2009), and partly because populations can only persist in the warmest of the local microclimates (Thomas et al. 1999). One of the first impacts of climate change may be that a greater proportion of the local landscape is suitable, and this can soon lead to larger and better connected populations, as has been shown for the butterfly *Hesperia comma* (Davies et al. 2006). This increased landscape carrying capacity could accelerate range expansion (Pateman et al. 2012), but for some species it still might not cause sufficient expansion to be detected in coarse scale records.

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In recent years, tools to model microclimate have progressed rapidly and can give detailed downscalings of near ground temperature at high resolution for large landscapes (Bennie et al. 2008). Several studies have linked species' distribution changes to more realistic assessments of their thermal tolerances (Wetthey and Woodin 2008, Beever et al. 2010, Buckley et al. 2010, Kearney et al. 2010), and one has tested model predictions against independent data from another time period (Buckley et al. 2010), although this was not done at a fine spatial resolution. We have found that models incorporating even a simple relationship between microclimate and population growth rate can lead to more accurate predictions of patch-scale dynamics into the future for the butterfly *H. comma*, which has been expanding its distribution in southern England (Bennie et al. 2013).

In the present study, we investigate the relationship between fine resolution distribution and microclimate for the butterfly *Plebejus argus*, which has not shown a large scale range expansion in the UK (Fox et al. 2006), even though it would be expected to have benefitted from regional warming (Thomas et al. 1999). This butterfly's growth is likely to be strongly dependent on temperatures close to the ground, similarly to many small bodied animals with limited powers of dispersal, and many plants. Butterflies make convenient subjects for this kind of study mainly because of the wealth of background information on their distribution and their ecology. *Plebejus argus* in Britain is restricted to seminatural habitats (unimproved calcareous grassland and heathland) which have become very scarce and fragmented in the last century. We statistically link the contemporary distribution of this species in the north Wales region to microclimate and other factors at 100 m resolution, and use this model to hindcast the distribution 30 and 40 yr ago, given the cooler regional climate then. We compare these predictions to historical colony maps at 100 m resolution or better. We show that, though the distribution has not changed very much, changes are consistent with a response to climate change at fine scales.

## Methods

A flow diagram of all described analyses is provided in Supplementary material Appendix 1, Fig. A1.

### Field survey

The northern coastal region of Wales is near the north-western range limit for the butterfly *Plebejus argus*. We studied two main concentrations of populations on calcareous grassland (henceforth termed localities): a coastal limestone headland called the Great Orme (53.33°N, -3.86°E), and limestone outcrops on either side of the Dulas Valley (53.28°N, -3.63°E), about 15 km away, where the species was introduced in the 1940s (Marchant 1956). *Plebejus argus* is univoltine in the UK and flies from late May to early July in our study region.

Between 27 May and 28 June 2011 we surveyed the entire distribution of adult *P. argus* on calcareous grassland in north Wales, and nearby unoccupied habitat, defined as

calcareous grassland containing one or more of the butterfly's host plants. In every 100 m square containing suitable vegetation, a transect walk of 300 m was taken according to standard methodology (Pollard 1977) (between 10 am and 5 pm, at minimum air temperature of 17°C if sunny or 19°C if cloudy, when wind speed less than Beaufort 4), counting all individuals within 2.5 m of the walker. Transect length was reduced proportionally if habitat did not cover the whole square, down to a minimum of 100 m. Average vegetation height and bare ground cover were recorded from a 25 × 25 m quadrat in the centre of the 100 m square (or, if the centre was not habitat, from the centre of a randomly chosen quadrant of the square which was habitat).

### Historical *P. argus* occupancy

Surveys of the occurrence of adult *P. argus* were carried out by C. D. Thomas in 1983 (Thomas 1985) and by R. L. H. Dennis in 1971–1972 (Dennis 1977), and these authors hand drew colony outlines on 1:25 000 Ordnance Survey maps. We geo-referenced and traced copies of the maps from these surveys using ArcGIS 9.3 (ESRI, Redlands, CA) (there is essentially no loss of precision in this procedure, because the maps are easy to align with the latest digital OS map). To compare previously mapped patches with our model predictions for 100 m squares in this study (see hindcasting section, below), we regarded a square to be occupied if its centre fell within the digitized shape outline.

### Microclimate

We used the mechanistic microclimate model of Bennie et al (2008) to predict vegetation surface-level temperatures in the limestone grassland for the months April–July at 5 m resolution for the years 1983–2009. The inputs to the model were a DEM (at 5 m horizontal resolution with a nominal vertical accuracy of +/- 60 cm), interpolated monthly mean temperature surfaces at 5 km resolution from the Met Office, and hourly wind speed and cloud cover data from RAF Valley airfield weather station (53.25°N, -4.53°E).

To summarize model outputs in a manner relevant to butterfly physiology, we summed degree-hours above 15°C for the months of April and May, the period when caterpillars are developing fastest, and hours above 15°C for June and July, when adults are active. Each 2011 *P. argus* transect and its associated vegetation quadrat was linked to the spatial average of microclimate within 50 m of the quadrat centre.

There was high year-to-year variability in temperature (SD ~0.9°C for mean daily maximum temperature of April and May, slightly less for June and July; Fig. 1a) around the long-term warming trend in this region. Given this variability, and given that we were most interested in predicting *P. argus*' response to the long-term trend, we decided a priori to correlate *P. argus* abundances in 2011 to each square's average microclimate between 1997 and 2009 for each given month (e.g. coloured circles in Fig. 2). This temporal averaging makes very little difference to the fit of the 2011 model (see next section) because the spatial pattern of microclimate (which squares are warmer than others) remains very similar from year to year. However using microclimate averaged

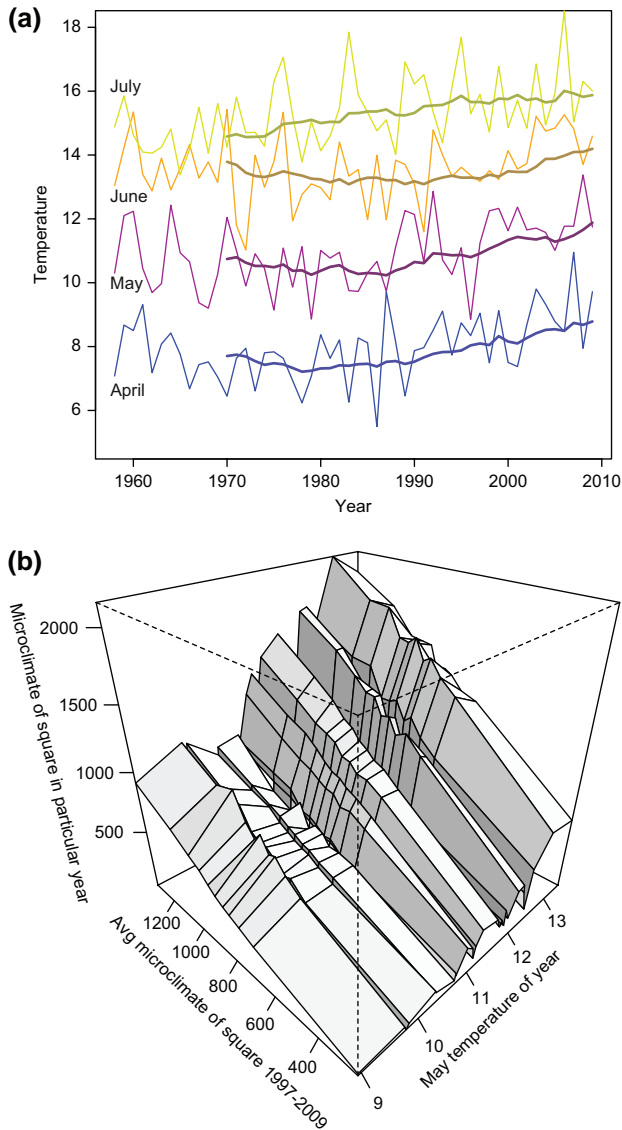


Figure 1. Regional climate and microclimate data used in this study. (a) Time series of Met Office UKCIP09 data for our study areas in north Wales: mean daily maximum air temperature for each month. Thin lines show the raw data, and thick lines show a running average of the previous 13 yr. (b) Microclimate conditions (degree-hours above 15°C in May), calculated for individual 50 m squares from the physically based model of Bennie et al. (2008) for the years 1983–2009 (vertical axis). We illustrate that this specific microclimate can be fairly well predicted from the Met office May temperature of the particular year (lower-right axis) and the average microclimate of the square throughout 1997–2009 (an indicator of the relative warmth of the square; lower-left axis). This correlative model was used to hindcast microclimate before 1983. For clarity of this plot only 11 squares are shown, every 10th percentile from the coolest to the warmest, but 7000 squares were used in fitting.

over 13 yr inevitably affects model predictions for past years (see hindcasting section below and Supplementary material Appendix 1, Fig. A1). Unfortunately, without further years of detailed population density data, it is not possible to test whether 13 yr, or some other time window, is most appropriate. Figure 1a shows that a 13-yr running average reveals a consistent warming trend in this region, especially for April and May.

## Statistical fitting of 2011 *P. argus* abundance

We fit generalized linear models with negative binomial error structure to explain variation in *P. argus* transect counts observed in 2011, using R 2.13.0 (R Development Core Team) (Supplementary material Appendix 1, Fig. A1). We used log length of the transect in m as an offset term, meaning that counts were forced to be directly proportional to this, for any given combination of other variables. Therefore this can be understood as a model of population density, or abundance per m of transect, henceforth termed ‘abundance’. The explanatory variables tested were: vegetation height; bare ground cover; elevation; aspect; slope; locality; date of survey and microclimate variables from April, May, June and July as described above. Non-significant variables were removed in a backwards stepwise manner from the full model. After examining plots of residuals we introduced a quadratic function of elevation because the relationship was clearly non-linear. Additional procedures such as model averaging did not seem warranted because firstly, the dropped variables all had very weak support ( $p > 0.14$ ) when we retested them by addition to the minimum adequate model, secondly all but one of the retained variables had very strong support, and thirdly the inclusion or exclusion of the one marginal variable (vegetation height) made no difference to the other model coefficients.

We examined the residuals of our minimum adequate model for spatial autocorrelation, which could affect the model’s inferences and predictions. There was weak (maximum 0.15) but significant positive autocorrelation between neighbouring points (Supplementary material Appendix 1, Fig. A2a). However, when we fitted a generalized linear mixed model that included spatial autocorrelation in residuals (using function `glmmPQL` in R package MASS (Venables and Ripley 2002)), this did not materially change the model’s predictions (Supplementary material Appendix 1, Fig. A2b). Therefore, for simplicity, we henceforth report the results of the generalized linear model.

## Hindcasting

*Plebejus argus* abundance in 2011 was found (Results) to be a function of the local microclimate in May, for which we had taken the 1997–2009 average. Therefore, to hindcast the distribution in 1983 we required May microclimate from 1969–1981, and for 1972 we required May microclimate from 1958–1970 (Supplementary material Appendix 1, Fig. A1). The hourly weather data from Valley which underpin the microclimate calculations were not available pre-1983. Therefore, to hindcast the *P. argus* distribution, we had to build a correlative model predicting microclimate based on a monthly temperature record (Fig. 1a) that extends back to the 1950s. We used a generalized additive mixed model (Wood 2004) with identity of year as a random factor, and a two-dimensional smooth term including the regional May air temperature of the year of observation, and the long-term average May microclimate of the particular 100 m square. The data used for this model are summarised in Fig. 1b. The fitted model explained 70% of the variation in microclimate for individual squares and years during the period

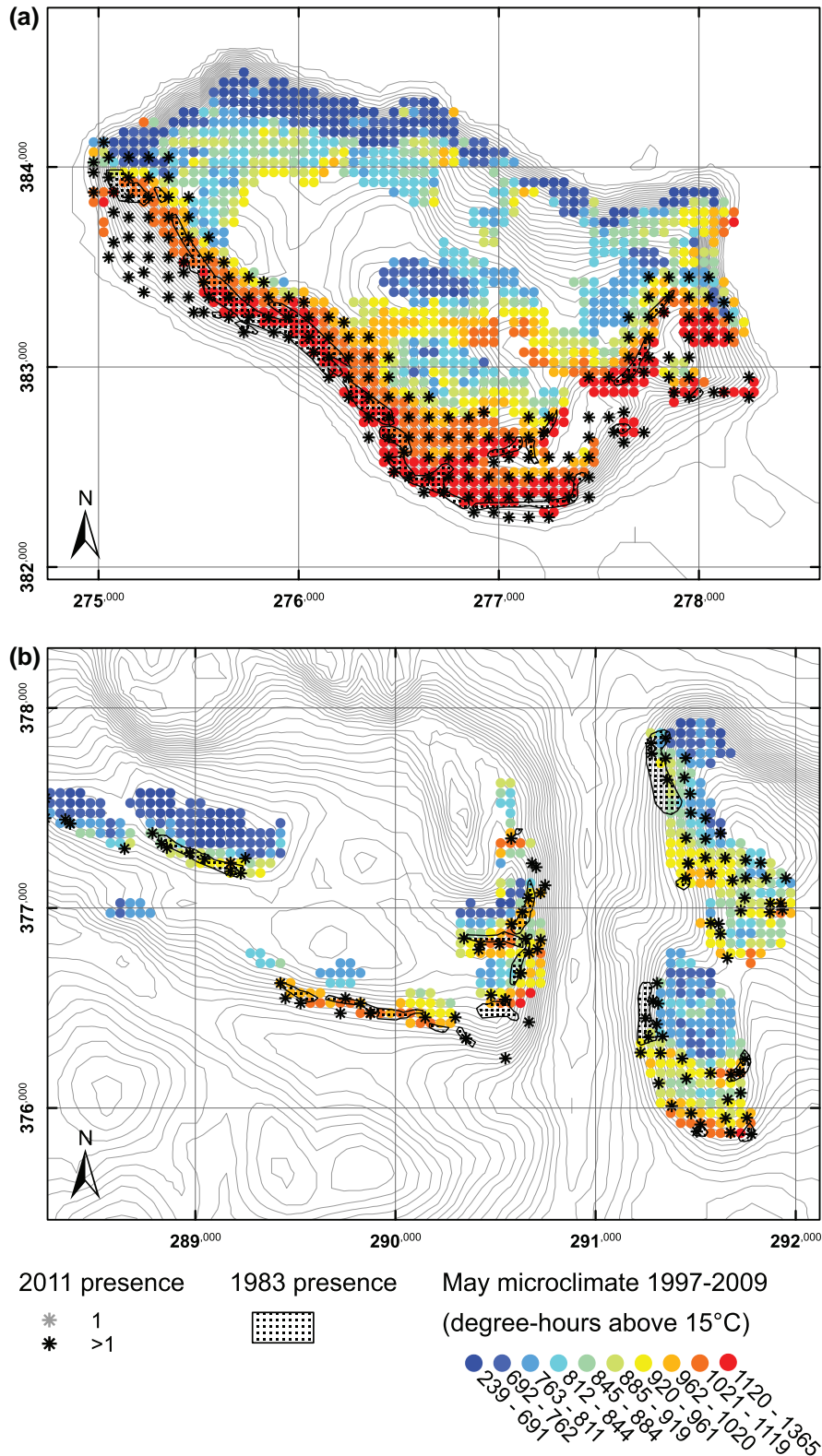


Figure 2. *Plebejus argus* distribution in 2011 and 1983 at the Great Orme (a) and the Dulas Valley (b) with underlying colours showing the May microclimate (degree-hours above 15°C per 50 × 50 m cell, averaged over 1997–2009) and 5 m contours showing the topography. Coordinates of the British National Grid are shown in metres (grid lines every km).



1983–2009. The regional May temperatures for 1969–1981 were 1.44°C cooler than 1997–2009, and those for 1958–1970 were 1.15°C cooler than 1997–2009 (Fig. 1a). We used the GAMM to predict each square’s average may microclimate for these past periods. As mentioned above, we cannot be sure that the *P. argus* distribution responds to the 13-yr average as opposed to some other function of the recent climate. However, one advantage of using this metric is that we can be more confident of the 13-yr mean microclimate of historic periods, based on our GAMM, than we could be of the prediction for any single year, because of the random inter-year variability.

We predicted *P. argus* abundance for a nominal 100 m transect in each survey square in 1983 and 1972 by substituting historical May microclimate values for the ones on which the abundance GLM was fitted. To quantify how much fit was improved, we also generated predictions without changing May microclimate. We used the GLM-predicted mean abundance ( $a$ ) and the negative binomial dispersion parameter ( $\theta$ ) to calculate the probability of seeing at least one individual as  $1 - \left(\frac{\theta}{\theta + a}\right)^\theta$ , and hence the likelihood of the actual historical observations of presence/absence given the model. We report differences between models in terms of AIC, which is simply calculated from the log likelihood, and in terms of a more intuitive percentage of predictions matching observations when we score  $a \geq 1$  as presence.

## Results

We walked transects in two hundred and ninety four 100 m squares containing potential *P. argus* habitat between 27 May and 28 June 2011. Of these, 224 squares were found to be occupied (Fig. 2). The abundance of adult *P. argus* on these transects was best explained by a combination of vegetation height (negative effect), elevation (non-linear negative effect captured by a two degree polynomial) and near-ground temperatures in May (positive effect) (Table 1; Fig. 2). There were also significant differences among survey days (due probably to a combination of weather and phenology) and between the Great Orme and the Dulas Valley localities (Table 1).

Hindcasting the 1983 distribution based on the model for 2011 (reducing May temperature but keeping all other variables the same) gave results that agreed well with the mapped occupied patches in 1983. The occupancy of 230 comparable squares in 1983 was correctly predicted in 67% of squares (assuming that predicted abundance  $\geq 1$  corresponds to presence). Without changing May temperature in the model, 56% of squares were predicted correctly and the

difference in AIC obtained from these two alternative predictions was 116. This very large difference in AIC means that we can be very confident that the predictions were changing in the right direction, even allowing for some AIC inflation due to spatial autocorrelation. The distribution of micro-sites that was occupied was predicted very accurately (Fig. 3a).

Hindcasting the 1972 distribution based on the model for 2011 gave equivocal results. On one hand, the distribution of micro-sites that were occupied was predicted well (Fig. 3b). On the other hand, overall occupancy was substantially over-estimated (Fig. 3b). The model predicted 50% of 218 comparable 1972 observations correctly. Without changing May temperature, the model only predicted 38% correctly, accompanied by a substantial worsening in AIC of 194.

We can use our fitted relationship between regional May temperature and the microclimate of 100 m squares to illustrate how the landscape would change with further climate warming (Fig. 3c–d). There is no sharp cut-off in terms of the May microclimate which seems to be ‘suitable’ for *P. argus*, but most occupied sites have  $> 1000$  degree-hours above 15°C in May, on the 13-yr average (Fig. 3c). The availability of habitat above this microclimate threshold, which we could regard as ‘highly suitable’, has increased substantially in the period covered by this study, but is expected to increase even more steeply with any further regional climate warming (Fig. 3d), e.g. warming by a further 1°C would result in high suitability in more than 80% of squares.

## Discussion

Based on a relationship between *P. argus* distribution and May microclimate, we predicted that there would have been small-scale but noticeable changes to the species’ distribution in the last 40 yr. We found that historical observations were consistent with our predictions. Although these distribution changes are consistent with a response to climate change, it is difficult to rule out alternative explanations. We were relying on the distribution of adult butterflies at 100 m resolution to infer a functional relationship with microclimate which might be consistent over long time periods. However, the distribution at 100 m resolution will fluctuate to some extent on a year-to-year or even day-to-day basis because of individual movements driven by weather (Dennis and Sparks 2006), even though *P. argus* rarely disperse more than 100 m (Lewis et al. 1997). We still expect that average abundance would indicate the fundamental relationship between microclimate and population performance, but such short-term fluctuations in distribution will have added noise and thus uncertainty to our statistical fits. Note, however, that

Table 1. Best fitting model of *P. argus* abundance in 2011 at 100 m resolution, and significance of individual terms according to likelihood ratio tests. Model structure was a generalized linear model with negative binomial errors and a log link, appropriate for over-dispersed count data;  $n = 230$ .

Term(s)	Coefficients (not standardized)	DF	Likelihood ratio stat.	p-value
Elevation, m	+0.039 E – 0.00029 E <sup>2</sup>	2	60.7	<0.00001
Day of survey as factor	Vary by up to 3.5	17	81.6	<0.00001
Locality as factor (Dulas Valley vs Great Orme)	+1.6	1	39.6	<0.00001
May degree-hours above 15°C	+0.0049	1	22.9	<0.00001
Vegetation height, cm	-0.016	1	3.6	0.058

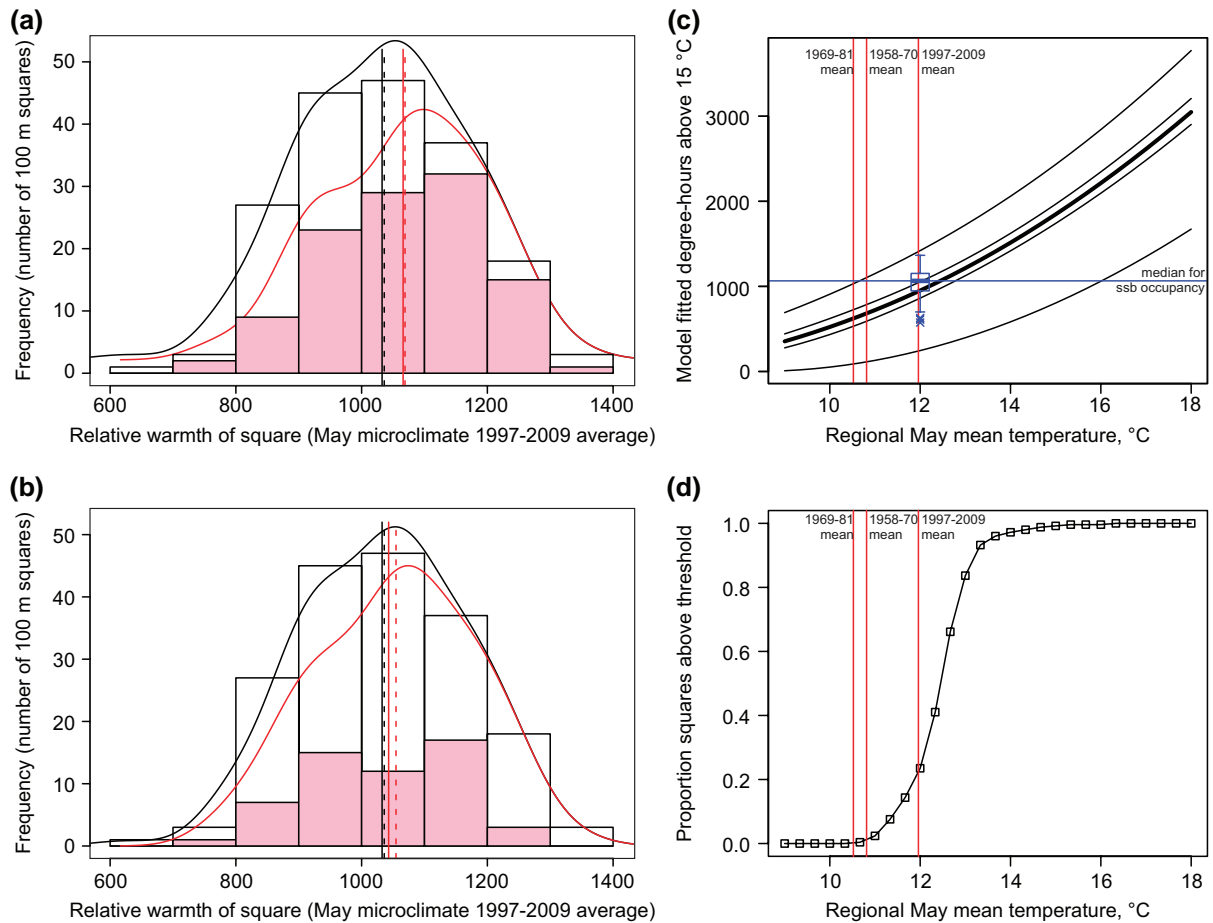


Figure 3. Microclimates predicted and observed to be occupied by *P. argus*. (a) The relative warmth of 100 m cells were predicted (smoothed density curves with dashed line at the mean) or observed (histograms with solid line at the mean) to be occupied in 1983 (pink) compared to 2011 (black). Warmth is measured in terms of the cell's microclimate in the latest time period, 1997–2009, but the ordering of cells does not change between time periods. (b) 1972 compared to 2011 with symbols as in (a). (c) The expected relationship between the regional May mean temperature and the distribution of microclimates across all limestone grassland habitat squares, to illustrate what may happen with future warming. Black lines are shown for the overall coolest square, the warmest square, and the quartiles, with a thicker line at the median. A blue boxplot of microclimates of squares that were occupied in 2011 is shown to indicate roughly what is 'suitable'. Red vertical lines indicate the observed temperatures of the periods used for fitting and predicting in this study. (d) Using the median microclimate of squares occupied in 2011 as a threshold for 'high suitability', the proportion of habitat squares above this threshold as regional May temperature increases. Red vertical lines as in (c).

the statistical relationship between 2011 distribution and microclimate is very strong (Table 1), even in addition to a relationship with elevation. It is also interesting that the May temperatures (when larvae and pupae are present) were most predictive of the adults' distribution, rather than conditions during the flight period. The strongest indication that the model has some functional validity is its ability to predict independent historical data, and the fact that predictions are significantly better when historical rather than current microclimate is used. Given our results, it seems reasonable to predict that *P. argus* will continue to respond to warming climate by increasing its local distribution, in the first instance to more easterly and westerly slopes.

The smaller-than-predicted distribution in 1972 could be explained by many things, including vegetation change, bad weather at the particular time of survey, or differing methodology between Dennis (Dennis 1977) and Thomas (Thomas 1985) (in terms of survey effort and/or what was counted as a colony). Roger Dennis reports that his survey of each piece

of potential habitat was necessarily brief, and also suspects that changes in habitat management by grazing may also have affected the distribution (R. L. H Dennis pers. comm. 2013); unfortunately we have no directly comparable vegetation data to test this hypothesis. It is reassuring that, despite this difference in the total area occupied, the distribution of microclimates occupied was still predicted well by the model (Fig. 3b).

Our study is unusual in being able to test predictions of a microclimate-based model against independent data separated by several decades (see also Bennie et al. 2013). These tests may be seen as weak in the sense that a multitude of similar models could have given similar predictions. However, we still believe that such tests should be employed whenever enough biologically relevant data are available, because they are the only way to gain confidence that species' responses to climate change can be usefully projected into the future. Our results give some useful insight to the conservation managers in north Wales, where *P. argus* is a priority species. Firstly, managers should not be concerned

that the *P. argus* distribution has not increased markedly so far, but secondly they should prepare for the possibility that expansion will soon accelerate, and check whether nearby habitat is managed appropriately to allow this to happen.

### Benefits of considering microclimate

This study contributes to a growing understanding of the relationship between species and microclimate (Davies et al. 2006, Anthes et al. 2008, Ashton et al. 2009, Kearney et al. 2010, Bradbury et al. 2011, Calladine and Bray 2012). Microclimate variables, such as degree-days available during larval development, as here, can be expected to have more direct ecological relevance than coarse climate measures (Buckley et al. 2011), and therefore models built from them ought to give better predictions into new situations, i.e. improved transferability (Dobrowski et al. 2011). As an example of these benefits, if we had tried to predict range change for *P. argus* in Wales on the basis of coarse-grained climate we could not have produced sensible results. As mentioned, regional May climate has warmed by more than 1°C in the last 40 yr in our study area. According to the UKCIP09 map at 5 km resolution, most of lowland central Britain is within  $\pm 0.5^\circ\text{C}$  of our study area, so May isotherms would have shifted at least 100 km north. A more mechanistic understanding of species' temperature tolerance can also lead to modelling of how alterations in habitat structure could exacerbate or mitigate the effects of climate warming (Menéndez and Gutiérrez 2004, Turlure et al. 2010, Larsen 2012, Suggitt et al. 2012, De Frenne et al. 2013).

When microclimate is considered, this can also help to explain why species are responding idiosyncratically or nonlinearly to climate change. The interaction between microclimates (as determined by slope and aspect) and regional macroclimate generates a non-linear change in the availability of thermally suitable habitats as the climate warms (see our example Fig. 3d). We suspect that the sigmoid pattern seen in Fig. 3d would be commonly found for other species and landscapes (and with other thresholds), and this could be part of the reason for the heterogeneity of species' apparent responses to climate change (Tomanek 2010, Chen et al. 2011). A similarly shaped relationship is likely to hold in reverse for cold-adapted species, for which little distribution decline might be noticed with initial warming, collapses in regional distributions with additional warming, followed by survival of localized populations in the coldest microclimates for a while thereafter (Hampe and Petit 2005, Gillingham et al. 2012). Improved understanding of these non-linear relationships could assist in adapting conservation actions in the face of climate change.

However, the most important message for conservation from this and other similar studies may be that strategies need to be robust to a very wide margin of uncertainty, and not rely on misleadingly precise predictions. Firstly, studies of organisms' responses to microclimate have highlighted that there are potentially hundreds more climate variables to choose from than are usually considered in traditional SDMs (e.g. temperature extremes rather than means, accumulated degrees over different time periods, night versus day temperatures, etc.). Studies of individual well known species can use

a few selected variables based on physiology and behaviour, but it would be difficult to apply this approach consistently to many species of conservation concern. Secondly, even if we are quite confident of the correct climate variables to use, the inflection point of the non-linear relationship mentioned above is likely to be very sensitive to the species' exact temperature response. Therefore, in many situations with limited data, we may have to accept that a species' rate of distribution change will be highly unpredictable even if the direction of change is known with high confidence.

There are a variety of suggested approaches for using microclimate information to set conservation priorities under climate change, including identifying microrefugia and microclimate-based stepping stones (Ashcroft 2010, Hannah et al. 2014). However, it is not known whether these approaches tend to be, or can be made to be, robust to uncertainty and applicable to a large enough fraction of species. The answer will depend on the strength of correlations between climate variables and between species at different spatial scales, and would be an important avenue for future research.

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### References

- Angert, A. L. et al. 2011. Do species' traits predict recent shifts at expanding range edges? – *Ecol. Lett.* 14: 677–689.
- Anthes, N. et al. 2008. The Duke of Burgundy butterfly and its dukedom: larval niche variation in *Hamearis lucina* across central Europe. – *J. Insect Conserv.* 12: 3–14.
- Ashcroft, M. B. 2010. Identifying refugia from climate change. – *J. Biogeogr.* 37: 1407–1413.
- Ashton, S. et al. 2009. Effects of temperature and elevation on habitat use by a rare mountain butterfly: implications for species responses to climate change. – *Ecol. Entomol.* 34: 437–446.
- Beever, E. A. et al. 2010. Testing alternative models of climate-mediated extirpations. – *Ecol. Appl.* 20: 164–178.
- Bennie, J. et al. 2008. Slope, aspect and climate: spatially explicit and implicit models of topographic microclimate in chalk grassland. – *Ecol. Model.* 216: 47–59.
- Bennie, J. J. et al. 2013. Range expansion through fragmented landscapes under a variable climate. – *Ecol. Lett.* 16: 921–929.
- Blois, J. L. et al. 2013. Space can substitute for time in predicting climate-change effects on biodiversity. – *Proc. Natl Acad. Sci. USA* 110: 9374–9379.
- Bradbury, R. B. et al. 2011. The influence of climate and topography in patterns of territory establishment in a range-expanding bird. – *Ibis* 153: 336–344.
- Buckley, L. B. et al. 2010. Can mechanism inform species' distribution models? – *Ecol. Lett.* 13: 1041–1054.
- Buckley, L. B. et al. 2011. Does including physiology improve species distribution model predictions of responses to recent climate change? – *Ecology* 92: 2214–2221.
- Calladine, J. and Bray, J. 2012. The importance of altitude and aspect for breeding whinchats *Saxicola rubetra* in the uplands:

- limitations of the uplands as a refuge for a declining, formerly widespread species? – *Bird Study* 59: 43–51.
- Chen, I. C. et al. 2011. Rapid range shifts of species associated with high levels of climate warming. – *Science* 333: 1024–1026.
- Cowley, M. J. R. et al. 2001. Density–distribution relationships in British butterflies. II. An assessment of mechanisms. – *J. Anim. Ecol.* 70: 426–441.
- Davies, Z. G. et al. 2006. Changing habitat associations of a thermally constrained species, the silver-spotted skipper butterfly, in response to climate warming. – *J. Anim. Ecol.* 75: 247–256.
- De Frenne, P. et al. 2013. Microclimate moderates plant responses to macroclimate warming. – *Proc. Natl Acad. Sci. USA* 110: 18561–18565.
- Dennis, R. L. H. 1977. The British butterflies – their origin and establishment. – EW Clasley.
- Dennis, R. L. H. and Sparks, T. H. 2006. When is a habitat not a habitat? Dramatic resource use changes under differing weather conditions for the butterfly *Plebejus argus*. – *Biol. Conserv.* 129: 291–301.
- Dobrowski, S. Z. et al. 2011. Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits. – *Ecol. Monogr.* 81: 241–257.
- Engler, R. et al. 2011. 21st century climate change threatens mountain flora unequally across Europe. – *Global Change Biol.* 17: 2330–2341.
- Fox, R. et al. 2006. The state of butterflies in Britain and Ireland. – Pisces Publications.
- Gillingham, P. K. et al. 2012. The effect of spatial resolution on projected responses to climate warming. – *Divers. Distrib.* 18: 990–1000.
- Gutiérrez, D. and Thomas, C. D. 2000. Marginal range expansion in a host-limited butterfly species *Gonepteryx rhamni*. – *Ecol. Entomol.* 25: 165–170.
- Hampe, A. and Petit, R. J. 2005. Conserving biodiversity under climate change: the rear edge matters. – *Ecol. Lett.* 8: 461–467.
- Hannah, L. et al. 2014. Fine-grain modeling of species' response to climate change: holdouts, stepping-stones, and microrefugia. – *Trends Ecol. Evol.* 29: 390–397.
- Hodgson, J. A. et al. 2012. The speed of range shifts in fragmented landscapes. – *PLoS One* 7: e47141.
- Kearney, M. R. et al. 2010. Correlative and mechanistic models of species distribution provide congruent forecasts under climate change. – *Conserv. Lett.* 3: 203–213.
- Larsen, T. H. 2012. Upslope range shifts of Andean dung beetles in response to deforestation: compounding and confounding effects of microclimatic change. – *Biotropica* 44: 82–89.
- Lenoir, J. et al. 2010. Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. – *Ecography* 33: 295–303.
- Lewis, O. T. et al. 1997. Three ways of assessing metapopulation structure in the butterfly *Plebejus argus*. – *Ecol. Entomol.* 22: 283–293.
- Marchant, A. J. 1956. *Plebejus argus caermensis* Thompson at Rhyd-y-foel and Llandulas. – *Entomologist* 89: 234.
- McInerney, G. et al. 2007. Range shifting on a fragmented landscape. – *Ecol. Inform.* 2: 1–8.
- Melles, S. J. et al. 2011. Expanding northward: influence of climate change, forest connectivity, and population processes on a threatened species' range shift. – *Global Change Biol.* 17: 17–31.
- Menéndez, R. and Gutiérrez, D. 2004. Shifts in habitat associations of dung beetles in northern Spain: climate change implications. – *Ecoscience* 11: 329–337.
- Merrill, R. M. et al. 2008. Combined effects of climate and biotic interactions on the elevational range of a phytophagous insect. – *J. Anim. Ecol.* 77: 145–155.
- Oliver, T. et al. 2009. Changes in habitat specificity of species at their climatic range boundaries. – *Ecol. Lett.* 12: 1091–1102.
- Pateman, R. M. et al. 2012. Temperature-dependent alterations in host use drive rapid range expansion in a butterfly. – *Science* 336: 1028–1030.
- Pearman, P. B. et al. 2008. Prediction of plant species distributions across six millennia. – *Ecol. Lett.* 11: 357–369.
- Pollard, E. 1977. A method for assessing changes in the abundance of butterflies. – *Biol. Conserv.* 12: 115–134.
- Randin, C. F. et al. 2009. Climate change and plant distribution: local models predict high-elevation persistence. – *Global Change Biol.* 15: 1557–1569.
- Rapacciuolo, G. et al. 2012. Climatic associations of British species distributions show good transferability in time but low predictive accuracy for range change. – *PLoS One* 7: e40212.
- Smith, A. B. et al. 2013. Evaluation of species distribution models by resampling of sites surveyed a century ago by Joseph Grinnell. – *Ecography* 36: 1017–1031.
- Suggitt, A. J. et al. 2011. Habitat microclimates drive fine-scale variation in extreme temperatures. – *Oikos* 120: 1–8.
- Suggitt, A. J. et al. 2012. Habitat associations of species show consistent but weak responses to climate. – *Biol. Lett.* 8: 590–593.
- Thomas, C. D. 1985. The status and conservation of the butterfly *Plebejus argus* L (Lepidoptera, Lycaenidae) in north-west Britain. – *Biol. Conserv.* 33: 29–51.
- Thomas, J. A. et al. 1999. Intraspecific variation in habitat availability among ectothermic animals near their climatic limits and their centres of range. – *Funct. Ecol.* 13: 55–64.
- Tingley, M. W. et al. 2012. The push and pull of climate change causes heterogeneous shifts in avian elevational ranges. – *Global Change Biol.* 18: 3279–3290.
- Tomanek, L. 2010. Variation in the heat shock response and its implication for predicting the effect of global climate change on species' biogeographical distribution ranges and metabolic costs. – *J. Exp. Biol.* 213: 971–979.
- Turlure, C. et al. 2010. Microclimatic buffering and resource-based habitat in a glacial relict butterfly: significance for conservation under climate change. – *Global Change Biol.* 16: 1883–1893.
- Venables, W. N. and Ripley, B. D. 2002. Modern applied statistics with S, 4th ed. – Springer.
- Warren, M. S. et al. 2001. Rapid responses of British butterflies to opposing forces of climate and habitat change. – *Nature* 414: 65–69.
- Wetey, D. and Woodin, S. 2008. Ecological hindcasting of biogeographic responses to climate change in the European intertidal zone. – *Hydrobiologia* 606: 139–151.
- Wood, S. N. 2004. Stable and efficient multiple smoothing parameter estimation for generalized additive models. – *J. Am. Stat. Assoc.* 99: 673–686.
- Zhu, K. et al. 2012. Failure to migrate: lack of tree range expansion in response to climate change. – *Global Change Biol.* 18: 1042–1052.

Supplementary material (Appendix ECOG-00825 at <[www.ecography.org/readers/appendix](http://www.ecography.org/readers/appendix)>). Appendix 1.