

Does including physiology improve species distribution model predictions of responses to recent climate change?

LAUREN B. BUCKLEY,^{1,3} STEPHANIE A. WAASER,¹ HEIDI J. MACLEAN,¹ AND RICHARD FOX²

¹Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599 USA

²Butterfly Conservation, Manor Yard, East Lulworth, Wareham, Dorset BH20 5QP United Kingdom

Abstract. Thermal constraints on development are often invoked to predict insect distributions. These constraints tend to be characterized in species distribution models (SDMs) by calculating development time based on a constant lower development temperature (LDT). Here, we assessed whether species-specific estimates of LDT based on laboratory experiments can improve the ability of SDMs to predict the distribution shifts of six U.K. butterflies in response to recent climate warming. We find that species-specific and constant (5°C) LDT degree-day models perform similarly at predicting distributions during the period of 1970–1982. However, when the models for the 1970–1982 period are projected to predict distributions in 1995–1999 and 2000–2004, species-specific LDT degree-day models modestly outperform constant LDT degree-day models. Our results suggest that, while including species-specific physiology in correlative models may enhance predictions of species' distribution responses to climate change, more detailed models may be needed to adequately account for interspecific physiological differences.

Key words: butterflies; degree-days; hybrid models; larval development; lower developmental threshold; phenology; range shifts; species distribution models; thermal constraints; United Kingdom; voltinism.

INTRODUCTION

The relative merits of two distinct approaches to predicting species' distribution shifts in response to climate change have been recently debated (Kearney and Porter 2009, reviewed in Buckley et al. 2010). Correlative models estimate parameters phenomenologically by statistically relating current distributions to environmental conditions. Mechanistic models incorporate explicit relationships between environmental conditions and organismal performance estimated independently of current distributions. While ideal mechanistic models may more appropriately model the dynamics of range limitations through time (Buckley et al. 2010), they require extensive organismal and climate data for parameterization and often need to be tailored to particular applications. Correlative models can be readily applied to any application for which locality and climate data is available. Reviews have largely concluded that the two approaches are complementary and might be united in a "hybrid" model (Midgley et al. 2007, Kearney and Porter 2009, Morin and Thuiller 2009, Buckley et al. 2010).

Hybrid models incorporate the output of a mechanistic model as a predictor in a correlative model (Kearney and Porter 2009, Buckley et al. 2010). These models enable more biologically informed distribution models to be readily implemented. The outputs of a mechanistic

(ecophysiological) model for cane toads were chosen to be important predictors in a correlative model, but did not alter model predictions (Elith et al. 2010). Related approaches include linking stochastic population growth to the probability of occurrence predicted by correlative models (Smith et al. 2001, Keith et al. 2008) and estimating development and growth rates and stress from observed distributions (CLIMEX; Sutherst and Maywald 1985). In our hybrid modeling approach, we developed simple models of development time (degree-days; accumulated development time above a lower developmental time [LDT] temperature) based on laboratory experiments for particular species. We incorporated predictions of degree-days into Maxent correlative species distribution models (SDMs).

The ability of SDMs to predict responses to recent climate change has seldom been tested (Nog Nogués-Bravo 2009) despite the recognized importance of testing their ability to make dynamic range predictions (Buckley et al. 2010). Our analysis focuses on U.K. butterflies, which have served as a flagship for understanding species responses to recent environmental change (Dennis 1993, Parmesan et al. 1999, Roy and Sparks 2000, Warren et al. 2001, Hill et al. 2002, Franco et al. 2006). Our study extends and integrates previous work for U.K. butterflies by Hill et al. (2002), which hindcasted SDMs based on a constant LDT, and Bryant et al. (2002), which examined whether species-specific degree-day (dd) requirements limit distributions. Bryant et al. (2002) concluded that species-specific behavior and life history factors into species distributions. Hill et al. (2002) examined distribu-

Manuscript received 13 January 2011; revised 27 June 2011; accepted 28 June 2011; final version received 9 August 2011.
Corresponding Editor: S. J. Simpson.

³ E-mail: buckley@bio.unc.edu

tional shifts for U.K. butterflies between 1970–1982 and 1995–1999 using SDMs which incorporated dd with a 5°C LDT base, coldest month mean temperature, and moisture availability. Similar climate variables (dd with a 5°C base, coldest month mean temperature, and annual precipitation) were successfully used by Luoto et al. (2006) to predict the distributions of Finnish butterflies. Kearney et al. (2010) integrated laboratory measurements of the temperature dependence of larval development and a biophysical model to attribute a butterfly's advancement in phenology to climate change.

Here we investigated whether including species-specific degree-day measures can better predict the geographic responses of U.K. butterflies to climate change. We compared the performance of SDM models based on fixed (5°C) and species-specific LDT at predicting distributions in 1970–1982 based on climate data during the same time period (i.e., 1970–1982 now-casting). We then assessed the performance of those SDMs when projected to predict distributions in 1995–1999 and 2000–2004. Notably, warming on the order of 1°C has occurred in the United Kingdom between our testing and projection period (Perry 2006).

METHODS

Species data

Butterfly distribution data for 51 species in Britain were obtained from data sets compiled by the Biological Records Centre (CEH, Monks Wood, United Kingdom), and Butterfly Conservation. Records are from two time periods (1970–1982 and 1995–1999) of comparable and intensive recording effort preceding the publication of national distribution atlases (Heath et al. 1984, Asher et al. 2001). An additional time period (2000–2004) with comparable recording effort (R. Fox, *personal observation*) was also examined. Records were reported within the 10 × 10 km grid cells of the United Kingdom National Grid. Grid IDs were converted into geographic (UTM) coordinates in R (R Development Core Team 2011). We equalized recording effort between observation periods by subsampling the 1995–1999 and 2000–2004 data sets to the number of observations in 1970–1982 for each species in each model run.

Our analysis focused on six resident species for which laboratory data on lower developmental temperatures (LDT) thresholds for larval development were available (Table 1). We additionally provide values for LDT and degree-day requirements for development of combined larval and pupa stages for comparison (Appendix: Table A1). The laboratory studies examined larval development time for at least three constant temperatures. For the two species for which LDT was not reported directly (*Aricia agestis*, *Pieris brassicae*), we used a well-established relationship between development rate (R , 1/development time, d^{-1}) and temperature (T , °C) to estimate LDT (Campbell et al. 1974, Lamb 1992, Bryant et al. 1997): $R = a + bT$. The parameters a and b are estimated via linear regressions (Appendix: Table A2). LDT is estimated as

the y -intercept ($-a/b$). The degree-day requirement for larval development can be estimated as the reciprocal of the slope ($1/b$). We note that this commonly implemented technique for estimating LDT can sometimes produce underestimates of LDT due to temperature thresholds (Bergant and Trdan 2006). All species are bivoltine or have two flight periods annually in the United Kingdom.

Climate data

Climate data (daily maximum, minimum, and mean temperatures and annual precipitation) gridded over a 5 × 5 km United Kingdom Climate Projections (UKCP09) grid were obtained from the United Kingdom Met Office. Degree-days were calculated in R as the accumulated product of time and temperature above the LDT for each day. We calculated dd using a single-sine approximation (Allen 1976) based on daily minimum and maximum temperatures and a fixed spacing of 12 hours between temperature minima and maxima. Although larval development is generally restricted to the spring and summer, we calculated annual degree-days for consistency with Hill et al. (2002) and Luoto et al. (2006). We calculated degree-days with a 5°C base, degree-days with a species-specific LDT, coldest month mean temperature, and annual precipitation as the five-year mean of climate data within the center of the study period (1974–1978, 1995–1999, and 2000–2004).

Larval body temperatures may deviate from environmental temperatures and influence dd predictions due to microclimate effects mediated by thermoregulatory behavior (Bryant et al. 2002). The microclimate of host plants is sufficiently complex that physical rather than biophysical models are generally used to estimate microclimates (Kingsolver 2000). We thus accounted for thermoregulation by examining the two extreme scenarios (perfect thermoregulation and no thermoregulation: body = air temperature) for a subset of thermoregulating species with known preferred temperatures. We used UKCP09 grid monthly average estimates of the duration (hours per day) of bright sunshine. We assumed that the bright sunshine occurs over the hottest part of the day and that the species is able to thermoregulate to its preferred temperature over this duration. We added the additional degree-days accumulated by thermoregulation to the single-sine wave calculation of dd. Gregarious *Aglais urticae* and *Inachis io* were observed to thermoregulate to their preferred temperatures (32.5°C and 31.5°C, respectively) during sunshine irrespective of ambient temperatures, whereas the body temperature of the solitary *Polygonia c-album* largely followed ambient temperatures (Bryant et al. 2000).

Species distribution models and assessment

We ran Maxent SDMs (Phillips et al. 2006) in the R package *dismo* (version 0.7-1; *available online*).⁴ First,

⁴ (<https://r-forge.r-project.org/projects/dismo/>)

TABLE 1. Lower developmental temperatures (LDT) and degree-days required for development (dd) for the larval stage.

Species	Thresholds		Contribution			1970–1982		
	LDT (°C)	dd	Pre	Temp	dd	κ	Cor	AUC
Species-specific LDT								
<i>Aglais urticae</i>	10.3	205.6	60.6	17.5	21.9	0.13 ± 0.0013	0.15 ± 0.0013	0.58 ± 0.0008
<i>Aricia agestis</i>	10.8	247.2	16.0	1.2	82.8	0.60 ± 0.0024	0.64 ± 0.0019	0.83 ± 0.0014
<i>Inachis io</i>	8.3	315.2	5.6	19.8	74.6	0.16 ± 0.0015	0.19 ± 0.0015	0.60 ± 0.0009
<i>Pieris brassicae</i>	6.9	236.7	40.1	6.7	53.3	0.20 ± 0.0014	0.24 ± 0.0014	0.62 ± 0.0009
<i>Pieris rapae</i>	10.0	157.0	10.0	7.4	82.5	0.24 ± 0.0015	0.28 ± 0.0015	0.64 ± 0.001
<i>Polygonia c-album</i>	7.0	281.2	12.2	6.4	81.4	0.34 ± 0.0017	0.38 ± 0.0016	0.70 ± 0.0011
With thermoregulation								
<i>Aglais urticae</i>			84.4	4.8	10.8	0.14 ± 0.0014	0.17 ± 0.0014	0.59 ± 0.0008
<i>Inachis io</i>			1.4	84.4	14.3	0.32 ± 0.0016	0.37 ± 0.0015	0.68 ± 0.001
5°C LDT								
<i>Aglais urticae</i>			42.7	17.6	39.7	0.12 ± 0.0013	0.16 ± 0.0013	0.58 ± 0.0008
<i>Aricia agestis</i>			27.8	1.7	70.4	0.58 ± 0.0025	0.63 ± 0.002	0.82 ± 0.0014
<i>Inachis io</i>			13.4	21.1	65.4	0.16 ± 0.0014	0.19 ± 0.0014	0.60 ± 0.0009
<i>Pieris brassicae</i>			44.4	7.4	48.2	0.20 ± 0.0015	0.24 ± 0.0015	0.62 ± 0.0009
<i>Pieris rapae</i>			20.0	9.9	70.2	0.24 ± 0.0015	0.28 ± 0.0015	0.64 ± 0.001
<i>Polygonia c-album</i>			15.4	7.0	77.6	0.34 ± 0.0017	0.38 ± 0.0016	0.70 ± 0.0011

Notes: The performance of Maxent models (κ [kappa], Cor [correlation], and area under the curve [AUC] ± SE) for testing in 1970–1982 and projection to 1995–1999 and 2000–2004. The proportional contribution of precipitation (Pre), mean temperature of the coldest month (Temp), and degree-days are included for models run with species-specific estimates of LDT and a fixed 5°C cutoff.

we used 100% of records for the 1970–1982 period to calibrate models, and then projected these models onto the independent data sets for the 1995–1999 and 2000–2004 periods for testing. Subsequently, we used 80% of records for the 1970–1982 period to calibrate models and the remaining 20% for model testing. We also projected these models to 1995–1999 and 2000–2004. Models were run with two sets of environmental variables: (1) degree-days, mean temperature of the coldest month, and mean annual precipitation (as in Hill et al. 2002, Luoto et al. 2006), and (2) degree-days only.

Our analysis and assessment follows that in Araujo et al. (2005). We evaluated model performance in each time period by randomly generating a number of pseudo-absences equal to half of the presence points using the RandomPoints function in dismo. We tested agreement between observed and predicted distributions using Cohen's κ statistic of similarity (κ) and the area under curve (AUC) of the receiver operating characteristic (ROC) approach (Fielding and Bell 1997, but see Lobo et al. 2008 for a critique of the commonly used AUC). We also assessed the correlation (Cor) between a model's predictions and presence/absence in the test data by calculating a Pearson correlation coefficient (Phillips and Dudík 2008). We used the prevalence of presences in the 1970–1982 period as calculated in Maxent (Phillips and Dudík 2008) as a presence threshold (Liu et al. 2005). We averaged the performance statistics over five iterations of the model runs and 100 iterations of evaluations for each model run to account for variance due to partitioning test and training data. AUC values ranged from 0.5 and 1, and κ values ranged from 0 to 1 for perfect and no predictive

ability, respectively. AUC values may be interpreted as excellent (AUC > 0.90), good (0.80 < AUC < 0.90), fair (0.70 < AUC < 0.80), poor (0.60 < AUC < 0.70), and fail (0.50 < AUC < 0.60) (Swets 1988). Values of κ may be interpreted as excellent (κ > 0.75), good (0.40 < κ < 0.75), and poor (0.00 < κ < 0.40) (Landis and Koch 1977).

RESULTS

Degree-day estimates and range limits

The lower development temperatures documented in the literature are all higher than the 5°C threshold (Table 1). Maps of accumulated degree-days differ markedly between species (Fig. 1 and Appendix: Fig. A1). The annual number of degree-days available increased markedly from 1970–1982 levels in 1995–1999 and 2000–2004. For several species, butterfly distributions did correspond well to areas predicted to have a sufficient number of degree-days annually to complete two generations (Appendix: Fig. A2).

SDM predictions of current distributions

The Maxent models exhibit fairly weak performance for most species according to both κ and AUC performance metrics (Table 1, Fig. 2, and Appendix: Figs. A3 and A7). Performances were similar whether the models are parameterized with degree-days, temperature, and precipitation, or with degree-days only (Table 1 and Appendix: Fig. A3). The weak performance of the models may occur because a large proportion of the species cover most of the available range extent in the United Kingdom. Indeed, the most restricted species, *A. agestis* and *P. c-album*, exhibit the highest performance.

TABLE 1. Extended.

1995–1999			2000–2004		
κ	Cor	AUC	κ	Cor	AUC
0.10 ± 0.0013	0.11 ± 0.0014	0.56 ± 0.0008	0.11 ± 0.0014	0.13 ± 0.0014	0.57 ± 0.0009
0.52 ± 0.0024	0.60 ± 0.0021	0.78 ± 0.0016	0.54 ± 0.0026	0.61 ± 0.0021	0.80 ± 0.0016
0.17 ± 0.0015	0.24 ± 0.0015	0.62 ± 0.0009	0.15 ± 0.0015	0.17 ± 0.0015	0.59 ± 0.0009
0.15 ± 0.0014	0.19 ± 0.0014	0.60 ± 0.0009	0.18 ± 0.0014	0.22 ± 0.0014	0.61 ± 0.0009
0.18 ± 0.0015	0.24 ± 0.0014	0.61 ± 0.0009	0.21 ± 0.0015	0.26 ± 0.0014	0.63 ± 0.0009
0.29 ± 0.0017	0.41 ± 0.0015	0.70 ± 0.0011	0.29 ± 0.0018	0.38 ± 0.0016	0.69 ± 0.0011
0.08 ± 0.0015	0.10 ± 0.0014	0.56 ± 0.0009	0.09 ± 0.0012	0.12 ± 0.0014	0.57 ± 0.0009
0.19 ± 0.0016	0.23 ± 0.0016	0.62 ± 0.0001	0.12 ± 0.0015	0.14 ± 0.0017	0.58 ± 0.0011
0.07 ± 0.0013	0.09 ± 0.0013	0.55 ± 0.0008	0.10 ± 0.0013	0.11 ± 0.0013	0.56 ± 0.0008
0.50 ± 0.0027	0.60 ± 0.0021	0.80 ± 0.0015	0.51 ± 0.0026	0.61 ± 0.002	0.81 ± 0.0015
0.12 ± 0.0014	0.20 ± 0.0014	0.61 ± 0.0009	0.12 ± 0.0015	0.14 ± 0.0014	0.58 ± 0.0009
0.13 ± 0.0014	0.17 ± 0.0014	0.59 ± 0.0009	0.15 ± 0.0015	0.20 ± 0.0015	0.60 ± 0.0009
0.15 ± 0.0015	0.21 ± 0.0014	0.61 ± 0.0009	0.17 ± 0.0015	0.22 ± 0.0015	0.62 ± 0.0009
0.29 ± 0.0018	0.38 ± 0.0016	0.69 ± 0.0011	0.28 ± 0.0018	0.35 ± 0.0017	0.68 ± 0.0011

The proportions of true and false absences and presences were similar whether or not species-specific estimates of LDT were included (Appendix: Fig. A4). The contribution of degree-days to the Maxent model increased when species-specific estimates of LDT were included relative to a fixed 5°C threshold (Table 1). However, we note that the species-specific and fixed 5°C threshold degree-day estimates are highly correlated (Spearman correlation coefficient = 0.98 average across species and time periods). In several cases, including species-specific degree-days estimates improved the performance of the Maxent model for the 1970–1982 period (particularly for the degree-day only models; Fig. 3C, D). However, performances were generally similar between the two estimation methods for degree-days. All results were confirmed when using 80% of the 1970–1982 data set for model testing and 20% for training (Appendix: Fig. A5).

SDM projections

Model performance tended to decrease when projecting the Maxent models parameterized for the 1970–1982 time periods to future time periods (Fig. 3). Models parameterized with species-specific estimates of LDT modestly, but significantly, outperform those parameterized with a fixed 5°C LDT when projected to the 1995–1999 and 2000–2004 period (pairwise *t* test, Fig. 3; see also standard errors, Table 1). This performance difference is most pronounced when the models are parameterized with degree-days alone (Appendix: Fig. A3).

Thermoregulation increased our dd estimates by an average of 20.5% and 18.1% for *A. urticae* and *I. io*, respectively, but maps and model predictions were similar (Appendix: Figs. A8–A10). While the models with thermoregulation performed similarly for *A.*

urticae, model performance for *I. io* improved in 1970–1982, but then declined considerably in extrapolation to values similar to the values without thermoregulation (Table 1). Notably, the relative contribution of dd declined somewhat for *A. urticae* and dramatically for *I. io* when accounting for thermoregulation (Table 1).

DISCUSSION

Including species-specific physiological measurements in Maxent models significantly improved model performance in projection, albeit modestly. Findings are consistent with our hypothesis that species-specific physiological information may better characterize the underlying climatic constraint on species' distributions. If this is the case, we would expect little performance improvement when SDMs are tested against current distributions. This is because both generic and species-specific parameters have similar spatial structure and are likely to correlate equally well with observed distributions. We would expect the performance advantage to occur in extrapolation. A modest performance advantage was indeed observed when we projected the models to 1995–1999 and 2000–2004. Monthly mean temperatures averaged across the United Kingdom were considerably warmer during the two more recent time periods than 1970–1982 (Perry 2006). Our findings are consistent with a potential advantage of incorporating species-specific physiological data in SDMs. The advantage could potentially be enhanced by using more detailed biophysical models to account for larval microclimate (Bryant et al. 2002). However, incorporating thermoregulation in the dd calculations for two species improved performance only for a single species in the initial time period.

We expect the performance advantages to increase when the models are projected further into the future.

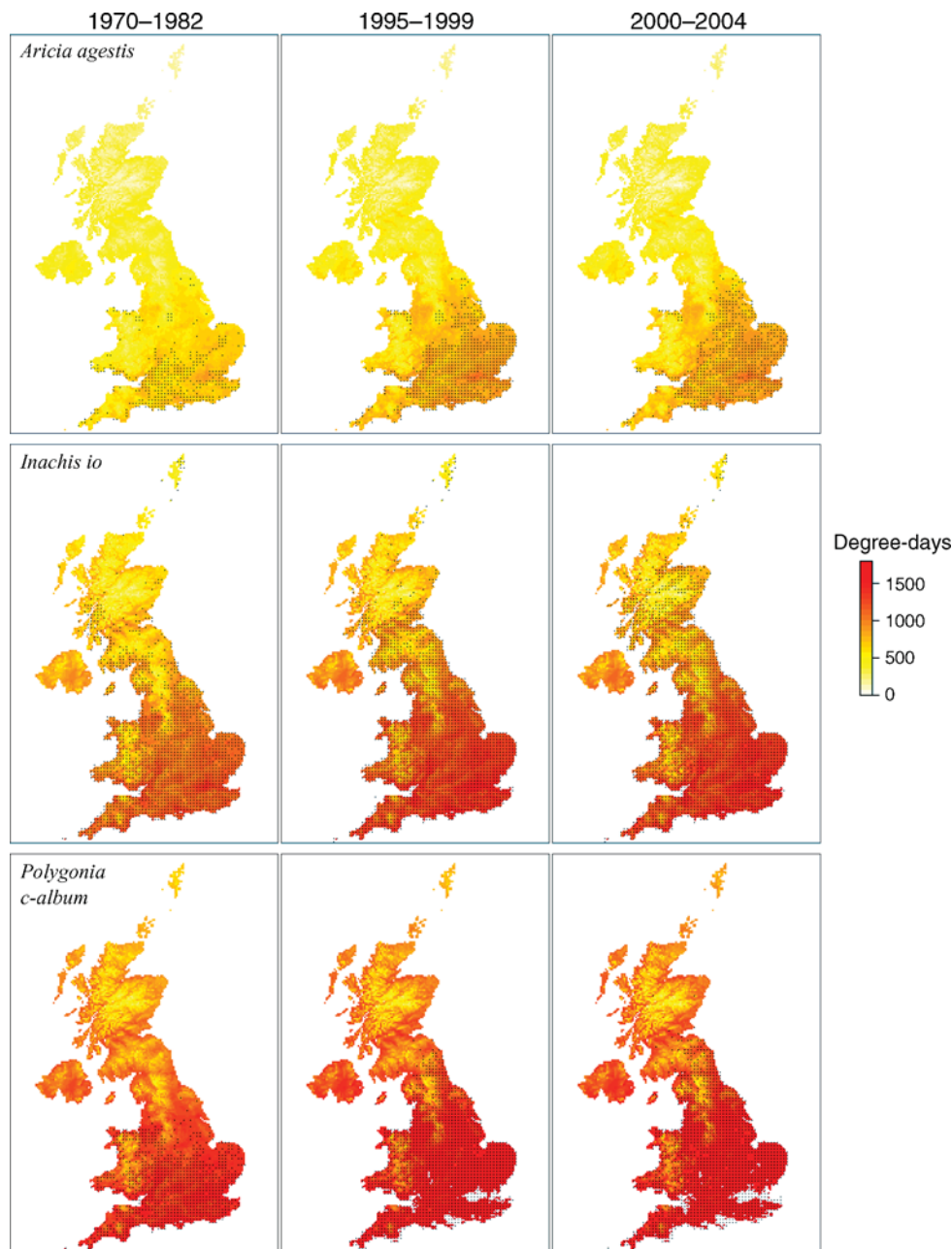


FIG. 1. Annual degree-days (accumulated degrees across time above a lower developmental temperature threshold) accumulated using species-specific lower developmental thresholds for butterflies *Aricia agestis*, *Inachis io*, and *Polygonia c-album* in the United Kingdom. Occurrences in each time period are depicted (black dots). (See Appendix Fig. A1 for all species and Appendix Fig. A2 for estimates of potential generations.)

Performance advantages are likely to be particularly apparent when the correlation between environmental variables becomes uncoupled in novel environments (Williams and Jackson 2007). Hindcasting performance tends to be best for those species with stable climatic constraints over time (Pearman et al. 2008, Nogués-Bravo 2009). Spatial autocorrelation may minimize differences in performance between species-specific and

constant LDT models by accounting for a large proportion of model performance. If spatial autocorrelation remains similar between the time periods, it may not matter what particular environmental variable is being used in the model (Segurado et al. 2006, Beale et al. 2008). Indeed, an analysis for bird abundance found that a model based purely on spatial autocorrelation outperformed an environmental niche model based on

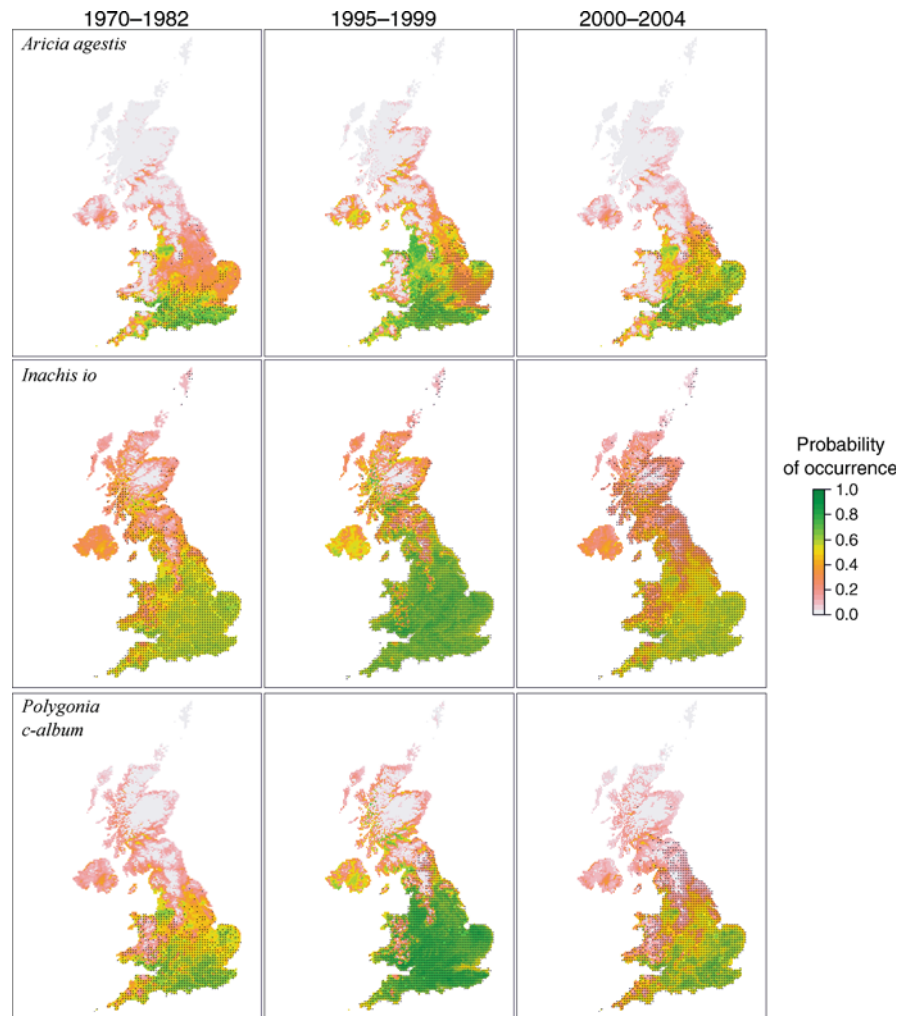


FIG. 2. The probability of occurrence predicted by Maxent species distribution models (SDMs) and observed distributions (black dots) for 1970–1982. (See Appendix Fig. A6 for additional distribution maps and Appendix Fig. A7 for a depiction of the Maxent models parameterized with 1970–1982 distribution data and projected to 1995–1999 and 2000–2004 for all species.)

spatial autocorrelation (Bahn and McGill 2007). The reliance of correlative models on correlation structure is suggested by the greater performance advantage of species-specific degree estimates in the degree-day only models. Including space has been demonstrated to improve the ability of SDMs to predict distributions out of equilibrium (De Marco et al. 2008).

Findings were generally similar across species. However, model performance was highest for *A. agestis*, which had the smallest initial range and has undergone a substantial range expansion. This finding may be due to *A. agestis* diversifying its host plant use and expanding to areas lacking its preferred host plant (Thomas et al. 2001). This expansion may have been enabled by a reduction in thermal stress and may have resulted in range boundaries better corresponding to absolute physiological limits. Additionally, range expansion may have been facilitated by an escape from parasitism

(Menéndez et al. 2008). Life history trade-offs can result in different range constraints acting across a range and complicate predictions of range dynamics (Burke et al. 2005).

A previous, detailed examination of the ability of degree-days to predict the distributions of U.K. butterflies found that degree-days failed to accurately predict distributions when other factors constrained distributions (Bryant et al. 1997). While maps of potential generations correspond reasonably well to observed distributions (Appendix: Fig. A2), estimates of potential generations may become less informative as butterflies alter their voltinism in response to climate change (Altermatt 2009). Increases in the number of generations per year may enhance population growth and facilitate range expansion (Altermatt 2009). Larval thermoregulation was also observed to result in range underestimates (e.g., for *A. urticae* and *I. io*) based on

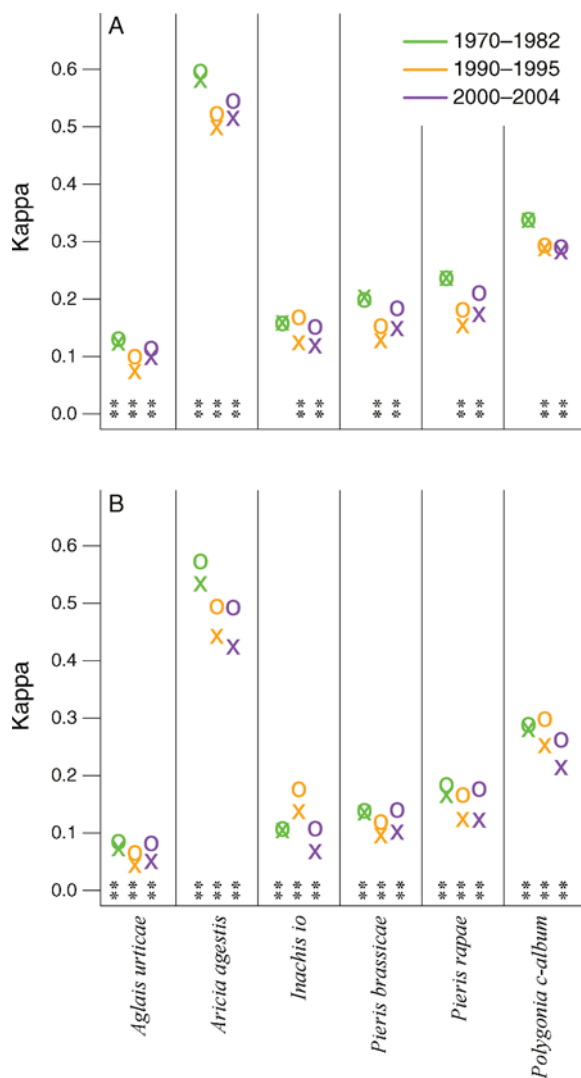


FIG. 3. SDM performance (κ [kappa]) for Maxent models parameterized with (A) degree-days, temperature, and precipitation and (B) degree-days only. SDMs incorporating degree-day estimates based on species-specific estimates of lower development temperature (open circles) tend to outperform those based on a fixed 5°C threshold (X's), particularly when projecting to future time periods and when parameterizing the models with degree-days only. Cases in which the performance of the models based on the fixed 5°C threshold is significantly lower ($P < 0.01$ in pairwise t test) are depicted with asterisks along the base. Significance should be interpreted conservatively as we are comparing iterations of models based on a single observed data set to assess significance.

degree-day calculations (Bryant et al. 1997, 2002). Ongoing human landscape modifications can drive substantial divergences from distribution predictions based on climate (Warren et al. 2001), but are unlikely to have substantially impacted our focal species (R. Fox, *personal observation*). Additionally, butterfly expansions may lag behind the expansion of thermally suitable habitat (Menéndez et al. 2006, Willis et al. 2009).

Our analysis suggests the viability of hybrid models. It is relatively straightforward to include the output of simple mechanistic models (e.g., degree-day models) in correlative models. While the performance advantages of including species-specific traits were modest in our analysis, the performance advantage is consistent with our expectation that species-specific traits can better characterize range constraints. Further analysis for different groups, locations, and hindcasting duration is warranted. Appropriately characterizing range constraints is likely to increase in importance in the novel environmental conditions that are likely to occur over longer-term extrapolation.

ACKNOWLEDGMENTS

We thank the countless volunteers who contributed to collecting the butterfly data. Thanks to A. Hurlbert, J. Kingsolver, D. McGlinn, J. Stegen, and reviewers for comments.

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APPENDIX

Supporting tables including lower development temperature and development times, and supporting figures depicting degree-days, available generations, model predictions, and model performance (*Ecological Archives* E092-192-A1).