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Dissecting the Contributions of Plasticity and Local Adaptation to the Phenology of a Butterfly and Its Host Plants

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abstract: Phenology affects the abiotic and biotic conditions that an organism encounters and, consequently, its fitness. For populations of high-latitude species, spring phenology often occurs earlier in warmer years and regions. Here we apply a novel approach, a comparison of slope of phenology on temperature over space versus over time, to identify the relative roles of plasticity and local adaptation in generating spatial phenological variation in three interacting species, a butterfly, *Anthocharis cardamines*, and its two host plants, *Cardamine pratensis* and *Alliaria petiolata*. All three species overlap in the time window over which mean temperatures best predict variation in phenology, and we find little evidence that a day length requirement causes the sensitive time window to be delayed as latitude increases. The focal species all show pronounced temperature-mediated phenological plasticity of similar magnitude. While we find no evidence for local adaptation in the flowering times of the plants, geographic variation in the phenology of the butterfly is consistent with countergradient local adaptation. The butterfly's phenology appears to be better predicted by temperature than it is by the flowering times of either host plant, and we find no evidence that coevolution has generated geographic variation in adaptive phenological plasticity.

Keywords: plasticity, local adaptation, space-for-time substitution, phenology, plant-herbivore, coevolution.

The seasonal timing at which an organism expresses a phenotype has the potential to affect the abiotic conditions to which it is exposed and interactions with con- and heterospecific individuals (Elzinga et al. 2007; Gilman et al. 2010). Over the past 15 years, interest in phenology has steadily grown, stimulated by observations across many high-latitude taxa that, coincident with the recent rise in global temperatures, spring phenology has become earlier and autumn phenology later (Parmesan and Yohe 2003).

At high latitudes, intraspecific variation in the timing of spring life-history events, such as flowering, egg laying, or migration, is often observed to correlate negatively with spring temperatures across space (Jackson 1966; Carroll et al. 2009) and time (Roy and Sparks 2000; Miller-Rushing and Primack 2008), consistent with temperature being a phenological cue. A correlation between an environmental variable and phenology is likely to arise via a combination of the effects of phenotypic plasticity and adaptive microevolution (Gienapp et al. 2008). Plasticity and genetic change may also interact; if additive genetic variation in phenological plasticity exists, then plasticity can evolve under selection (Lande 2009), meaning that interspecific and interpopulation variation in the slopes of reaction norms may reflect adaptation (Visser 2008).

The degree to which the slope of phenology on temperature is due to plasticity versus adaptive microevolution can help us predict the fate of a population or species if the climate changes (Davis et al. 2005; Phillimore et al. 2010). Consider the situation where the optimal phenology covaries with temperature and any deviation of the mean phenology of the population from this optimum reduces the mean of the absolute finesses of members of a population (for a quantitative genetic model exploring such a scenario more fully, see Chevin et al. 2010). Under this scenario, if the optimum is shifted and the mean phenology of the population does not track this optimum, the population's fate will depend on the degree to which absolute fitness is reduced and the capacity of the population for adaptive evolution. If the population tracks or partially tracks the optimum via plasticity, mean population fitness will decrease less, though plasticity may be costly (Chevin et al. 2010). Based on the above scenario, if we can quantify (i) the degree to which the optimum phenology covaries with temperature and (ii) the degree of plasticity, we can identify species for which changes in temperature may be most detrimental. While quantifying phenological plastic-

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ity of individuals or populations is quite straightforward, quantifying how absolute fitness changes with temperature and phenology requires that selection on a phenotype is quantified along a temperature gradient (Chevin et al. 2010). We can, however, use space-for-time substitution to gain some insight here. If geographic variation in phenology reflects local adaptation to average temperature, then we anticipate that a shift in the interannual average temperatures may reduce the mean fitness of populations in the short term (Davis et al. 2005; Phillimore et al. 2010; but for a critique of the practice of substituting space for time, see Hansen et al. 2012).

In the scenario outlined above, the optimum phenology is influenced by a single abiotic variable. However, phenology is also key to the matching or mismatching of interspecific ecological interactions, from the mutually beneficial to the mutually detrimental (Forrest and Miller-Rushing 2010). Therefore, the fitness landscape of phenology in a focal species will also be affected by the phenology of other species and their responses to environmental change (Stenseth and Mysterud 2002; Visser et al. 2004). Even if we want to model only the effects of a change in average temperature on the phenology and fitness of populations of two interacting species, we need estimates for several additional parameters. For instance, in addition to knowing how the optimum phenology for each species covaries with temperature, we need to know how the optimum phenology changes depending on the phenology of the other species. Because interspecific interactions are important to all species and because phenology must affect and be affected by such interactions, there is great value in considering multiple interacting species when analyzing the processes responsible for the spatial and temporal correlations between temperature and phenology.

Here we focus on the correlations between spring temperatures, the emergence time of the orange-tip butterfly (*Anthocharis cardamines*), and the flowering times of its Brassicaceae hosts, the cuckoo flower (*Cardamine pratensis*) and garlic mustard (*Alliaria petiolata*). Across its Eurasian range, *A. cardamines* is polyphagous and univoltine, with the female laying a single egg on a variety of Brassicaceae hosts during the flowering period (Wiklund and Ahrberg 1978; Courtney 1981). In Britain, *A. cardamines* chiefly utilizes two host plants, preferring *C. pratensis* in the north and west and *A. petiolata* in the south (Courtney and Duggan 1983). A study focusing on the interaction between *A. cardamines* and *C. pratensis* revealed a narrow window during which the butterfly lays its eggs; large young flower heads were preferred, and the survival of larva was best on flowers less than 8 days old (Dempster 1997). After hatching, the larva is wholly dependent on its host plant for nutrition, consuming first the flower head and then the seedpods. Thus, hosting a larva means a substantial, sometimes complete, loss of seeds for the plant (Courtney 1982). The larvae of Pierinae butterflies are the main herbivores feeding on Brassicaceae in Britain (Chew and Courtney 1991). Butterfly emergence times may therefore be under selection to match the host flowering times, while the reverse may be true of the plants.

In addition to playing a role as a phenological cue, the thermal environment may directly or indirectly exert selection on phenology. For example, it may be advantageous for an organism to have early phenology relative to other individuals to minimize intra- and interspecific competition and extend the time available for growth, but the earlier the phenology, the greater the risk of exposure to frost. Under such a simple model, the optimum phenology across time and space would covary with temperature and risk of frost. In southern Britain, *C. pratensis* and *A. petiolata* tend to begin flowering in early to mid-April, whereas flowering may be about a month later in the north. *Anthocharis cardamines* also shows geographic variation in its phenology across Britain, with first flying dates typically around mid- to late April in the south and early to mid-May in the north. Interannual variation in the phenology of all three species in Britain has been found to correlate negatively with spring average monthly temperatures (Sparks and Yates 1997). Mean first flowering of *C. pratensis* was predicted by January, February, and March temperatures, with March temperatures being the strongest predictor (Sparks and Yates 1997). Average March temperature was also identified as the strongest predictor of *A. petiolata* flowering times, with January, February, and April mean temperatures also in the best model. April temperature was the strongest predictor of first appearance of *A. cardamines*, with March temperatures also included in the best multipredictor model (Sparks and Yates 1997). In a different study addressing the first flying dates of *A. cardamines* based on a UK-wide survey, Roy and Sparks (2000) identified average February temperature as the strongest predictor. In addition to the effect of temperature, day length is known to influence the phenology of many species, including the Brassicaceae *Arabidopsis thaliana* (Metcalf and Mitchell-Olds 2009; Wilczek et al. 2010). Latitudinal variation in spring day lengths may therefore contribute to spatial variation in phenology of some species, for instance, by delaying the time period over which phenology is sensitive to temperature. To date, few macroecological studies exploring phenological variation have integrated day length and temperature information (e.g., Caffara et al. 2011) or tested whether the time period over which phenology is sensitive to temperature varies geographically (e.g., Husby et al. 2010).

In this study, we aim to distinguish between three types of explanations for observed phenological trends in *A.*

cardamines, *C. pratensis*, and *A. petiolata*. Identifying how the interactions among these species may potentially be affected under future climate change scenarios depends on the degree to which each of the following hypotheses is operating: (i) the plastic hypothesis, under which all three species respond with similar plasticity to similar cues and there is no evidence for local adaptation with respect to temperature or the phenology of other species or of adaptive plasticity; (ii) the temperature-mediated local adaptation hypothesis, under which the optimum phenology varies spatially with average temperature and population means track local thermal optima; and (iii) the biotic adaptation hypothesis, under which local adaption and adaptive plasticity in butterfly emergence times are driven by flower availability.

We combine spatiotemporal phenological data from across Britain with daily mean temperature data and day length information. To these data we apply a new statistical approach that allows us to estimate temperature-mediated plasticity and local adaptation from the slope of phenology on temperature over space and time for each species (Phillimore et al. 2010; fig. 1*A*, 1*B*). In order to identify the time window over which phenology is most sensitive to temperature, we conduct an extensive search over different time windows, including allowing the position of the time window to shift latitudinally with day length. We then test whether the emergence time of the butterfly is plastic or locally adapted with respect to the flowering time of either host plant (fig. 1*C*, 1*D*). Finally, we ask whether slopes of phenology on temperature at colocations are positively correlated between the butterfly and its host plants, as expected if plant-herbivore interactions have driven adaptive evolution of phenological plasticity.

Methods

Data

We considered spatially referenced observations of first appearance (*Anthocharis cardamines*, $n = 14{,}524$) and first flowering (*Cardamine pratensis*, $n = 9{,}994$; *Alliaria petiolata*, $n = 9{,}790$) from across the United Kingdom over the period 1996–2009. These observations were made by citizen scientists and collated by the UK Phenology Network (UKPN, http://www.naturescalendar.org.uk). Each observation represents the first event seen by an individual observer in a year. We converted dates to ordinal dates, starting with January 1 as day 1, and excluded observations made on or after day 200 for *A. cardamines* ($n = 2$) and day 175 for the plant species (*C. pratensis*, $n = 4$; *A. petiolata*, $n = 2$). While the use of first dates to quantify variation in phenology has been criticized (Moussus et al. 2010), we use simulations to show that under most scenarios slope estimates will be unbiased (app. A, available online; see also Clark and Thompson 2011). A bias will be introduced if there is a correlation between temperature and the number of individuals encountered, which is itself the product of local abundance and recorder effort.

We used UK Met Office daily mean temperatures interpolated over a grid at 5 × 5-km resolution (© British Crown Copyright [2009], the Met Office; Perry et al. 2009; http://www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09/). Phenological observations were assigned to the 5 × 5-km grid cells in which they were reported. This meant that a single 5 × 5-km cell could potentially include several observations in a single year. Observations were excluded for a few locations that lacked interpolated climate data. Day length (time from sunrise to sunset) in minutes was calculated for each day by applying sunrise and sunset equations (Meeus 1991) to the centroid of every 5 × 5-km grid cell.

Our analyses require the delimitation of populations. We therefore assigned 5 × 5-km grid cells to larger 150 × 150-km grid cells, which we treated as random effects in statistical analyses (fig. B4, available online). While the 150 × 150-km grid cells delimit populations in an arbitrary way, we chose cells of this size to provide a balance between number of populations and number of years of observations per population and to minimize the influence that spatial measurement error in temperature will have on slopes. We used the spatial relational database PostgreSQL, version 8.3.5 (PostgreSQL Global Development Group), and PostGIS, version 1.3.4, to store and query the data via the RpostgreSQL R package.

Model for Estimating Plasticity and Local Adaptation

If we can identify the proximate environmental cue used to predict phenology—here we assume that this is the average temperature during a particular time window—and this cue varies over time and space, then it is possible to separate the contributions that plasticity and local adaptation make to spatiotemporal variation in phenology (Phillimore et al. 2010). In order to separate the two requires that we assume that all populations have the same linear slope (or population mean reaction norm) of the mean population phenological response on average temperature (which we term “mean plasticity”). The slope of phenology on temperature through time, the temporal slope, will be due to mean plasticity plus any association between breeding values and temperature, that is, adaptive microevolution. It is possible that, in addition to the contribution of individual plasticity, mean plasticity may also be affected by changes in the stage structure of a population if the phenology of an individual depends on its age (Ozgul et al. 2009; van de Pol et al. 2012). Such a

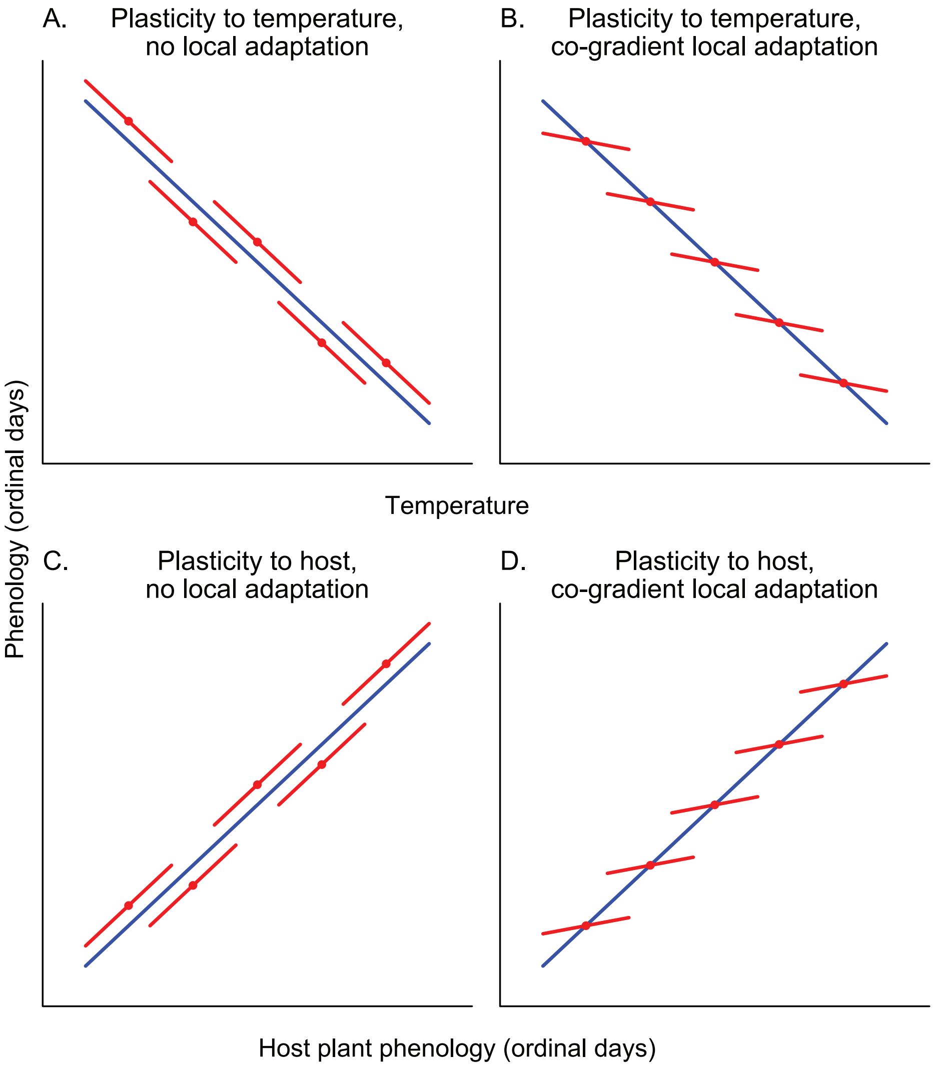

Figure 1: Schematic showing slopes of phenology on temperature (*A*, *B*) and phenology (*C*, *D*) of a host plant. In each plot the red lines correspond to the mean within-population reaction norms through time (temporal slopes), and the blue line corresponds to the between-population reaction norm (over space). If the temporal slopes are estimated over a limited number of years relative to the focal species' generation time, they provide an estimate of mean population phenological plasticity. The spatial slope should arise due to mean population phenological plasticity plus local adaptation. Therefore, if the spatial slope differs from the temporal slope, this reveals local adaptation (see "Methods" for further details). *A* corresponds to phenological plasticity with respect to temperature and no local adaptation. *B* reveals phenological plasticity with respect to temperature plus cogradient local adaptation. *C* corresponds to phenological plasticity with respect to host plant phenology and no local adaptation. *D* reveals some plasticity plus cogradient local adaptation with respect to host plant phenology. For depiction of further scenarios, we refer readers to figure 1 in Phillimore et al. (2010).

process could contribute to the temporal slope estimated for the perennial *C. pratensis* but can be discounted in the case of the univoltine butterfly and biennial *A. petiolata*.

If the time series spans few generations and the interannual relationship between time and temperature is not monotonic, then it may be reasonable to assume that the contribution made by microevolution is small to negligible and the temporal slope will therefore provide an estimate of mean plasticity. On the basis of the similarity between individual and population phenological reaction norms (Charmantier et al. 2008) and the paucity of evidence for adaptive phenological microevolution over ecological timescales even from long-term studies (Merilä 2012), we suggest that this assumption may not be unreasonable.

Where a temporally consistent geographic cline in environment exists, as is often the case for temperature, over generations an association between breeding values and the long-term average temperature in a location, that is, local adaptation, may develop. Therefore, the slope of phenology on temperature between populations, the spatial slope, should be the result of mean plasticity plus local adaptation. We treat the difference between the temporal and spatial slopes as an estimate of the degree of local adaptation with respect to temperature (see fig. 1*A*, 1*B*).

Statistical Analysis

In order to estimate slopes at two hierarchical levels simultaneously, we followed the approach outlined by Phillimore et al. (2010), implementing a generalized linear mixed model (GLMM) with bivariate response using the MCMCglmm R package (Hadfield 2010). We treated phenology (P) and average temperature in a specified time window (T) as a bivariate response and included three random effects: (i) 150 × 150-km grid cell, (ii) year, and (iii) a residual term. For each random effect (R), we obtained a posterior distribution for the variance and covariance between phenology and temperature:

$$\begin{bmatrix} \sigma^2_{PR} & \sigma_{PR,\,TR} \\ \sigma_{PR,\,TR} & \sigma^2_{TR} \end{bmatrix}. \tag{1}$$

The quantity $\sigma_{PR,\,TR}/\sigma^2_{TR}$ estimates the slope of phenology on temperature for a particular random effect. We estimated the spatial and temporal slope by treating grid cell and year, respectively, as random effects. The residual term estimates the spatial slope within a grid cell in a single year, though this slope is likely to be an underestimate of the true slope due to measurement error in the interpolated temperatures. We obtained a posterior distribution for each slope estimate and report the 95% highest posterior density (HPD). We also estimated the 95% HPD for the slope difference (Δb), which is the spatial slope minus the temporal slope. In this statistical framework, we are currently unable to deal with spatial autocorrelation of observations among grid cells or, related to this, nonindependence of populations caused by gene flow (Stone et al. 2011).

The MCMCglmm approach estimates the spatial and temporal variance in a bivariate response, while we are interested in the degree to which one of these response variables (temperature) explains the other (phenology). For this reason, the standard measures of model fit are not useful here. Instead, we compare models based on pseudo-R^2 (Phillimore et al. 2010), where we quantify the proportion of the total variance in phenology across k random effects that can be explained by temperature:

$$R^2 = \frac{\sum (\sigma^2_{PR_k,\,TR_k}/\sigma^2_{TR_k})}{\sum \sigma^2_{PR_k}}. \tag{2}$$

We used the following protocol to identify the latitudinally invariant time window (LITW) over which average temperatures best predicted spatiotemporal variation in phenology. For each species, we considered all combinations of starting points (from day 1 to day 101 in 5-day iterations) and durations of time windows (from day 10 to day 120 in 5-day iterations), subject to the constraint that the time window could not extend beyond the 97.5th percentile of the observed phenological distribution. We ran the MCMCglmm for 23,000 iterations for each time window with the default priors (for [co]variance components, they are drawn from the inverse-Wishart distribution with $V = 1$ and $\nu = 0.0002$; for the mean, they are drawn from a normal distribution with mean $= 0$ and variance $= 10^8$). We sampled every 10 iterations and removed the first 3,000 iterations as burn-in. To assess model mixing, we plotted the traces of the posterior distributions for means and variance-covariance components. In addition, we checked the degree of autocorrelation in the posterior sampling. We used our measure of pseudo-R^2 to identify the time window over which average temperatures best predict spatiotemporal variation in phenology. As many overlapping time windows yielded similar R^2 values, to capture model uncertainty, we report slope estimates across all models within 0.02 R^2 units of the highest value (note that this is an arbitrary choice of cutoff).

We also implemented a day length–initiated time window (DLTW) model, where the starting day of the time window was initiated when a certain day length threshold was reached. In these models, starting point refers to the start date in the southernmost grid cell. We then calculated the day length for this ordinal day in this cell, and the starting point for all other cells was the date on which this day length was first reached/exceed. We considered the same range of starting points and time window durations outlined above for LITW models. As the end date of the time window varies latitudinally in the DLTW models, we considered it more biologically appropriate to model the phenological response as a lag time (i.e., date of phenology minus end date of time window in that particular 5 × 5-km grid cell) rather than as an ordinal date. The measure of pseudo-R^2 (eq. [2]) proved inadequate for comparisons among DLTW models and between these models and the LITW models. This is because by analyzing lag times rather than ordinal dates, we tended to reduce the spatial variation in phenology that could be explained by temperature, thereby reducing the pseudo-R^2. As a remedy, for model comparisons involving DLTW models we considered only the temporal correlation between temperature and lag time/phenology, estimating a temporal pseudo-R^2 by including year as the only random effect in equation (2) (i.e., excluding the spatial and residual terms). The advantage of this is that year-to-year variation in day length, and therefore the end of the time window at a single site, is negligible. While this approach is not ideal, as the R^2 does not include spatial and residual variance, it is broadly similar to the approach recently applied to identify the most predictive time windows for two geographically separated populations of *Parus major* (Husby et al. 2010).

Phenological observations were distributed heterogeneously over space and time (figs. B1–B3, available online). Although our approach can handle unbalanced data, if temporal slopes vary among locations, our temporal slope estimate will tend toward that found in better-sampled locations. Also, if there is nonstationarity of the spatial or temporal slope, the estimated slope will tend toward the slope estimated for better-sampled locations or years.

Extending the Model to a Multispecies Framework

To explore local adaptation and plasticity of the phenology of the butterfly with respect to host plant phenology, we can substitute spatiotemporal variation in host plant phenology for temperature in the model outlined above (fig. 1*C*, 1*D*). We extended the test outlined by Phillimore et al. (2010) for estimating temperature-mediated plasticity and local adaptation for a single species to a multispecies framework. This allowed us to test whether *A. cardamines* is locally adapted to the phenology of one of its host plants or to local average temperatures. We included data on the phenology of all three species plus temperature data (average temperatures for the LITW that best predicted *A. cardamines* phenology) as a multivariate response. In addition, we included 150-km grid cell and year as random effects. The multivariate response variable included a lot of missing data for phenology. For example, when phenology of one species was entered, temperature was present, but the phenology of the two other species was missing. The MCMCglmm approach was able to deal with this by treating such cases as missing at random (Nakagawa and Freckleton 2008); that is, data were updated conditional on the model. We ran MCMCglmm (Hadfield 2010) using the default prior described above for 23,000 iterations, removing the first 3,000 as burn-in.

For each random effect, R, we estimated the posterior distribution of a 4 × 4 variance-covariance matrix, wherein the phenology of the butterfly (A) and host plants (C and G) are denoted with subscripts:

$$\begin{bmatrix} \sigma^2_{AR} & \sigma_{AR,\,CR} & \sigma_{AR,\,GR} & \sigma_{AR,\,TR} \\ \sigma_{AR,\,CR} & \sigma^2_{CR} & \sigma_{CR,\,GR} & \sigma_{CR,\,TR} \\ \sigma_{AR,\,GR} & \sigma_{CR,\,GR} & \sigma^2_{GR} & \sigma_{GR,\,TR} \\ \sigma_{AR,\,TR} & \sigma_{CR,\,TR} & \sigma_{GR,\,TR} & \sigma^2_{TR} \end{bmatrix}. \tag{3}$$

Using the posterior distributions of the variance-covariance matrix for each random effect, we were able to estimate the degree to which the host plants' phenology predicted the phenology of the butterfly ($\sigma_{AR,\,CR}/\sigma^2_{CR}$ and $\sigma_{AR,\,GR}/\sigma^2_{GR}$) over space and time and Δb, which tests whether spatial variation in the butterfly's phenology shows local adaptation to the phenology of the host. If plant and butterfly populations were to respond with the same plasticity to the same environmental cue, the slopes over space and time would be the same. Alternatively, if the optimum timing for butterfly emergence is set by the flowering time of the host, and assuming the cue used for butterfly emergence does not allow perfect prediction of the host plant phenology, local adaptation may result in the spatial slope (of butterfly phenology regressed on host phenology) being steeper than the temporal slope (fig. 1*D*; Lande 2009; Phillimore et al. 2010).

However, if the phenology of the two host plants and the butterfly all correlated with one another and temperature across space and time, bivariate analyses could have been misleading. To address this problem, we employed a multiple regression approach. We estimated **A** (eq. [4]), the variance-covariance matrix among predictors (plant phenology and temperature), and **B** (eq. [5]), the covariance between the response (*A. cardamines* phenology) and the predictors for two random effects, grid cell and year:

$$\mathbf{A}_R = \begin{bmatrix} \sigma^2_{CR} & \sigma_{CR,\,GR} & \sigma_{CR,\,TR} \\ \sigma_{CR,\,GR} & \sigma^2_{GR} & \sigma_{GR,\,TR} \\ \sigma_{CR,\,TR} & \sigma_{GR,\,TR} & \sigma^2_{TR} \end{bmatrix}, \tag{4}$$

$$\mathbf{B}_R = \begin{bmatrix} \sigma_{AR,\,CR} & \sigma_{AR,\,GR} & \sigma_{AR,\,TR} \end{bmatrix}, \tag{5}$$

where $\mathbf{A}_R^{-1}\mathbf{B}_R$ yields the multiple regression coefficients treating plant phenology and temperature as predictors of *A. cardamines* phenology. This calculation was repeated across the posterior distribution of $\mathbf{A}_R$ and $\mathbf{B}_R$ to obtain estimates of the 95% HPD for each coefficient. For each predictor we also estimated the posterior distribution for Δb, and if the 95% HPD did not overlap 0, this would support the hypothesis that local adaptation is with respect to that predictor.

We also assessed the correlations among species and temperature over space and time by transforming each posterior sample of variances and covariances into a correlation matrix. To examine the consequences of spatial and temporal variation in phenology for interspecies synchrony, we assessed the reduced major axis slope between the butterfly and two plant species over space and time. This was estimated as the slope of the phenology of *A. cardamines* regressed on that of one of its host plants, divided by the correlation coefficient between the butterfly and the host plant.

Test for the Influence of Coevolution

Above we have assumed that phenological plasticity with respect to temperature is a constant across populations, but it is possible that plasticity may vary among populations as a form of local adaptation. Local interactions between a host plant and a butterfly may exert strong reciprocal selection on the phenology of each species. For instance, if seed predation by *A. cardamines* leads to a population of one host plant evolving a shallower (or steeper) mean plastic response with respect to temperature, this may in turn exert selection for a shallower (or steeper) plastic response in the butterfly. Thus, if adaptation in the butterfly keeps up with changes in the host plant phenology, we anticipate that a positive correlation may arise between the temporal slopes estimated for butterfly populations and host plant populations in the same location. However, even if a positive correlation were detected, we would still need to be cautious in interpreting this as evidence for coevolution for two reasons. First, it is possible that other geographically varying drivers cause evolution of either the host plant's or the butterfly's phenological plasticity. The positive correlation could therefore be the sole result of adaptation of the butterfly to the host plant or vice versa rather than being reciprocal, as coevolution implies (Janzen 1980; Nuismer et al. 2010). Second, it is possible that other geographically varying variables affect the temporal slope of both species simultaneously (Janzen 1980; Nuismer et al. 2010); for example, measurement error in temperature may vary among grid cells.

We estimated the slope of phenology on average temperature for 150 × 150-km grid cells that each had 50 or more phenological observations for a species drawn from at least 5 years. We selected the time window over which *A. cardamines* is most sensitive to temperature as the predictor for all species. This will tend to slightly depress the temporal slopes estimated for the plants. We calculated the yearly mean temperature in a grid cell and assigned this to all observations in that year. We then estimated the temporal slope for each grid cell in a mixed-effects model with yearly mean temperatures as a predictor and year as a random effect. Finally, we examined the intergrid cell correlation between the temporal slope estimated for each *A. cardamines* population and for each of the host plants.

All analyses were conducted in the R statistical programming environment (v2.14.1; R Development Core Team 2011). R code for latitudinally invariant models is available online.[1] Phenology and average temperature data during the LITW that best predicted each species' phenology can be downloaded from Dryad (http://dx.doi.org/10.5061/dryad.733d9).

Results

Temperature and Phenology

LITW. For all three species, spatiotemporal variation in phenology was strongly predicted ($R^2 > 0.29$) by models that included the average temperature over an LITW (fig. 2*A*–2*C*), and the best time windows overlapped substantially among species. The time windows over which average temperature best predicted phenology all started before the phenological events but showed some overlap with the distribution of phenology. Average temperatures over the period from day 61 to day 125 best predicted the flight times of *Anthocharis cardamines* (fig. 2*A*; $R^2 = 0.38$), while the time window that best predicted the flowering times of *Cardamine pratensis* and *Alliaria petiolata* ended a little sooner, spanning the periods from day 61 to day 95 and from day 46 to day 95, with $R^2 = 0.30$ and 0.42, respectively. In all cases, there were several other overlapping time periods over which the predictive power of average temperature, measured as pseudo-R^2, was similar. In general, there was a tendency for slope estimates across time and space to become steeper with increasing pseudo-R^2. Over each of the best-predicting time periods, temperatures varied a little more among years than grid cells (table 1).

The phenology of *A. cardamines* over space and time was more advanced when spring temperatures were higher. Across space (best model posterior median $b = -3.94$, 95% HPD $= -5.60$ to -1.97) and time ($b = -8.34$, 95% HPD $= -10.21$ to -6.75), the slope departed significantly from 0 (fig. 2*D*, 2*G*). The steep slope across time is consistent with pronounced phenological plasticity and was significantly steeper than the slope across space ($\Delta b = 4.48$, 95% HPD $= 2.13$–7.07), indicating that countergradient local adaptation had counteracted some of the effects of plasticity over space, thereby reducing spatial variation in phenology. For all models with an R^2 within 0.02 of the best model, Δb was significant (fig. 2*D*). The residual term in the best model was weakly but significantly negative ($b = -0.77$, 95% HPD $= -1.09$ to -0.43).

Flowering times of *C. pratensis* exhibited a pronounced negative relationship with average spring temperatures (fig. 2*E*, 2*H*). For the highest pseudo-R^2 model, the slopes across space ($b = -5.54$, 95% HPD $= -8.85$ to -2.06) and time ($b = -6.07$, 95% HPD $= -7.91$ to -4.43) were similar ($\Delta b = 0.49$, 95% HPD $= -2.81$–4.60), consistent with the null hypothesis that phenological plasticity can account for all of the spatiotemporal variation in phe-

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[1] Code that appears in the *American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

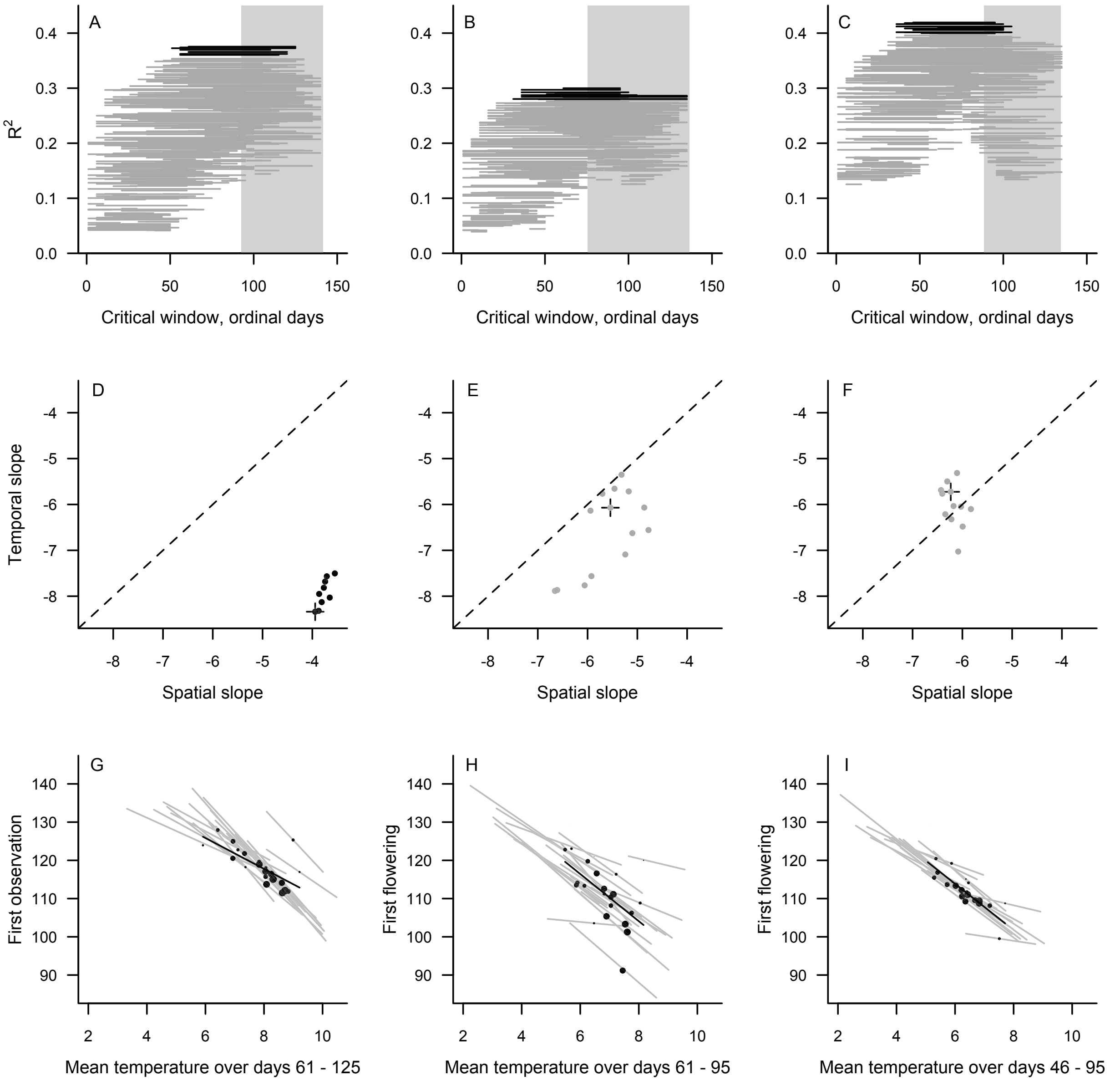

Figure 2: Variation in model fit (as measured by pseudo-R^2) of MCMCglmm bivariate model across different time windows for *Anthocharis cardamines* (*A*; 347 models), *Cardamine pratensis* (*B*; 330 models), and *Alliaria petiolata* (*C*; 330 models). The gray boxes delimit the 2.5th and 97.5th percentiles for the distribution of observed first phenology dates. Black horizontal lines correspond to the values that have a pseudo-R^2 within 0.02 of the best model (high-R^2 models). *D–F* report the slope estimates of phenology on temperature over space and time from the high-R^2 models. The parameters estimated under the best model are denoted with a plus sign, and black dots are used to denote models for which the 95% highest posterior density of the difference between the spatial slope and the temporal slope does not include 0. Slope estimates over space (black lines) and time (gray lines) for the time window that yielded the highest pseudo-R^2 are shown in *G–I*. Each data point represents the mean estimated for a grid cell, with a diameter proportional to the log of the number of observations. The black lines correspond to the slope of phenology on temperature across space obtained from a linear mixed-effects model using the mean temperature for each 150-km grid cell and including grid cell as a random effect. The gray lines correspond to the slope of phenology on temperature within populations (temporal slope) obtained from a linear mixed-effects model using the mean temperature for each year and including year as a random effect. Temporal slopes were estimated only for grid cells with observations from 5 years or more.

Table 1: Estimated variances in average temperatures (°C) across time and space for the time periods that best predict the phenology of the three focal species

Species	Time period (days)	Variance over space	Variance over time	Residual variance
Anthocharis cardamines	61–125	.72	.94	.28
Cardamine pratensis	61–95	.69	1.71	.34
Alliaria petiolata	46–95	.58	1.91	.29

Note: Variances were estimated from cells and years where the focal species was recorded, rather than every 5 km × year combination. Estimates are from the MCMCglmm used to estimate slopes.

nology. These patterns broadly held across models with R^2 within 0.02 of the best model (fig. 2*E*). The slope for the residual term ($b = -2.40$, 95% HPD $= -2.82$ to -1.97) was negative and departed significantly from 0.

Alliaria petiolata flowered earlier when spring conditions were warmer (fig. 2*F*, 2*I*). Across space ($b = -6.23$, 95% HPD $= -7.66$ to -4.73) and time ($b = -5.72$, 95% HPD $= -7.15$ to -4.22), the slopes of phenology on temperature for the highest pseudo-R^2 model were similar ($\Delta b = -0.53$, 95% HPD $= -2.60$–1.48), consistent with the null hypothesis of plasticity and no local adaptation. Note also the similarity of these slopes to those estimated for *C. pratensis*. There was little variation in slope estimates across models with an R^2 within 0.02 of the best model (fig. 2*F*). The residual slope was negative and departed significantly from 0 ($b = -2.59$, 95% HPD $= -2.96$ to -2.15).

DLTW. The best DLTW for *A. cardamines* started on day 56 in the far south (day 63 in the far north), where the day length was 642 min, and extended to day 115 (day 122 in the north; fig. 3*E*, 3*G*). Over this period the temporal R^2 was 0.95 (fig. 3*D*). Adoption of this time window led to a slightly shallower spatial slope estimate ($b = -2.14$, 95% HPD $= -4.36$ to -0.10) and a temporal slope similar to that estimated using the best LITW ($b = -8.03$, 95% HPD $= -9.35$ to -6.78); the slope difference remained significant. In comparison, the highest temporal R^2 for an LITW model was 0.95 for days 56–125, and for days 61–125 (identified as the highest pseudo-R^2 model above), the temporal R^2 was 0.93.

For *C. pratensis* the highest temporal R^2 DLTW model was 0.95 for days 56–95 in the most southerly cell (days 64–103 in the most northerly cell; day length = 642 min; fig. 3*E*). The parameter estimates obtained for this time window were substantially shallower over space ($b = -3.71$, 95% HPD $= -7.42$–0.09) than time ($b = -5.97$, 95% HPD $= -7.35$ to -4.65), though not significantly so. The LITW model with the highest temporal R^2 ($=0.95$) also ran from day 56 to day 95 (fig. 3*B*) and corresponded to the third-highest full model pseudo-R^2 ($=0.29$). In comparison, for the period from day 61 to day 95 (identified as the highest pseudo-R^2 model above), the temporal R^2 was 0.92.

The best DLTW for *A. petiolata* was identical to that identified for *C. pratensis*, spanning the period from day 56 to day 95 in the southernmost cell (from day 63 to day 102 in the northernmost cell; day length = 643 min; fig. 3*I*), with a temporal R^2 of 0.92 (fig. 3*F*). Also consistent with the findings for *C. pratensis*, adoption of this DLTW led to a quantitative change in slope estimates, with the spatial slope shallower than estimated for the best LITW (spatial $b = -4.65$, 95% HPD $= -6.31$ to -3.12; temporal $b = -5.89$, 95% HPD $= -7.42$ to -4.45), but the slope difference remained nonsignificant. The highest pseudo-R^2 LITW model also returned the highest temporal R^2, 0.93 (fig. 3*C*).

Is Local Adaptation of the Butterfly to Temperature or Host Plant Phenology?

When the phenology of either of the host plants was considered as a predictor of the phenology of *A. cardamines*, slope estimates were positive, with the slope over space significantly shallower than the slope over time in both cases (fig. 4). However, the bivariate tests of temperature and host phenology show that these variables are also correlated over time and space. Therefore, to distinguish whether *A. cardamines* was locally adapted to average temperature (over days 61–125 LITW) or the phenology of one of the host plants, we estimated partial correlations across time and space (fig. 4). While the slope estimates for *C. pratensis* remained positive, they were substantially shallower and there was no evidence for local adaptation. There was no evidence for local adaptation to *A. petiolata* or average temperature, but the spatial slope estimates departed substantially from those estimated using bivariate analyses, and in one case the spatial slope estimate for *A. petiolata* was positive. Multicollinearity appears to be a likely explanation, given the very high correlation between temperature and *A. petiolata* across space ($r = -0.94$). After removing *A. petiolata* from the analysis, we obtained slope estimates for temperature and *C. pratensis* across

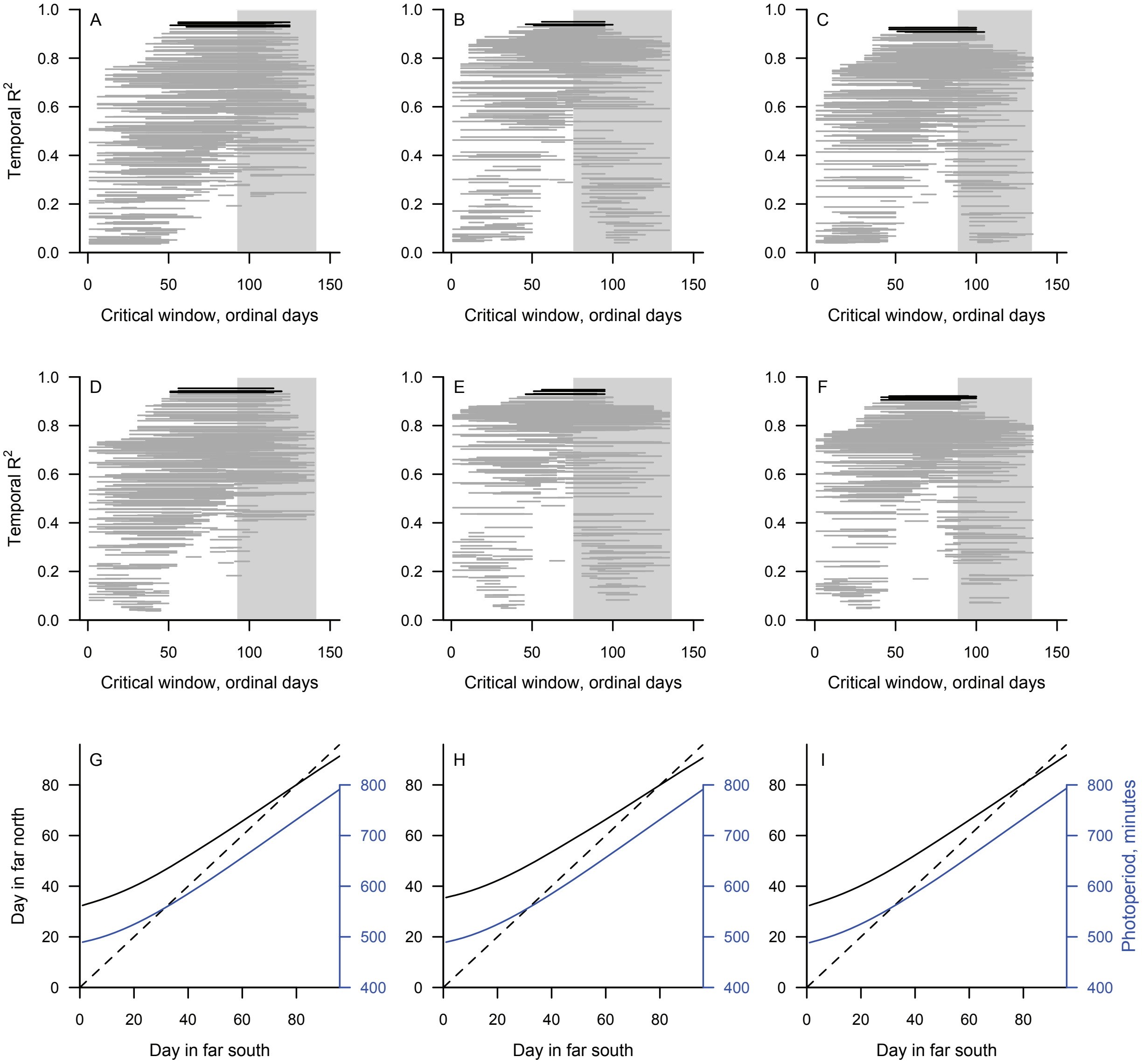

Figure 3: Variation in model fit (as measured by temporal R^2) of MCMCglmm bivariate model across latitudinally invariant (*A–C*) and day length–initiated (*D–F*) time windows for *Anthocharis cardamines* (*A*, *D*), *Cardamine pratensis* (*B*, *E*), and *Alliaria petiolata* (*C*, *F*). The gray box delimits the 2.5th and 97.5th percentiles for the distribution of observed first phenology dates. Black horizontal lines correspond to the values that have a pseudo-R^2 within 0.02 of the best model (high-R^2 models). *G–I* show the relationship between the day in the most southerly grid cell with phenology data for each species and day length (blue line) and the ordinal day in the most northerly cell that is of equal day length (black line).

space and time that were more in keeping with the slopes estimated in bivariate analyses (fig. 4). The slope of flight times for *A. cardamines* on temperature was significantly negative over space and time, with the latter slope being significantly steeper than the former. The slopes estimated for *C. pratensis* were almost identical over space and time.

Regardless of the cues and mechanisms involved in the butterfly's phenological plasticity, one of its primary roles is likely to be in synchronizing with the host plants' phenology. Reduced major axis regression between *A. cardamines* and its host plants revealed that while the slope was shallower than 1 over space (*C. pratensis* = 0.59, 95% HPD = 0.42–0.83; *A. petiolata* = 0.85, 95% HPD = 0.52–1.27), it marginally and nonsignificantly exceeded 1 over

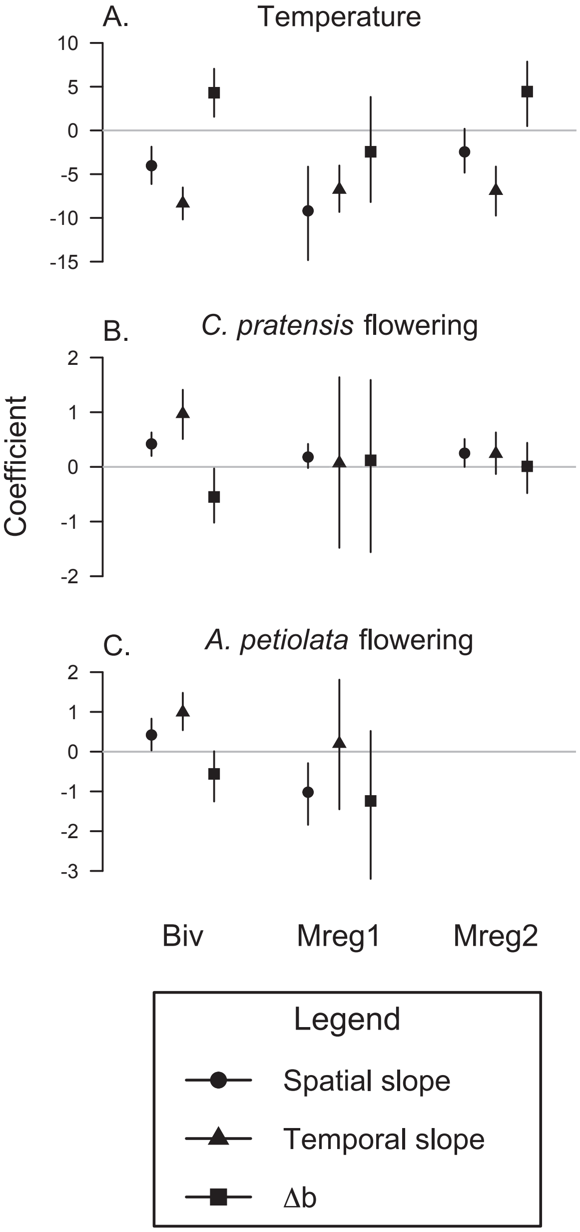

Figure 4: Coefficients over space and time and the slope difference obtained using average temperature (*A*) and host plant phenology (*B*, *C*) as predictors of *Anthocharis cardamines* phenology. Error bars indicate 95% highest posterior density. Biv = bivariate response models; Mreg1 = multiple regression including temperature and the phenology of both host plants; Mreg2 = multiple regression including temperature and *Cardamine pratensis* phenology.

time (*C. pratensis* = 1.15, 95% HPD = 0.73–1.60; *A. petiolata* = 1.17, 95% HPD = 0.77–1.68). This means that while first flowering of the host plants occurs well before the butterfly is observed flying in the warmer southwest of the United Kingdom, in the colder north the first flying date coincides with the first flowering dates (fig. 5). As the temporal slope does not depart from 1, this suggests that the species in a particular area experience a fairly consistent degree of matching/mismatching in different years.

Does Geographic Variation in Plasticity Contain a Signature of Coevolution?

There is little intraspecific variation in temporal slope estimates (fig. 2*G*–2*I*), much of which may be attributable to estimation error only. This suggests that there is little, if any, local adaptation in plasticity. Consistent with this interpretation, we found no evidence for a positive correlation between the temporal slopes estimated for *A. cardamines* populations and those of either host plant (fig. 6).

Discussion

We find most support for the hypothesis that plasticity maintains spatiotemporal interactions between the butterfly and the plants. All three species respond to a largely temporally overlapping thermal cue and with similar plasticity. There is some support for temperature-mediated local adaptation in *Anthocharis cardamines*, but we find no evidence that biotic interactions are driving adaptive evolution in this system. Adaptive evolution of the butterfly's phenology in the distant past may explain the congruence between butterfly and host plant phenology. However, we cannot discount species sorting and happenstance during postglacial range expansion as an alternative explanation; perhaps the apparent specialization of the butterfly on these host plants arose because they happen to have similar temperature-mediated phenological plasticity.

All three species show a strong phenological response to spring temperatures during a short time period running between approximately days 46–95 for the plants and days 61–125 for the butterfly, though there is some uncertainty regarding the exact period for each species. For none of the species did we find evidence to prefer a model where the time window varied latitudinally, initiated by a day length threshold, over a model where the time window was latitudinally invariant. For *A. cardamines*, the most likely explanation is that while day length is used by butterflies as a cue for various life-history stages (e.g., Gotthard et al. 1999), ambient temperature is the chief cue determining emergence dates in temperate species (Bryant et al. 2002). Given the evidence that day length effects the timing of flowering in *Arabidopsis thaliana* (Metcalf and Mitchell-Olds 2009), the absence of evidence for day length being important in determining the time window

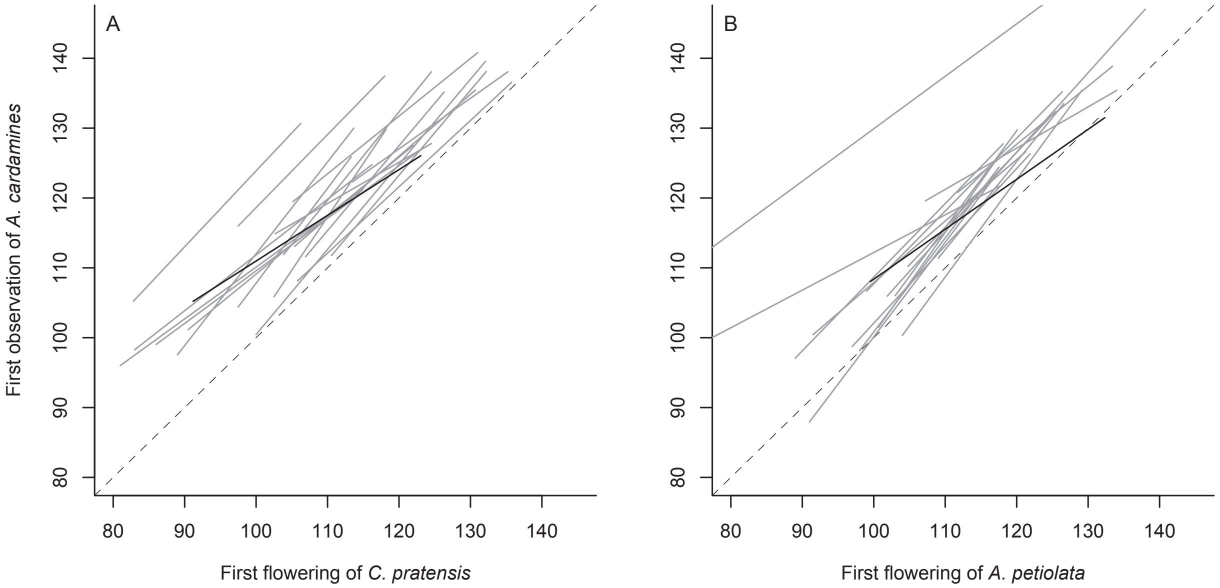

Figure 5: Correspondence between the mean phenology of *Anthocharis cardamines* and its host plants, *Cardamine pratensis* (*A*) and *Alliaria petiolata* (*B*), over space and time. Over space, the relationship (black lines) is between the mean phenology of the butterfly and host plant per grid cell. Over time the relationships (gray lines) are between the mean phenology of the butterfly and host plant per year in a single grid cell. Temporal slopes were estimated only for grid cells with 50 or more observations of phenology of each species data from 5 years or more. Slopes and intercepts were estimated via reduced major axis regression.

for the two Brassicacea warrants deeper consideration. One possible explanation is statistical power. Indeed, the most predictive time windows all start during a period when the latitudinal cline in day length across the United Kingdom is relatively shallow (fig. 3*G*–3*I*). Alternatively, the explanation may instead reflect biology; perhaps a day length requirement operates independently of the time window and is met at all latitudes before the first flowering date at any latitude, in which case it will not contribute to spatial variation in phenology.

Our slope estimates are consistent with spring temperature-mediated phenological plasticity dominating spatial variation in the emergence time of *A. cardamines* and flowering times of *Cardamine pratensis* and *Alliaria petiolata.* For the two Brassicaceae, we have no evidence for local adaptation. Thus, we predict that if individuals of either species were transplanted from the north to the warmer south of Britain, they would flower earlier than individuals at the home locality but at the same time as the southern population. The slope estimates for *C. pratensis* and *A. petiolata* flowering times (~6-day advance per 1°C increase in mean temperature) correspond closely to those estimated for a longer UK-based time series (Sparks and Yates 1997). Across the locations and years where observations were made, the mean temperature in the time windows that best predicted the phenology of the plant species varied substantially more over time than space (ratio of variance in temperature over time versus that over space equals 2.48 in *C. pratensis* and 3.29 in *A. petiolata*). Such a ratio of time-varying selection to spatially varying selection is not conducive to local adaptation (Kawecki and Ebert 2004).

Unlike the phenology of its host plants, the phenology of *A. cardamines* appears to be locally adapted to temperature in a countergradient pattern (Conover and Schulz 1995), meaning that adaptive genetic change over space counteracts or compensates for the plastic change of phenology with temperature (Grether 2005). Multiple-regression-based analyses suggest that local adaptation is with respect to temperature rather than host plant phenology. It remains possible that populations could be locally adapted to the phenology of different plant species in different areas (e.g., *C. pratensis* in the north and *A. petiolata* in the south) or to a wider time window corresponding to the period where either host plant is available. We anticipate that the effect of local adaptation means that if *A. cardamines* individuals were transplanted from northern Britain to southern Britain, the translocated individuals should emerge earlier than the local population. A similar countergradient pattern has been observed in the devel-

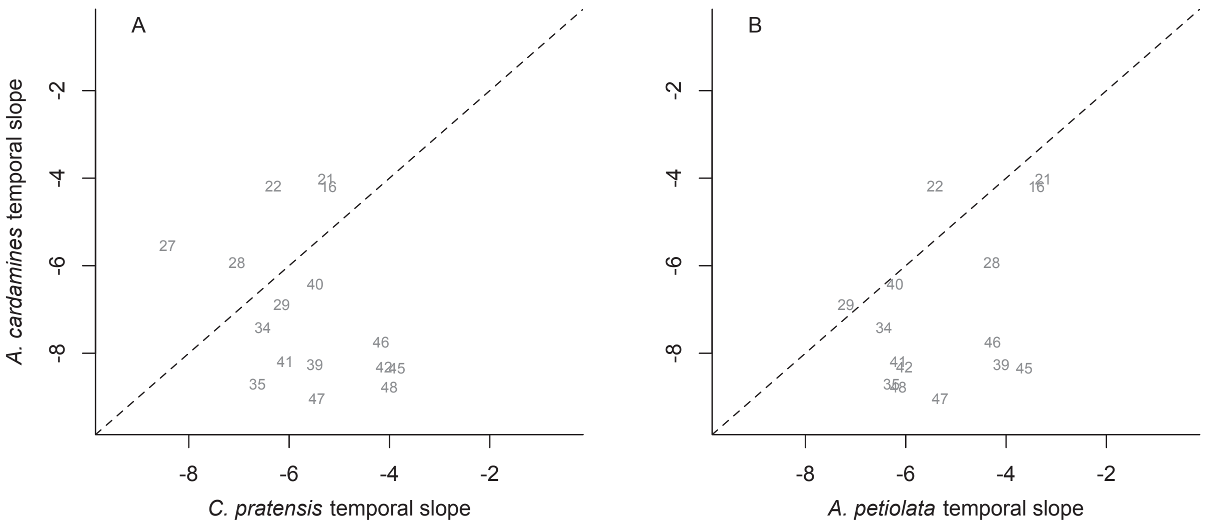

Figure 6: Relationship between the temporal slopes (of phenology on temperature) for different populations of *Anthocharis cardamines* versus different populations *Cardamine pratensis* (*A*) and *Alliaria petiolata* (*B*). Populations are defined as 150 × 150-km grid squares, and data point numbers correspond to grid cell locations (fig. B4, available online), with numbers ascending from north to south. The correlation is nonsignificant in both cases.

opment times of other high-latitude ectotherms, for example, *Rana temporaria*, and is hypothesized to arise due to time constraints imposed by a shorter summer in the north (Laugen et al. 2003). Interestingly, Roy and Asher (2003) observed that while the phenology of several British butterfly species is strongly correlated with temperature through time, across different latitudes and longitudes, over which there are pronounced temperature clines, the mean phenology of many species shows remarkably little variation. One interpretation of these findings is that countergradient local adaptation in the form of faster development in colder areas may be widespread among high-latitude Lepidoptera (Roy and Asher 2003). While evidence for local adaptation on this mesoscale was somewhat surprising to us in light of the mobility of *A. cardamines* and the greater temporal than spatial heterogeneity in average temperatures, reciprocal transplant studies have revealed local adaptation of butterflies to temperature on a comparable spatial scale (Pelini et al. 2009). However, Roy and Asher (2003) also raised an alternative explanation for the difference between spatial and temporal slopes: that larvae inhabiting colder areas may select warmer microclimates for pupation. This means that we would overestimate the spatial variance in temperature to which the pupae are exposed and underestimate the spatial slope. It is plausible that such thermotaxic behavior by the larvae could be a consistent and plastic response to the environment. Unfortunately, we are unable to distinguish between these hypotheses using the broad-scale climatic and phenological data at hand.

A consequence of the spatial slope in *A. cardamines* being shallower than that of its hosts is that the interval between the hosts' first flowering date and the butterfly's first flying is shorter in the colder north (fig. 5), with butterflies seen before the first flowering of *A. petiolata* in some instances. Host availability rather than host preference may therefore explain the tendency of *A. cardamines* to exploit *A. petiolata* in the south and west and *C. pratensis* further north and east (Courtney and Duggan 1983). If the sole selection pressure acting on the butterfly's phenology was host availability and the butterfly and its host plants responded to the same environmental cue, we might expect all populations of the butterfly to exhibit the same reaction norm with respect to temperature (i.e., show no local adaptation) and emerge around peak flowering date. The fact that the spatial slope is shallower than the temporal slope in *A. cardamines* suggests that another selection pressure may shape spatial variation in the butterfly's phenology. Perhaps spatial variation in *A. cardamines* flying times is the result of a trade-off between an advantage of emerging later to maximize host availability and an advantage of flying earlier to maximize the time available for larval development. If this is the case, an increase in spring temperatures may relax the selection that favors early emergence in the north of Britain, which could increase mean population fitness and potentially lead to greater success of individuals that move northward.

The temperature-mediated plasticity that the plants and butterfly exhibit may itself be adaptive. Earlier flowering in many plants is associated with increased pollination and reduced seed predation (Elzinga et al. 2007), and plasticity in the butterfly allows the population to track interannual variation in host availability. Further evidence for adaptive plasticity in plant phenology comes from a long-term study in Thoreau's woods, Massachusetts; plant species that had a steeper slope of mean flowering phenology on interannual spring temperature were found to be the least prone to declines in abundance as temperatures have risen in recent years (Willis et al. 2008). We did not formally test whether there was any evidence for populations of the plants or the butterfly species differing in their plasticity because the standard method of detection, within-subject mean centering and random regression (van de Pol and Wright 2009), is anticonservative when sample sizes are spatially heterogeneous (Phillimore et al. 2010). Visual inspection of figure 2*G*–2*I*, however, reveals remarkably little intraspecific geographic variation in temporal slope estimates. Thus, it is unsurprising that we found no significant cross population correlation between the plasticity shown by the butterfly and either host plant. As antagonistic coevolution can give rise to the interspecies correlation between population means being negative, positive, and everything in between (Nuismer et al. 2010), on the basis of finding no correlation, we are able to infer little about the contribution that coevolution has made.

Unlike the majority of associative studies exploring aspects of climate as a predictor of phenotype, we use daily rather than monthly temperature data and explore the performance of a wide range of sliding time windows. Van de Pol and Cockburn (2011) identify two drawbacks of an associative model approach using sliding time windows: (i) that each day is allowed to contribute equally and (ii) that the start point and the end point are often constrained to when months begin and end. Our approach of using daily temperature data addresses only the latter of these two concerns. Nonetheless, the high explanatory power of our models (as measured by pseudo-R^2) was encouraging. Our sliding time window approach also revealed that slope estimates were sensitive to the position and duration of the time window, as has also been shown for the first egg dates of *Parus major* (Husby et al. 2010). For instance, we estimated the temporal slope of flowering time on average temperature during the period from day 46 to day 95 in *A. petiolata* to be -5.72, whereas if we had considered the period from day 56 to day 85, which corresponds approximately to March, the slope is estimated as -4.12. Harrington et al. (1999) used March temperatures to predict the phenology of *A. petiolata* and identified a nonlinear relationship, flattening at high and low March average temperatures. However, over the longer period that we identify as most predictive, we see no evidence for nonlinearity. Troubling from a biological, if not statistical, perspective is our finding that the best-predicting time window overlaps with the distribution of first phenological events. How can phenological events occur before the putative cue? One possibility is that because temperatures are highly correlated from one day to the next, when temperatures in the early part of the time window are especially warm, then temperature averaged over the entire time window may be, to a large degree, predestined. In such years, it is possible that a shorter time period may act as the cue.

As discussed elsewhere (van de Pol and Wright 2009; Phillimore et al. 2010), a corollary of the slope of phenology on temperature differing over time and space is that analyses of spatiotemporal data that do not take this into account will be biased toward estimating an intermediate slope. Based on our findings, we suggest it would be acceptable to apply space-for-time substitution to model the response of phenology to temperature in *C. pratensis* and *A. petiolata* but not for *A. cardamines*.

Summary

The interactions between the three species considered in our study are often cited as being unlikely to be disrupted by climate change (Sparks and Yates 1997; Harrington et al. 1999); we find no evidence to contradict this conclusion. In particular, our findings that the phenology of all three species correlated with temperatures in an overlapping time window and exhibited similar plasticity imply that an increase in temperature will affect all three species in a similar way. In addition, the tendency for *Alliaria petiolata* to flower earlier than *Cardamine pratensis* widens the window over which suitable flower heads are available to the butterfly and may serve to buffer small differences in plasticity between the butterfly and its hosts. We only find evidence for local adaptation in the butterfly, and it appears more likely that this is driven by constraints placed by a colder climate in the north rather than adaptation to the host plants. We detect no convincing evidence for coadaptation between plant and herbivore. Although it remains possible that the similar mean plasticity shown by these species was itself shaped by coadaptation, we note that there is little hint of different populations showing different reaction norms or a correlation between geographic variation in the reaction norm of the butterfly and plants, as might be expected if coevolution had played a dominant role in determining phenology.

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Literature Cited

Bryant, S. R., C. D. Thomas, and J. S. Bale. 2002. The influence of thermal ecology on the distribution of three nymphalid butterflies. Journal of Applied Ecology 39:43–55.

Caffara, A., A. Donnelly, and I. Chuine. 2011. Modelling the timing of *Betula pubescens* budburst. II. Integrating complex effects of photoperiod into process-based models. Climate Research 46:159–170.

Carroll, E. A., T. H. Sparks, N. Collinson, and T. J. C. Beebee. 2009. Influence of temperature on the spatial distribution of first spawning dates of the common frog (*Rana temporaria*) in the UK. Global Change Biology 15:467–473.

Charmantier, A., R. H. McCleery, L. R. Cole, C. Perrins, L. E. B. Kruuk, and B. C. Sheldon. 2008. Adaptive phenotypic plasticity in response to climate change in a wild bird population. Science 320:800–803.

Chevin, L.-M., G. M. Mace, and R. Lande. 2010. Adaptation, plasticity, and extinction in a changing environment: towards a predictive theory. PLoS Biology 8:e1000357.

Chew, F. S., and S. P. Courtney. 1991. Plant apparency and evolutionary escape from insect herbivory. American Naturalist 138: 729–750.

Clark, R. M., and R. Thompson. 2011. Sampling bias in the determination of first and last occurrences. Plant Ecology and Diversity 4:201–211.

Conover, D. O., and E. T. Schulz. 1995. Phenotypic similarity and the evolutionary significance of countergradient variation. Trends in Ecology & Evolution 10:248–252.

Courtney, S. P. 1981. Coevolution of pierid butterflies and their cruciferous foodplants. 3. *Anthocharis cardamines* (L.) survival, development and oviposition on different hostplants. Oecologia (Berlin) 51:91–96.

———. 1982. Coevolution of pierid butterflies and their cruciferous foodplants. 4. Crucifer apparency and *Anthocharis cardamines* (L.) oviposition. Oecologia (Berlin) 52:258–265.

Courtney, S. P., and A. E. Duggan. 1983. The population biology of the orange tip butterfly *Anthocharis cardamines* in Britain. Ecological Entomology 8:271–281.

Davis, M., R. Shaw, and J. Etterson. 2005. Evolutionary responses to changing climate. Ecology 86:1704–1714.

Dempster, J. P. 1997. The role of larval food resources and adult movement in the population dynamics of the orange-tip butterfly (*Anthocharis cardamines*). Oecologia (Berlin) 111:549–556.

Elzinga, J. A., A. Atlan, A. Biere, L. Gigord, A. E. Weis, and G. Bernasconi. 2007. Time after time: flowering phenology and biotic interactions. Trends in Ecology & Evolution 22:432–439.

Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3101–3112.

Gienapp, P., C. Teplitsky, J. S. Alho, J. A. Mills, and J. Merila. 2008. Climate change and evolution: disentangling environmental and genetic responses. Molecular Ecology 17:167–178.

Gilman, S. E., M. C. Urban, J. Tewksbury, G. W. Gilchrist, and R. D. Holt. 2010. A framework for community interactions under climate change. Trends in Ecology & Evolution 25:325–331.

Gotthard, K., S. Nylin, and C. Wiklund. 1999. Seasonal plasticity in two satyrine butterflies: state-dependent decision making in relation to daylength. Oikos 84:453–462.

Grether, G. F. 2005. Environmental change, phenotypic plasticity, and genetic compensation. American Naturalist 166:E115–E123.

Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. Journal of Statistical Software 33:1–22.

Hansen, M. M., I. Olivieri, D. M. Waller, E. E. Nielsen, and T. G. W. Group. 2012. Monitoring adaptive genetic responses to environmental change. Molecular Ecology 21:1311–1329.

Harrington, R., I. Woiwod, and T. Sparks. 1999. Climate change and trophic interactions. Trends in Ecology & Evolution 14:146–150.

Husby, A., D. H. Nussey, M. E. Visser, A. J. Wilson, B. C. Sheldon, and L. E. B. Kruuk. 2010. Contrasting patterns of phenotypic plasticity in reproductive traits in two great tit (*Parus major*) populations. Evolution 64:2221–2237.

Jackson, M. T. 1966. Effects of microclimate on spring flowering phenology. Ecology 47:407–415.

Janzen, D. H. 1980. When is it coevolution? Evolution 34:611–612.

Kawecki, T. J., and D. Ebert. 2004. Conceptual issues in local adaptation. Ecology Letters 7:1225–1241.

Lande, R. 2009. Adaptation to an extraordinary environment by evolution of phenotypic plasticity and genetic assimilation. Journal of Evolutionary Biology 22:1435–1446.

Laugen, A. T., A. Laurila, K. Rasanen, and J. Merila. 2003. Latitudinal countergradient variation in the common frog (*Rana temporaria*) development rates: evidence for local adaptation. Journal of Evolutionary Biology 16:996–1005.

Meeus, J. H. 1991. Astronomical algorithms. Willmann-Bell, Richmond, VA.

Merilä, J. 2012. Evolution in response to climate change: in pursuit of the missing evidence. Bioessays 34:811–818.

Metcalf, C., and T. Mitchell-Olds. 2009. Life history in a model system: opening the black box with *Arabidopsis thaliana*. Ecology Letters 12:593–600.

Miller-Rushing, A. J., and R. B. Primack. 2008. Global warming and flowering times in Thoreau's Concord: a community perspective. Ecology 89:332–341.

Moussus, J.-P., R. Juillard, and F. Jiguet. 2010. Featuring 10 phenological estimators using simulated data. Methods in Ecology and Evolution 1:140–150.

Nakagawa, S., and R. P. Freckleton. 2008. Missing inaction: the dangers of ignoring missing data. Trends in Ecology & Evolution 23: 592–596.

Nuismer, S. L., R. Gomulkiewicz, and B. J. Ridenhour. 2010. When is correlation coevolution? American Naturalist 175:525–537.

Ozgul, A., S. Tuljapurkar, T. G. Benton, J. M. Pemberton, T. H. Clutton-Brock, and T. Coulson. 2009. The dynamics of phenotypic change and the shrinking sheep of St. Kilda. Science 325:464–467.

Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. Nature 421:37–42.

Pelini, S. L., J. D. K. Dzurisin, K. M. Prior, C. M. Williams, T. D. Marsico, B. J. Sinclair, and J. J. Hellmann. 2009. Translocation experiments with butterflies reveal limits to enhancement of poleward populations under climate change. Proceedings of the National Academy of Sciences of the USA 106:11160–11165.

Perry, M., D. Hollis, and M. Elms. 2009. The generation of daily gridded datasets of temperature and rainfall for the UK. Climate memorandum no. 24. National Climate Information Centre, Met Office, Devon, UK.

Phillimore, A. B., J. D. Hadfield, O. R. Jones, and R. J. Smithers. 2010. Differences in spawning date between populations of common frog reveal local adaptation. Proceedings of the National Academy of Sciences of the USA 107:8292–8297.

R Development Core Team. 2011. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. http://www.R-project.org.

Roy, D. B., and J. Asher. 2003. Spatial trends in the sighting dates of British butterflies. International Journal of Biometeorology 47: 188–192.

Roy, D. B., and T. H. Sparks. 2000. Phenology of British butterflies and climate change. Global Change Biology 6:407–416.

Sparks, T. H., and T. J. Yates. 1997. The effect of spring temperature on the appearance dates of British butterflies 1883–1993. Ecography 20:368–374.

Stenseth, N. C., and A. Mysterud. 2002. Climate, changing phenology, and other life history traits: nonlinearity and match-mismatch to the environment. Proceedings of the National Academy of Sciences of the USA 99:13379–13381.

Stone, G. N., S. Nee, and J. Felsenstein. 2011. Controlling for nonindependence in comparative analysis of patterns across populations within species. Philosophical Transactions of the Royal Society B: Biological Sciences 366:1410–1424.

van de Pol, M., and A. Cockburn. 2011. Identifying the critical climatic window that affects trait expression. American Naturalist 177:698–707.

van de Pol, M., H. L. Osmond, and A. Cockburn. 2012. Fluctuations in population composition dampen the impact of phenotypic plasticity on trait dynamics in superb fairy-wrens. Journal of Animal Ecology 81:411–422.

van de Pol, M., and J. Wright. 2009. A simple method for distinguishing within- versus between-subject effects using mixed models. Animal Behaviour 77:753–758.

Visser, M. E. 2008. Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B: Biological Sciences 275:649–659.

Visser, M. E., C. Both, and M. M. Lambrechts. 2004. Global climate change leads to mistimed avian reproduction. Advances in Ecological Research 35:89–110.

Wiklund, C., and C. Ahrberg. 1978. Host plants, nectar source plant, and habitat selection of males and females of *Anthocharis cardamines* (Lepidoptera). Oikos 31:169–183.

Wilczek, A. M., L. T. Burghardt, A. R. Cobb, M. D. Cooper, S. M. Welch, and J. Schmitt. 2010. Genetic and physiological bases for phenological responses to current and predicted climates. Philosophical Transactions of the Royal Society B: Biological Sciences 365:3129–3147.

Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau's woods are driven by climate change. Proceedings of the National Academy of Sciences of the USA 105:17029–17033.

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Male orange-tip butterfly visiting a cuckoo flower. Photo by WTPL/Richard Becker.