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## RESEARCH ARTICLE

# Modelling thermal sensitivity in the full phenological distribution: A new approach applied to the spring arboreal caterpillar peak

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## Abstract

1. Advances in spring phenology are among the clearest biological responses to climate warming. There has been much interest in how climate impacts on phenology because the timings of key events have implications for species interactions, nutrient cycling and ecosystem services. To date most work has focused on only one aspect of population phenology, the effects of temperature on the average timing. In comparison, effects of temperature on the abundance of individuals and their seasonal spread are understudied, despite their potential to have profound impacts on species interactions.
2. Here we develop a new method that directly estimates the effect of spring temperatures on the timing, height and width of the phenological distribution and apply it to temperate forest caterpillars, a guild that has been the focus of much research on phenology and trophic mismatch.
3. We find that warmer spring conditions advance the timing of the phenological distribution of abundance by  $-4.96$  days  $^{\circ}\text{C}^{-1}$  and increase its height by 34%  $^{\circ}\text{C}^{-1}$  but have no significant effect on the duration of the distribution. An increase in the maximum density of arboreal caterpillars with rising temperatures has implications for understanding climate impacts on forest food chains, both in terms of herbivory pressure and the resources available to secondary consumers.
4. The new method we have developed allows the thermal sensitivity in the full phenological distribution to be modelled directly from raw data, providing a flexible approach that has broad applicability within global change research.

## KEYWORDS

caterpillar, phenology, spatiotemporal, thermal sensitivity, trophic match/mismatch

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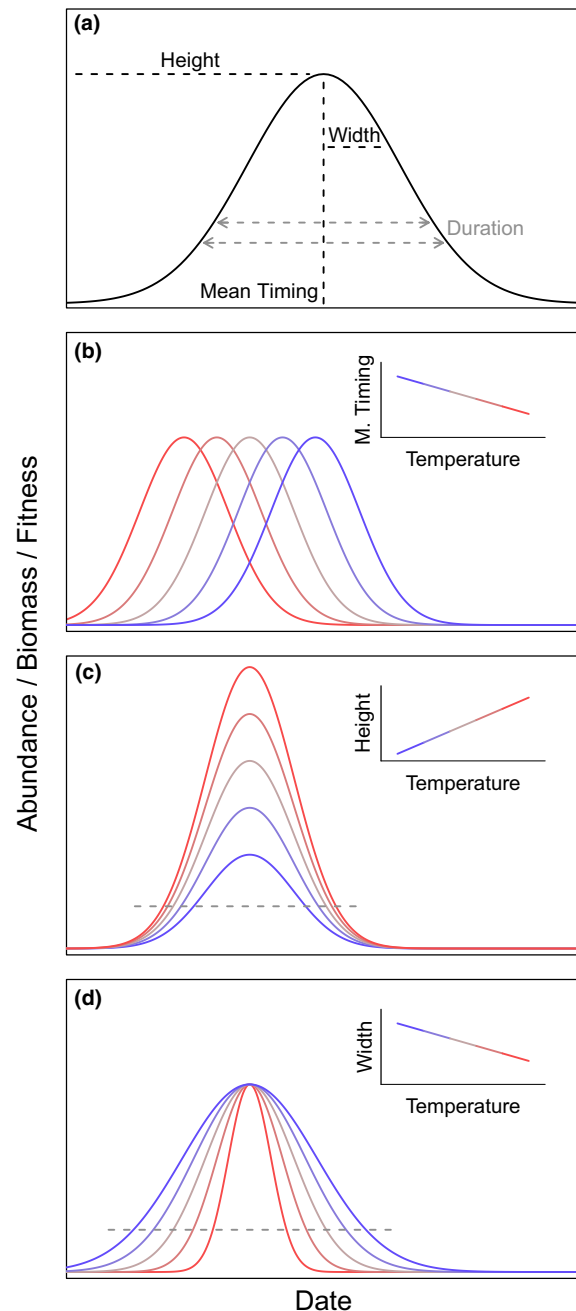
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## 1 | INTRODUCTION

Anthropogenic climate warming has profound impacts on ecological systems, with phenological shifts having become one of the most reported biotic responses (Parmesan & Yohe, 2003; Walther et al., 2002). Temperature is a key driver of phenology for extra-tropical taxa, though there is heterogeneity in thermal sensitivity among species and trophic levels (Cohen et al., 2018; Roslin et al., 2021; Thackeray et al., 2016). The outcome of many species interactions depend on synchrony between ephemeral life history events and, as the thermal sensitivity of interacting species or guilds may differ, warming temperatures have the potential to alter interactions, including those between consumers and their resources (Kharouba et al., 2018; Samplonius et al., 2020; Thackeray et al., 2016).

Phenology is frequently quantified as the mean or first timing of an event (Figure 1a) among individuals in a population (Both et al., 2009; Burgess et al., 2018; Charmantier et al., 2008; Reed et al., 2013; Roslin et al., 2021; Thackeray et al., 2016; Thomas et al., 2001) and the thermal sensitivity of mean (or first) timing has been examined for many species and guilds (Cohen et al., 2018; Roslin et al., 2021; Thackeray et al., 2016). In comparison, very few phenology-focused studies have addressed how temperature affects other parameters that determine the full phenological distribution, namely the abundance of individuals exhibiting the mean timing (height), how the timing within a population or guild is spread around the mean (width), or the length of time over which the frequency of a phenological event falls above a given threshold (duration) (Figure 1a). Beyond a phenological context, there is evidence across a range of taxa that temperature affects interannual trends in abundance (Bowler et al., 2017). Previous work also finds spatial and temporal trends in the duration of life history events (Ahmad et al., 2021; Møller et al., 2010; Vitasse et al., 2009), although responses vary among species and events. For example, the grasshopper community is abundant for a longer duration in warmer years in Colorado (Buckley et al., 2021) and the deciduous tree canopy duration is longer in warmer years in the Pyrenees (Vitasse et al., 2009), while warmer conditions drive shorter flowering durations for a range of flowing plant species observed on Guernsey (Bock et al., 2014) and in Finland more bird species have seen a reduction in the duration of breeding over time than an increase (Hällfors et al., 2020).

In the context of research on phenology and the match/mismatch hypothesis (MMH—the hypothesis that phenological asynchrony between consumer demand and an ephemeral resource impacts negatively on consumer fitness Cushing, 1969), the temperate forest tri-trophic chain of deciduous trees, caterpillars and cavity nesting passerines in spring has become a classic study system (Both et al., 2009; Charmantier et al., 2008; Cole et al., 2021; Thomas et al., 2001). Within this system the phenological distribution of caterpillars may have both top-down and bottom-up effects through interactions with both the leafing trees and breeding birds respectively. The phenological distribution of the caterpillar guild of primary consumers—comprised of many species (Shutt et al., 2019)—is usually summarised on the basis of mean timing, which has been found to advance by approximately



**FIGURE 1** (a) A Gaussian function showing the three parameters that govern the phenological distribution (black) of a life history event: Mean timing is the most common timing within the population/guild, height describes the maximum response (e.g. abundance, biomass or fitness) value reached, and width corresponds to the standard deviation of the function and therefore its curvature. Duration (a derived metric) describes the number of days where the response falls above a given threshold. The chosen threshold level will influence the duration, as illustrated by the two lines. (b–d) Examples of how a slope in thermal sensitivity for each parameter could influence the phenological distribution while the other parameters are held constant. The grey dashed lines in (c, d) show that a change in the height or width parameter both influence the duration at a given value and therefore duration is not defined by width alone, as it would be for a Gaussian distribution.

4–6 days  $^{\circ}\text{C}^{-1}$  (Burgess et al., 2018; Charmantier et al., 2008; Visser et al., 2006); largely tracking the shift in timing of deciduous tree leafing, but a little steeper than the advance of insectivorous passerine breeding (Both et al., 2009; Burgess et al., 2018; Cole et al., 2021). Effects of spring temperature on the height or width of the caterpillar phenological distribution have been largely overlooked. The exceptions are a study that reported no correlation between spring temperature and the height of the caterpillar biomass distribution over 16 years in Poland (Nadolski et al., 2021) and studies that found the width of the biomass distribution to be narrower under warmer spring conditions across nine years in the Netherlands (Visser et al., 2006) and across 19 sites in the UK (Smith et al., 2011). However, all previous studies are low-powered ( $n \leq 20$ ) and relied on a two-step analytical approach whereby phenological parameters were estimated for each site-year combination and then estimates were treated as data in a subsequent model, ignoring measurement error. This two-step approach will underestimate the true error in slopes. One reason for the scarcity of phenological research beyond mean timing is that the field has lacked a statistical framework for directly examining the thermal sensitivity of all three parameters that govern the phenological distribution.

Spring temperatures could affect the phenological distribution of the arboreal caterpillar guild abundance throughout spring via various intraspecific and interspecific effects. Warmer temperatures have been shown to drive earlier emergence for species that overwinter as eggs or larvae (Charmantier et al., 2008; Visser et al., 2006), shifting the mean timing of the guild phenology. Temperature could affect the width of the phenological distribution by changing intraspecific variation in larval emergence—though no effect was found in previous work on *Malacosoma disstria* (Uelmen et al., 2016). Temperature could also affect the period over which each individual feeds prior to pupation through altering the rate of development (Buse et al., 1999; Stamp, 1990), which is predicted to narrow the width and reduce the duration, consistent with the findings of previous work (Smith et al., 2011; Visser et al., 2006). There are multiple mechanisms that

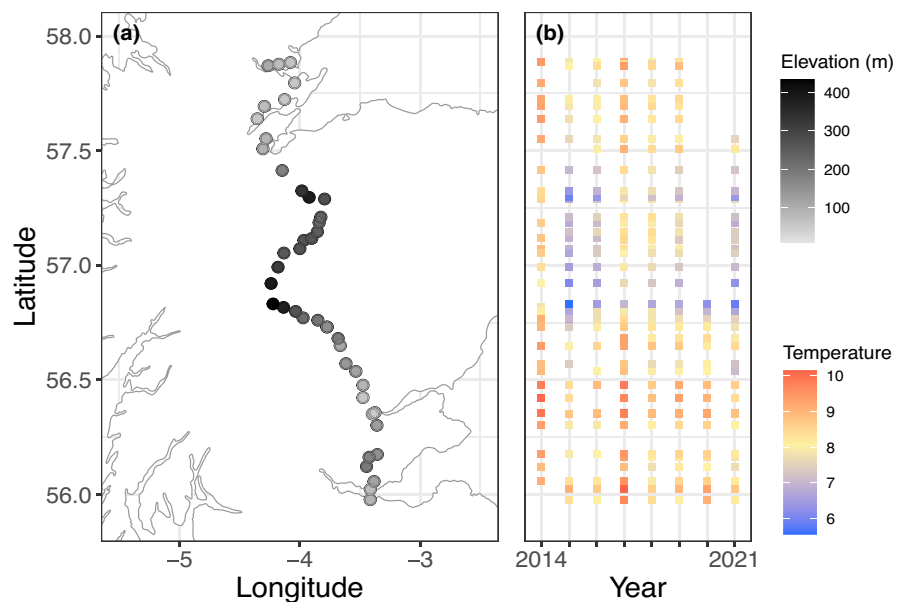
could drive a relationship between temperature and the height of the phenological distribution. For instance, if low temperatures presents a constraint on development, an increase in temperature may increase pre- and post-emergence survival and post-emergence growth (Battisti et al., 2005), such that increasing temperatures could increase the guild abundance and distribution height. However, colder temperatures can increase the starvation tolerance of caterpillars (Abarca & Lill, 2015), such that the phenological synchrony between caterpillars and their hosts may alter the effect of temperature on the distribution height. Interspecific differences in the magnitude or direction of effect for each of these mechanisms would also contribute to the thermal sensitivity of the phenological distribution of the full caterpillar guild.

Here, we use data on temperature and caterpillar abundance throughout spring, collected at 44 sites across 8 years (Figure 2), yielding 293 site-by-year combinations, to analyse the effect of temperature on the phenological distribution of 8196 arboreal caterpillars sampled from 37,674 branch beatings. We develop and apply a novel statistical method, using the Gaussian function, to estimate the thermal sensitivity of the three parameters that govern the phenology of abundance: mean timing, height and width (i.e. standard deviation; Figure 1). We also examine whether estimated thermal sensitivities over space and time are consistent with a causal effect (i.e. where slopes are similar in space and time Lovell et al., 2023). Finally, using derived parameters, we explore thermal sensitivity in the duration of and area under the full phenological distribution.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system

Data were collected between 2014 and 2021 at 44 deciduous woodland sites along a 220 km transect from Edinburgh (55°980 N, 3°400 W) to Dornoch (57°890 N, 4°080 W) in Scotland



**FIGURE 2** (a) Map of site locations in Scotland with elevation above sea level indicated by a scale of grey to black. (b) The mean annual temperatures from mid-Feb to late June for each site in each year by latitude. Gaps in the temperature data reveal years when sites were not monitored.

(Macphie et al., 2020; Shutt et al., 2018; Figure 2a). All field work was carried out with the permission of site landowners. The sites vary in temperature and extend across two degrees of latitude and a 440 m elevation range (Figure 2b). Two iButton temperature loggers, recording hourly temperature, were installed in mid-February at different locations at each site, on the north side of a tree and in a shaded area to avoid direct sunlight. The latest installation was ordinal date 58 (27th February) and recording continued until the end of the season with the earliest retrieval date among years being day 161 (9/10th June). As one site had no temperature data for 2017, we used temperature data for the nearest site in 2017, making a correction for the annual average difference in temperatures between the two sites.

We sampled caterpillars using a branch beating method, recording the abundance of caterpillars on each branch monitored on different dates throughout spring (Macphie et al., 2020; Shutt et al., 2019). This work defines the arboreal guild of caterpillars as the larvae of insect species that spend their larval stage on deciduous trees and are similar in appearance to Lepidopterans (Shutt et al., 2019). Previous sampling across these sites found 93% of the guild to be Lepidoptera, including 45 species, 78% of which were Geometrids (of which 45% were the most common species, *Operophtera brumata*) and 13% Noctuids, and the remaining 7% included species of Hymenoptera, Diptera and Coleoptera (Shutt et al., 2019). At each site, tree leafing phenology was monitored on a selection of trees and each year caterpillar sampling began once 45% of the trees had their first leaf across all sites. The branch beating continued until the end of the field season in mid/late June (2021 sampled from ordinal dates 133 to 157; see Macphie et al., 2020 for 2014–20 details). This sampling approach captures the beginning and end of the caterpillar season within the majority of site by year combinations. An average of 14 trees (range: 10–17) were sampled at each site in each year from 2017 to 21, prior to that, 5 trees per site (range: 3–7) were sampled from 2014 to 16. One branch on each tree was marked for sampling and the trees monitored represent the tree composition throughout each site, dominated by 10 taxa: alder (*Alnus glutinosa*), ash (*Fraxinus excelsior*), beech (*Fagus sylvatica*), birch (*Betula* spp.), elm (*Ulmus glabra*), hazel (*Corylus avellana*), oak (*Quercus* spp.), rowan (*Sorbus aucuparia*), sycamore (*Acer pseudoplatanus*) and willow (*Salix* spp.), which make up 98% of the trees sampled. Each site was visited every 2 days with half of the focal trees sampled on alternating visits, leaving 4 days between each branch beating to allow for recolonisation. The same branches were sampled across and within years unless damaged or dead.

## 2.2 | Replication statement

| Scale of inference      | Scale at which the factor of interest is applied | Number of replicates at the appropriate scale |
|-------------------------|--|---|
| Guild (of caterpillars) | Site by year combinations                        | 293   |

## 2.3 | Modelling the caterpillar peak as a Gaussian function

We modelled the number of caterpillars recorded on each branch as Poisson distributed with an expectation that follows a Gaussian function of scaled (mean=147.9, SD=14.1) ordinal date ( $x$ ; Equation 1) using the RStan package (Stan Development Team, 2020). The Gaussian function (Equation 1) is well-suited to describing the phenological distribution of caterpillar abundance over time as it consists of three parameters that describe the mean timing ( $\mu$ ), height ( $A_{\max}$ ) and width ( $\sigma$ ) (Figure 1a; see also Dennis et al., 2016 and de Villemereuil et al., 2020 for earlier work on phenology using the Gaussian function):

$$A(x) = A_{\max} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right). \quad (1)$$

(Equation 1) can be rearranged into (Equation 2) allowing the height and width parameters to be modelled on the log scale:

$$A(x) = \exp\left(\log A_{\max} - \frac{(x-\mu)^2}{2\exp(\log \sigma)^2}\right). \quad (2)$$

Spatiotemporal temperature model (Figure S1): For our main analysis, we modelled  $\log A_{\max}$ ,  $\log \sigma$  and  $\mu$  (the phenological parameters) using a generalised non-linear mixed model with fixed effects including an intercept and a temperature slope for each phenological parameter, allowing a change in each parameter with temperature (Figure 1b–d). The periods over which mean temperatures best predicted the three phenological parameters were identified using a sliding window approach (Figure S1; see section below regarding the determination of temperature predictors). The temperature variables were mean centred for the analysis and differed between the phenological parameters, each comprising the mean site by year daily temperatures from periods identified using the sliding window approach. Site, year and site by year interaction effects were fitted as random for each phenological parameter, and the covariance between the phenological parameters for each of these terms was calculated from a single correlation matrix, assuming the same correlation structure among random terms, with term-specific variances. Each day at each site in each year, unique tree identity, recorder of the sample and each observation were also fitted as random terms for  $\log A_{\max}$  to account for other important sources of variance in caterpillar abundance (Macphie et al., 2020), the latter term dealing with any over-dispersion with respect to the Poisson error distribution. The full analysis framework is outlined in Figure S1 in Appendix S1, Supplementary Information and the spatiotemporal model notation can be found in Appendix S2. To assess the fit of the temperature slope for each phenological parameter to the parameters estimates for each site by year combination we calculated a pseudo- $R^2$  which represents the proportion of site by year variance that is explained by the slope; details can be found in Appendix S3.

Where phenological data are replicated across thermal environments in space and time, it is possible to estimate separate regressions of biotic responses on temperature in both space and in time. Where the effect of temperature is similar in space and time, this increases our confidence that the effect is causal and the processes involved in space and time are similar (Dunne et al., 2004; Phillimore et al., 2010). Alternatively, a difference in the effect of temperature over space versus time may indicate that different processes are operating over space and time, such as local adaptation or species turnover in space but not time, or that a third variable correlated with temperature and the biotic response is at play (Tansey et al., 2017).

Space versus time temperature model (Figure S1): To test for any difference in the thermal sensitivity of the caterpillar phenological distribution in space and time, we included two fixed effect temperature slopes for each phenological parameter: one using the site mean temperatures and another for the annual deviations from the mean of each site (Figure S1); employing within-site centring (Van De Pol & Wright, 2009). As the among site variance in our temperature estimates is quite high, we anticipate that site estimates of mean temperatures will be quite close to the true mean and slope estimates will be largely unbiased (Phillimore et al., 2010; Westneat et al., 2020). The site mean temperatures were attained from a linear mixed-model using the lme4 package (Bates et al., 2015) to estimate a mean site temperature, which is not biased by the years in which each site has been monitored (Figure 2b). Separate linear mixed models were used for the temperature associated with each Gaussian function parameter and included temperature as the response variable with site and year random intercepts. The mean site temperatures from the models were mean-centred for use in the model, summarised below. The random term structure was the same as in the spatiotemporal temperature model. The difference between the spatial and temporal temperature slopes for each phenological parameter was determined by subtracting the temporal slope estimate from the spatial slope estimate for each iteration of the posterior distributions.

## 2.4 | Derived parameters

Duration: The width parameter is equivalent to a standard deviation, describing the curvature of the distribution, meaning that when the height is held constant a change in the width parameter defines a change in duration (Figure 1d). When the height parameter changes with a constant width this also alters the duration (Figure 1c), so by allowing slopes of change in both the height and the width parameters with temperature, changes in the width parameter do not uniquely define changes in duration, but this can be calculated post-hoc. We define the duration of the distribution as the number of days that the expected abundance exceeds some threshold. The choice of abundance threshold is arbitrary without an informed reason, and the relative difference in duration between distributions will differ depending on the threshold at which it is calculated.

Area under the phenological distribution: The formula for the area under the Gaussian function ( $T$ ) can be obtained by rearranging the integral of the Gaussian function (Equation 3) and Gaussian probability function (Equation 4), for which the area is equal to one,

$$T = \int_{-\infty}^{\infty} A_{\max} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) dx, \quad (3)$$

$$1 = \int_{-\infty}^{\infty} \frac{1}{\sigma\sqrt{2\pi}} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) dx, \quad (4)$$

$$\sigma\sqrt{2\pi} = \int_{-\infty}^{\infty} \exp\left(-\frac{(x-\mu)^2}{2\sigma^2}\right) dx.$$

Combining (Equations 3 and 4) shows that the area under the distribution can be described by (Equation 5), which rearranges to (Equation 6) when the height and width parameters are estimated on the log scale.

$$T = A_{\max} \sigma \sqrt{2\pi}, \quad (5)$$

$$T = \exp\left(\log A_{\max} + \log \sigma + \log(\sqrt{2\pi})\right). \quad (6)$$

This shows the area under the phenological distribution depends log-linearly on temperature with a slope equal to the sum of the log-scale slope estimates for the change in height and width. Slopes for the change in the area under the distribution with changing temperature were calculated for the spatiotemporal temperature model and both components of the space versus time temperature model (Table 1).

## 2.5 | Mean expectations on the arithmetic scale

When a variable is normally distributed on the log-scale, the mean on the arithmetic scale is equal to the sum of the log-scale mean and half of the log-scale distribution variance exponentiated. Within our models the height and width parameters are assumed to come from a log-normal distribution, meaning that the expectation on the arithmetic scale across site by years must include half of the variance attributed to the random terms being marginalised. Details of the methods of estimation on the arithmetic scale for results shown in Figures 3 and 4 can be found in Appendix S4.

## 2.6 | Determination of temperature predictor using sliding windows

The periods during which temperatures have most effect on the mean timing, height and width of the phenological distribution may differ among the phenological parameters; therefore, we applied a sliding window approach simultaneously across all three parameters (Figure S1). In the interests of efficiency, we conducted model comparisons in a frequentist setting on the basis

**TABLE 1** Summary of results for the effect of temperature on the mean timing, height, width and area under the phenological distribution of spring arboreal caterpillars, showing posterior mean effect with 95% credible intervals (CI) in brackets beneath.

| Parameter   | Unit                          | Spatiotemporal slope   | Spatial slope          | Temporal slope         | Difference (S-T)       |
|-------------|-------------------------------|------------------------|------------------------|------------------------|------------------------|
| Mean timing | days °C <sup>-1</sup>         | -4.96 (-6.21 to -3.64) | -5.77 (-7.39 to -4.18) | -3.39 (-5.49 to -1.46) | -2.37 (-4.77 to 0.17)  |
| Height      | Prop. change °C <sup>-1</sup> | 1.34 (1.05 to 1.61)    | 1.66 (0.97 to 2.63)    | 1.17 (0.81 to 1.49)    | 0.49 (-0.31 to 1.55)   |
| Width       | Prop. change °C <sup>-1</sup> | 0.91 (0.83 to 0.99)    | 0.85 (0.75 to 0.96)    | 1.05 (0.89 to 1.21)    | -0.20 (-0.39 to -0.01) |
| Area        | Prop. change °C <sup>-1</sup> | 1.21 (0.97 to 1.44)    | 1.40 (0.90 to 2.12)    | 1.22 (0.89 to 1.53)    | 0.18 (-0.41 to 0.95)   |

Note: Spatiotemporal slopes come from a model using temperatures for each site-year to estimate the thermal sensitivity of the parameters. The spatial and temporal slopes come from a model employing a within-site centring approach to separate the effects in space and time. The difference column indicates the difference between the spatial and temporal slope estimates calculated from the spatial slope minus the temporal. Slope estimates are exponentiated or unscaled where applicable and 'prop.' in the unit column implies proportional changes (i.e. exponentiated slopes). For the mean timing parameter and the difference column CI removal from 0 suggests a significant effect, whereas for the three parameters in units of proportional change CI removal from 1 suggests significance.

of Akaike information criteria (AIC; Burnham & Anderson, 2004). We obtained estimates of the mean timing, height and width of the caterpillar phenological distribution at each site in each year using the site by year model (described in Appendix S5) and then passed these estimates and a measure of measurement uncertainty to a multi-variate meta-analytic model, using the metafor package (Viechtbauer, 2010). Within this framework we then ran over all combinations of sliding windows for the mean timing (start dates from 58 to 100 in steps of 7, durations from 28 to 98 days in steps of 14), height (start dates from 58 to 128 in steps of 14, durations from 28 to 98 days in steps of 14) and width (start dates from 58 to 128 in steps of 14, durations from 28 to 98 days in steps of 14), totalling 13,231 models. The mean daily temperature for each site by year combination during the identified windows were then used within the Gaussian function models described above (Figure S1).

All analyses used R version 4.0.2 (R Core Team, 2020), and models including the Gaussian function used the RStan package (Stan Development Team, 2020). Models were run using four chains with 2500 iterations after warmup with a thinning of 5; the spatiotemporal temperature model and space versus time model had a warmup of 2000 and the site by year model had a warmup of 1500 iterations. Convergence was checked using the Rhat (all <1.02) and through graphical inspection. Effective sample sizes were all over 600, and over 1100 for all focal coefficients. The space versus time temperature model had three divergent transitions after the warmup, which was 0.15% of the 2000 iterations retained.

### 3 | RESULTS

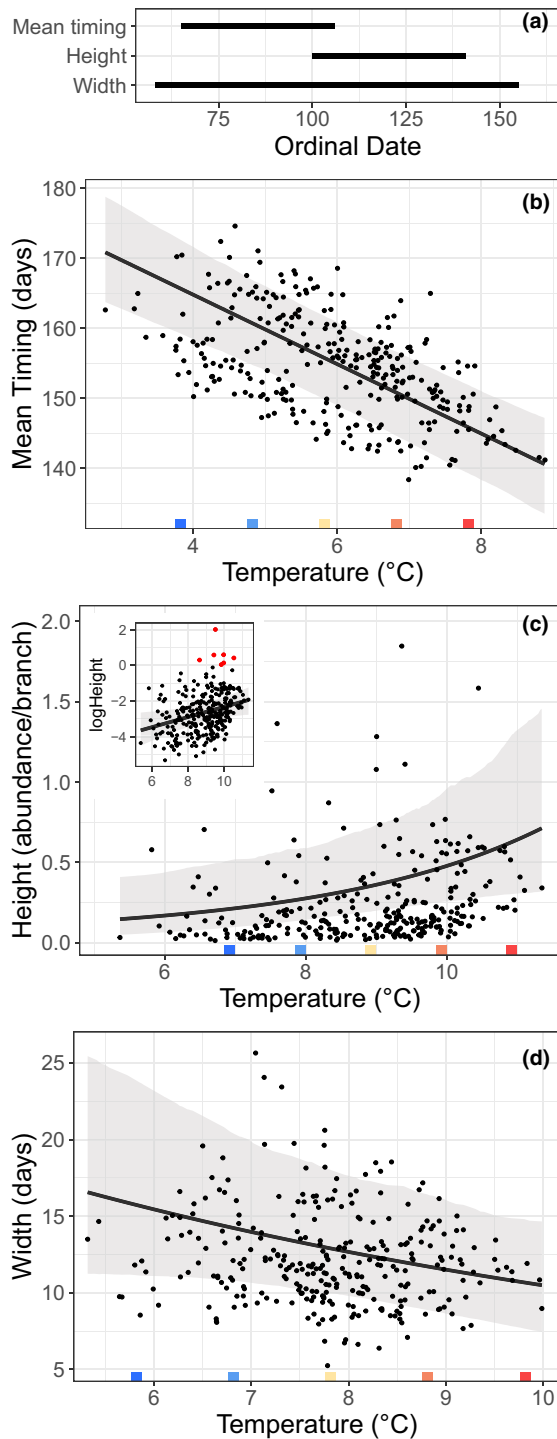
Of the 37,674 branch beatings, 3950 of the samples recorded one or more caterpillar totalling 8196 individuals. Of the samples in which one or more caterpillars were present, 69% recorded one and 16% recorded two, with a maximum abundance of 109.

In the sliding window analysis, mean timing was most sensitive to temperatures from early March to mid-April (ordinal dates 65–106, 5th March–15th April in non-leap year, Figure 3a, Figure S1), height was most sensitive to temperatures later in the spring (100–141,

9th April–20th May, Figure 3a, Figure S1) and width to temperatures that spanned the spring (58–155, 27th February–3rd June, Figure 3a, Figure S1). We used the mean temperature during each of these windows as the temperature variable for the respective Gaussian parameter in all subsequent analyses.

Spring temperatures had a significant effect on all three phenological parameters, with the most profound effects being that the caterpillar phenological distribution is both earlier and higher in warmer years (Figures 3b,c and 4a). We found that mean timing shifted by -4.96 days °C<sup>-1</sup> (95% credible intervals [CIs]: -6.21 to -3.64 days °C<sup>-1</sup>, Figure 3b). The bimodal pattern among the points in Figure 3b is caused by substantial year random effects (2014=0.25, 2016=0.62, 2017=0.25, 2018=0.11, 2019=-0.63, 2020=-0.55, 2021=-0.31 and 2022=0.24; scaled ordinal date effect sizes). When looking at the expected change in distribution height independently of the other parameters (see Appendix S4), the maximum abundance increased by 34% °C<sup>-1</sup> (CIs: 5%–61% °C<sup>-1</sup>, Figure 3c), though we still find substantial variation in height among sites, years and site-years (Table S3; differences in phenological parameter variances among sites and years from models with and without temperature are discussed further in Appendix S6). When we account for the uncertainty in all three parameters to attain the mean expectations of abundance on each day in spring (see Appendix S4), the distribution height increased by 28% (CIs: 1%–52%) when temperature increased by one degree above the mean (Figure 4a). The width parameter decreased by 9% °C<sup>-1</sup> (CIs: 1%–17% °C<sup>-1</sup>, Figure 3d), indicating the shape of the distribution narrows as spring temperature increases. The temperature slopes explained 34.93% (CIs: 13.62%–55.82%), 7.96% (CIs: 0.15%–19.17%) and 4.94% (CIs: 0.07%–14.97%) of the variance among site by year combinations for the mean timing, height and width parameters, respectively (Figure 3b–d; calculations described in Appendix S3).

The duration of the distribution will be affected by both the height and width parameters and varies depending on the abundance threshold at which it is calculated (Figure 1); we therefore chose to present duration at two thresholds. The purpose of quantifying duration was to assess any change in the period throughout which caterpillars are present, making lower abundance thresholds most informative; we chose 0.05 and 0.1 caterpillars per branch as in



**FIGURE 3** (a) Windows of time where spring temperature was identified as the best predictor of each parameter of the phenological distribution. (b–d) the model predictions (black points) for the mean timing, height and width of the caterpillar peak, as a function of temperature during the identified windows for each site by year combination. Mean estimate on the data scale (black line) and 95% credible intervals (grey band). (c) The inset plot shows log scale estimates and red points indicate points excluded from the data scale plot. Coloured squares along the x-axis show the mean temperature in yellow with  $\pm 1$  and  $2^\circ\text{C}$  in blues/reds which correspond to the plots in Figure 4.

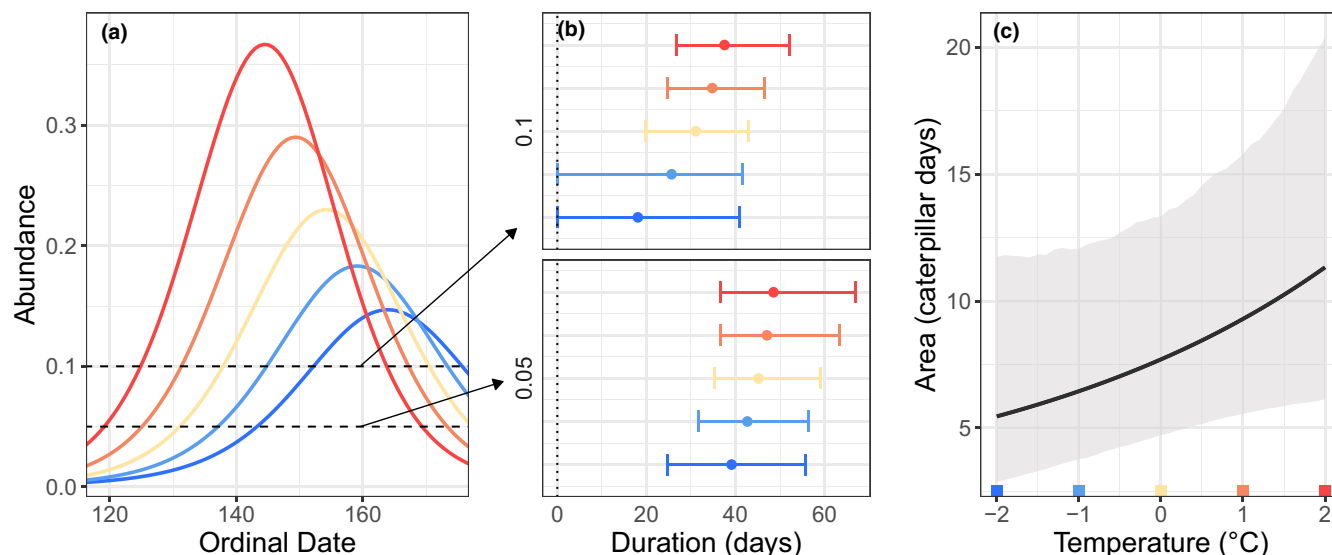
the absence of a biological motivation the choice of abundance was arbitrary and these allowed comparison across a  $4^\circ\text{C}$  range (blue to red lines in Figure 4a) that is within the temperature variation we find across sites and years within our study. We found no significant effect of temperature on duration at either threshold across the  $4^\circ\text{C}$  range within our data (Figure 4b; mean [CIs] difference between 2 and  $-2^\circ\text{C}$  at  $0.1 = 19.45$  days [ $-4.23$ – $47.90$ ]; at  $0.05 = 9.42$  days [ $-7.75$ – $29.58$ ]). While the change in duration at the chosen abundance levels was not significant, the mean point estimates show a slight increase with temperature, particularly at the higher threshold. This illustrates that while the shape of the peak is narrowing through a reduction in the width parameter, the substantial increase in height maintains (or may even increase) the duration when caterpillars are present above a particular abundance. The area under the phenological distribution increases by 1.21 times per  $^\circ\text{C}$  (derived on the log scale then exponentiated), though this effect was not significantly removed from 1 (CIs: 0.97–1.44, Figure 4c).

Spatial and temporal slopes were generally in the same direction as the main spatiotemporal model (Table 1), except for the temporal width parameter slope. For the mean timing parameter, estimates in space and time were not significantly different and both were in the same direction with CIs removed from zero. While there was no significant difference in the mean timing slopes across space and time, the difference in the point estimates were consistent with a co-gradient, a steeper spatial slope. For the thermal sensitivity of the distribution height, the spatial and temporal estimates did not significantly differ, and point estimates were in the same direction consistent with a co-gradient pattern; however the credible intervals for both terms included 0. The thermal sensitivity of the width parameter was significantly different in space versus time, with a significant negative spatial slope, but no effect of temperature across years. The effect of temperature on the area under the phenological distribution was similar in the main model and over space and time, all showing positive but non-significant effects.

## 4 | DISCUSSION

We found that spring temperatures have an effect on the mean timing, height and width of the caterpillar phenological distribution. In addition to the phenological mean timing shifting by  $-4.96$  days  $^\circ\text{C}^{-1}$ , which is consistent with results from previous studies (Burgess et al., 2018; Charmantier et al., 2008; Visser et al., 2006), the distribution height increases by  $34\%$   $^\circ\text{C}^{-1}$  and decreases in width by  $9\%$   $^\circ\text{C}^{-1}$  (Figure 3b–d). While the shape of the peak narrows through the decrease in width, when paired with the substantial increase in height we found no change in the duration of the distribution with changing temperature (Figure 4b). The results reveal substantial thermal sensitivity of the full phenological distribution, including effects that have been largely overlooked in earlier work on phenology and MMH research.





**FIGURE 4** (a) Posterior mean expected abundance on the data scale of the full phenological distribution at different temperatures: the mean of each temperature window (mean timing = 5.85°C, height = 8.92°C, width = 7.81°C; yellow), +1°C (orange), +2°C (red), -1°C (light blue) and -2°C (dark blue); calculated from the posterior predictive distribution. (b) The mean and 95% credible intervals (95% CIs) for the duration of the peak at an abundance of 0.1 and 0.05 caterpillars for distribution at each temperature calculated from the posterior distributions of the simulated expectations of abundance across dates. (c) The mean and 95% CIs for the area under the phenological distribution from -2 to 2°C around the mean (centred) temperature, calculated from the simulations under the model.

Our finding that spring temperatures have a substantial impact on the maximum height of the caterpillar guild phenological distribution (an increase of 34% °C<sup>-1</sup>) is likely to have cascading effects through interactions within the forest community. Even an increase in temperature of 1.5°C could yield more than a 50% increase in the maximum abundance of arboreal caterpillars. This is liable to lead to an increase in herbivory pressure that represents a potentially major indirect effect of temperature on the severity of tree defoliation (Kulman, 1971; Marquis & Whelan, 1994; Whitham et al., 1991; Whittaker & Warrington, 1985), though this effect will also depend on the thermal sensitivity of leaf toughness and palatability. The impact on tree defoliation and growth is likely to depend on how synchronous caterpillars are to the tree and the level of defences the leaves have acquired at the time of maximum herbivory (Bellemain-Noël et al., 2021; Schwartzberg et al., 2014). Should the increased maximum abundance translate to a greater prevalence of pest outbreaks and defoliation, further work into whether the change is driven by a few specific species or is consistent throughout the guild will be important for the design of effective and targeted pest management interventions. An increase in the height of the caterpillar phenological distribution is also liable to have profound consequences for secondary consumers, a theme to which we will return.

The positive effect of spring temperature on the height of phenological abundance distribution that we observe departs substantially from the Nadolski et al. (2021) report of no correlation between annual temperature variation and maximum caterpillar biomass in Poland across 16 years. While it is possible that this reflects true differences in the caterpillar thermal-response between Scotland and Poland, perhaps influenced by spatial patterns in the thermal sensitivity of defoliator populations (Netherer

& Schopf, 2010), it is possible that our slopes do not in fact differ from theirs. While Nadolski et al. do not report a slope or confidence interval, the interval is likely to be broad and therefore may overlap with our result.

By separating the effects of temperature in space and time we can gain a window into whether effects are likely to be causal and insights into the processes at play (Lovell et al., 2023). For the mean timing parameter, similar estimates in space and time suggest temperature has a causal effect and is consistent with plasticity being responsible for much of the spatiotemporal variation in mean timing (Phillimore et al., 2010). While non-significant, the difference in the point estimates was in a direction consistent with a co-gradient pattern, which may suggest some contribution of local adaptation or a difference in species turnover over space versus over time. For the thermal sensitivity of the distribution height, the general direction of the estimates and lack of difference in space versus time suggests a causal effect of temperature, with a possible co-gradient pattern; yet neither effect was significant when considered in isolation. For the thermal sensitivity of the width, the lack of a trend in time but significant negative effect in space were consistent with the findings of Smith et al. (2011). Such a difference between effects estimated over space and time suggests a non-causal relationship between temperature and distribution width in our main model. The positive but non-significant effect of temperature on the area under the phenological distribution was similar in both space and time and the spatiotemporal model; we therefore cannot conclude that there is any effect of temperature on the area under the curve within our dataset, though this presents an interesting avenue for future work. While point estimates for all temperature-phenology effects are in the same direction over space and time, the trends

are estimated with considerable uncertainty and we suggest there would be value in revisiting these analyses with greater temporal replication in the future.

Our spatiotemporal estimate of a shift in phenological mean of  $-4.96 \text{ days } ^\circ\text{C}^{-1}$  in the caterpillar guild is similar to estimates obtained for leaf out in oak trees and other deciduous species from previous studies across Europe (Roberts et al., 2015; Tansey et al., 2017; Vitasse et al., 2010). In contrast, our estimate of the temporal slope for mean caterpillar timing is shallower than some dominant UK trees, for example, *Quercus* sp. leaf-out found to have sensitivity to forcing temperatures of  $-8.81 \pm 0.52 \text{ days } ^\circ\text{C}^{-1}$  (Roberts et al., 2015). This means that increasing temperatures could alter the phenological (a) synchrony between caterpillars and deciduous trees, despite previous studies suggesting that caterpillars are maintaining synchrony with oak (Both et al., 2009; Burgess et al., 2018). An increase in tree-caterpillar asynchrony may impede the increase in the height of the caterpillar phenological distribution and prevent the most extreme detrimental effects for the trees (Schwartzberg et al., 2014), while greater synchrony could exacerbate the increase in herbivory pressure (Bellemin-Noël et al., 2021; Schwartzberg et al., 2014).

Moving up the food chain to the insectivorous bird-caterpillar trophic interaction, a study of bird species in UK and Netherlands (not limited to woodland passerines) showed an average advance in lay date of  $3.28 \text{ days } ^\circ\text{C}^{-1}$  for resident species and  $2.49 \text{ days } ^\circ\text{C}^{-1}$  for migratory species (McClean et al., 2022). Our temporal estimate for the shift in caterpillar mean timing is similar to the estimate for resident birds and the average migratory species slope falls within the temporal caterpillar slope CIs (McClean et al., 2022). The overlap between bird and caterpillar slope estimates suggests that average resident and migratory bird species may be able to track the change in caterpillar phenology from year to year.

Where the thermal sensitivity of phenology differs between trophic levels (Thackeray et al., 2016), changing temperatures will alter the asynchrony between a consumer and its resource (Kharouba et al., 2018). The MMH is most often studied through comparison of consumer phenology and fitness to the resource population/guild mean timing; yet, the height and width of the resource distribution determines the duration of time for which the resource is above a given threshold, the amount of food available (i) as the total among days throughout spring (the area under the phenological distribution) or (ii) given a particular amount of phenological asynchrony and how the relative amount of food available differs among synchronous and asynchronous consumers. For forest birds that rely on caterpillars as a food resource to feed nestlings, the impacts of temperature on the shape and height of the caterpillar peak could have stark consequences for how the MMH manifests. The increase in peak height means that under warmer spring conditions far more food is predicted to be available to consumers that remain approximately synchronous with the caterpillars. However, the reduction in peak width with increasing temperature means that resource abundance declines more steeply to either side of the mean timing under warmer conditions, affecting the relative abundance of food available to synchronous versus asynchronous consumers. Therefore,

the fitness consequences of asynchrony could change with temperature, potentially increasing the strength of stabilising or directional selection on consumer breeding phenology. In the future, the modelling framework we present here could be extended to model the impact of the three phenological parameters of the resource on the parameters that govern the phenological fitness function of consumers (or resources). Specifically under the MMH we predict that the mean timing, height and width of the resource should have causal effects on the optimum timing, maximum and width of the consumer phenological fitness function (Macphie, 2023b).

Through allowing temperature during different windows to affect each distribution parameter in the sliding window, we have gained new insights into the thermal sensitivity of the caterpillar phenological distribution. The window identified as most influential for mean timing falls prior to the onset of the main peak in abundance, most likely influencing hatching phenology rather than altering the mean timing through impact on developmental rate, and is similar to that identified as important in other European studies (Porlier et al., 2012; Simmonds et al., 2020; Visser et al., 2006). The height of the distribution however is most sensitive to temperatures around the onset of the peak and in the weeks following, suggesting the thermal sensitivity in height is driven more by thermal effects on the larvae (and potentially their host plants) than eggs. For width, our time window is broader than identified in Visser et al. (2006), though we note a high degree of uncertainty in the position of the window for this phenological parameter (Figure S2). The sliding window approach involves a very high-level of multiple testing (13,231 window combinations in our case; van de Pol et al., 2016), which inflates the type I errors. In the context of our study, we anticipate that this is most likely to affect the slope of temperature on the width parameter, which is the weakest of the correlations we identify. Avenues for future work include examining whether the most influential window of temperature will differ with elevation and latitude (Macphie, 2023b) or whether the window that most affects height and width is in fact relative to caterpillar mean timing.

Our approach is similar to the Gaussian model functions described in de Villemereuil et al. (2020) and Dennis et al. (2016), with the major difference being that we include linear effects of temperature on the three parameters that control the position, shape and height of the phenological distribution. The approach we present here offers great potential for modelling effects of climate (e.g. temperature, precipitation) or other continuous variables (e.g. year, density of conspecifics) on phenological distributions. Examples of seasonal events that could be approximated by a Gaussian phenological distribution include planktonic blooms, tree leafing and senescence, flowering, fruiting, fish or amphibian spawning events, migration and reproduction metrics for mammals or birds, and numbers of parasitised or diseased individuals. Further potential improvements to the approach include modelling of skewed phenological distributions and incorporation of spatiotemporal autocorrelation in parameters (particularly height, as abundance is expected to be correlated from 1 year to the next). In addition, inclusion of linear latitude and year effects would reduce the risk that the effects that we attribute to climate variables arise from third variables that exhibit spatial or temporal trends. The approach we describe has advantages over use of a GLM/GLMM with a Poisson response and

quadratic date term to estimate the effects of an environmental variable on mean timing (Chevin et al., 2015; Edwards & Crone, 2021), as we found that this approach forces an undesirable non-linear relationship between the environmental variable and height (see Appendix S7 for further details).

Introducing a new approach for estimating climate-phenology relationships, we have shown that temperature has an effect not only on the mean timing of the phenological distribution of spring arboreal caterpillars but also on the height and width of the peak. We report an increase in the height accompanied by a decrease in the width; resulting in a similar duration of the distribution as temperature increases. The alterations to the shape of the phenological distribution of caterpillars not only identifies shifts in dynamics within the caterpillar guild that are attributed to temperature, but it will also impact the herbivory pressure on deciduous trees and alter the food availability throughout spring for breeding birds with possible implications for the MMH. The methods we present have broad applicability to other systems and questions within phenology and the MMH, and we encourage more work to consider the full phenological distribution of biological events rather than focusing on mean timing. To predict the biotic impacts of ongoing climate warming, it will often be essential to take these additional components of change into account.

#### AUTHOR CONTRIBUTIONS

Kirsty H. Macphie, Albert B. Phillimore and Jelmer M. Samplonius collected the data. Kirsty H. Macphie, Albert B. Phillimore and Jarrod D. Hadfield designed the analyses. Kirsty H. Macphie conducted the analyses with input from Jarrod D. Hadfield and Joel L. Pick. Kirsty H. Macphie wrote the first draft and all authors contributed to editing and revisions.

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#### CONFLICT OF INTEREST STATEMENT

There are no conflicts of interest.

#### DATA AVAILABILITY STATEMENT

Data and code are available on Zenodo <https://doi.org/10.5281/zenodo.8335050> (Macphie, 2023a).

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

**Appendix S1.** Framework summary figure.

**Appendix S2.** Spatiotemporal temperature model notation.

**Appendix S3.** Pseudo- $R^2$  for phenological parameter-temperature slopes.

**Appendix S4.** Mean expectation on the arithmetic scale.

**Appendix S5.** Sliding window analysis.

**Appendix S6.** Site, year and site-year variance in models.

**Appendix S7.** Issues with a Poisson GLMM approach to modelling temperature effects.

**Figure S1.** Graphical outline of the methodological framework used to analyse the effect of temperature on the full phenological distribution. Raw data on the abundance of caterpillars on days throughout spring (*Caterpillar Data*) and daily mean temperatures (*Temperature Data*) were collected at each site over multiple years. The caterpillar data were used to estimate the mean timing, height and width of the phenological distribution at each site in each year (*Site by Year Model*). A multi-variate meta-analytical *Sliding Window Analysis* was used to estimate the *most predictive temperature windows*, allowing a separate window for each

phenological distribution parameter. The *Spatiotemporal Temperature Model* used site-by-year variation in average temperatures from these windows as predictors of each phenological distribution parameter estimated using raw caterpillar data (modelled as a Gaussian function of ordinal date). Site-by-year temperatures were *within-site centred*, with the site mean temperature and annual temperature deviations used as predictors of each phenological parameter in the *Space versus Time Model* (following the same approach as the spatiotemporal model).

**Figure S2.** Plot of the AICs from models using different windows of temperature (horizontal black lines) as predictors of the three parameters describing the phenological distribution of caterpillar abundance. All lines beneath the red dashed line are within two AICs of the model with the lowest AIC value. Cropped Y axis, only showing subset of models with lower AICs.

**Figure S3.** Plots of the minimum AIC from models using windows of temperature starting (blue) or ending (red) on each date for each parameter describing the phenological distribution of caterpillar abundance. Dashed vertical lines indicate the start and end dates with the lowest AICs.

**Table S1.** Window combinations for the models that did not converge in a sliding window analysis which allowed different temperature periods to predict the three parameters that describe the phenological distribution of caterpillar abundance. Shows the start date and duration of each window.

**Table S2.** Comparison of the best windows identified for each pair of parameters (timing, height and width). Proportional overlap is the number of days that intersect divided by the summed number of days. Temperature correlations capture the correlation between the average temperatures obtained for pairs of parameters and is partitioned into spatiotemporal (using site by year mean temperatures), spatial (using site means) and temporal (using annual deviations from site means) estimates.

**Table S3.** Posterior mode (95% credible intervals) for the variance attributed to the site, year and site-year (each site in each year) random terms for the timing, height and width parameters of the phenological distribution of caterpillars. Outlined for two models: the main spatiotemporal temperature model and the equivalent model that excludes the fixed effect temperature slopes for each parameter. As estimates are directly from the model the width and height terms are on the log-scale and the timing and width terms are scaled (original SD = 14.1).

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