Warmer springs lead to earlier and higher peaks of arboreal caterpillars

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Abstract

Advances in spring phenology are among the clearest biological responses to climate warming. In the ephemeral temperate deciduous forest food webs, at the vanguard of research on temperature's effect on trophic interactions, most work has focused on the average timing of phenological events. In comparison, effects of temperature on the abundance of individuals and their seasonal spread is understudied, despite the potential for profound impacts on trophic interactions. Here we use a new method to show that for the guild of forest caterpillars, warmer spring conditions not only advance the timing of the phenological distribution of abundance by -4.96 days $^{o}C^{-1}$, but also increase its height by 34% $^{o}C^{-1}$. This increase in the maximum density of caterpillars with rising temperatures is likely to have major implications for both herbivory pressure and the resources available to secondary consumers.

Main text

Anthropogenic climate warming is having profound impacts on ecological systems, with phenological shifts one of the most reported biotic responses[1,2]. Temperature is a key driver of phenology for extra-tropical taxa, though there is heterogeneity in thermal sensitivity among species and trophic levels[3–5]. 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 disrupt interactions, including those between consumers and their resources[5–7].

Phenology is most frequently quantified as the mean or first timing of an event (Fig. 1a) among individuals in a population[4,5,8–12] and the thermal sensitivity of mean (or first) timing has been examined for many species and guilds[3–5]. In comparison, very few phenology-focused studies have addressed how temperature affects 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)[13–17] (Fig 1a), all of which may impact on species interactions. Removed from a phenological context, there is evidence across a range of taxa that temperature affects temporal trends in abundance[18] and spatial and temporal trends in the duration of life history events[19–21], although responses vary among species and events.

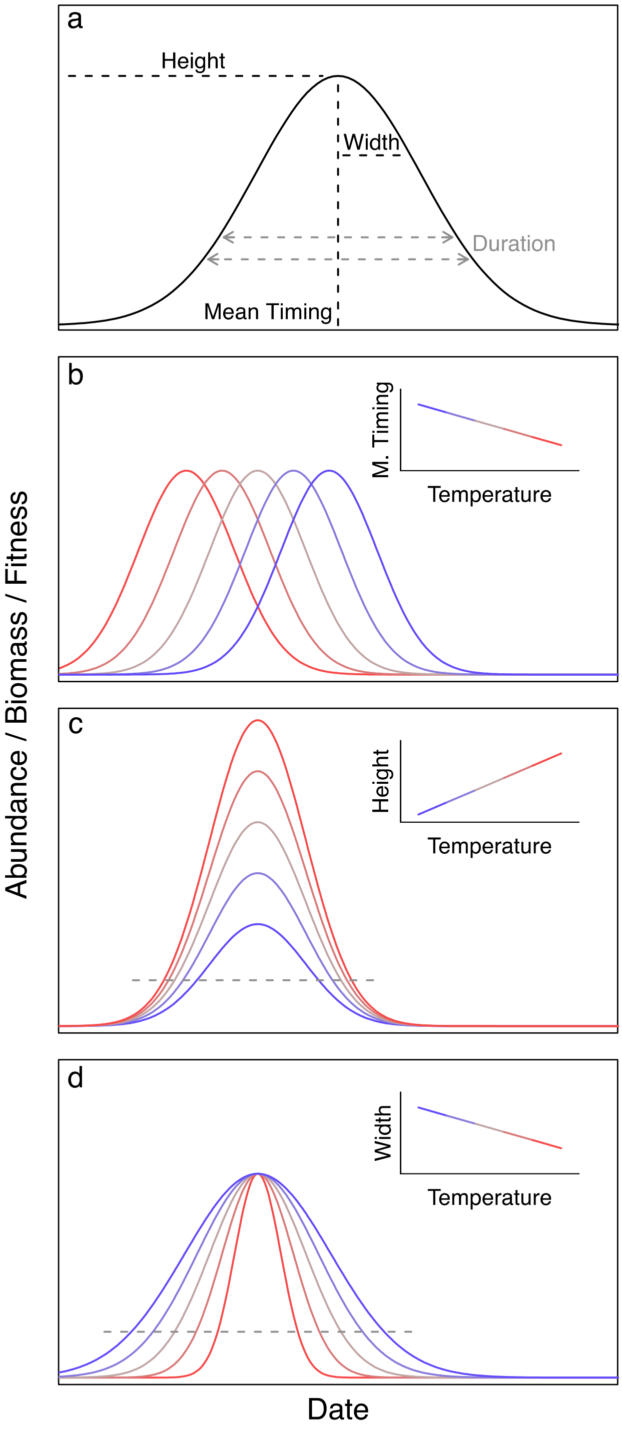

Figure 1: Using the Gaussian function to describe the peaked phenological distribution of an ephemeral life history event. a) a Gaussian function showing the three parameters that govern the phenological distribution (black) and a derived statistic of biological importance (grey): mean timing is the most common timing within the population/guild, height describes the maximum response (e.g. abundance, biomass or fitness) value reached, width corresponds to the standard deviation of the function and therefore it's curvature, and duration 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) Show 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) and 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 would be for a Gaussian distribution.

The match/mismatch hypothesis (MMH) outlines the importance of phenological synchrony for consumer fitness within seasonal trophic interactions[22]. Where the thermal sensitivity of phenology differs between trophic levels[5], this can alter the synchrony between many consumers and their resource[6]. The MMH is most often studied through comparison of consumer phenology to the resource population/guild mean timing; yet the height and width (Fig. 1a,c,d) of the resource distribution determines the duration of time for which the resource is above a given threshold, the amount of food available at a particular phenological asynchrony and how the relative amount of food available differs among synchronous and asynchronous consumers. Therefore, temperature-mediated shifts in the height and width of phenological distributions are also expected to have implications for trophic interactions, both from a bottom-up and top-down perspective[23,24].

In phenology and MMH research, the temperate forest system of deciduous trees, caterpillars and cavity nesting passerines in spring has become a classic system for studying the seasonality of the tri-trophic interactions[8,10,12,25]. 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[17] – is usually summarised on the basis of mean timing, which has been found to advance by approximately 4-6 days °C^{-1} [9,10,26]; largely tracking the shift in timing of deciduous tree leafing, but a little steeper than the advance of insectivorous passerine breeding[8,9,25]. 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[27], a study that shows some evidence of an increase in the average biomass across three sites of differing elevation in Austria[28], and studies that found the width of the biomass distribution to be narrower under warmer spring conditions across nine years in the Netherlands[26] and across 19 sites in the UK[29]. However, all previous studies are relatively 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. This two-step approach will underestimate the true error in slopes, in comparison to estimating all parameters of interest from the raw data within a single model. One reason for the scarcity of phenological research beyond mean timing is that the field has lacked a statistical framework for examining the thermal sensitivity of all three parameters that govern the phenological distribution.

There are multiple physiological and ecological mechanisms through which spring temperatures could affect the phenological distribution of the arboreal caterpillar guild abundance throughout spring. Warmer temperatures have been shown to drive earlier emergence for species that overwinter as eggs or larvae[10,26], shifting the mean timing of the guild phenology. Temperature could affect the width of the phenological distribution by changing the variation in emergence within the guild and the period over which each individual feeds prior to pupation. If development progresses according to a simple growing degree day model we would expect these timings to be more compressed under warmer temperatures. However, the only empirical study we are aware has tested this found no effect of temperature on the duration of hatching for the forest tent caterpillar, *Malacosoma disstriaI* [30]. Once larvae are feeding, increasing temperature increases the rate of development[31,32], reducing the period each individual is present and therefore, if the total guild abundance remains consistent, is predicted to narrow the width and reduce the duration of the phenological distribution, which is consistent with the findings of previous work[26,29]. Whilst the lack of correlation between spring temperatures and the height of arboreal caterpillar peak in biomass estimated in a previous study suggests height may be unaffected by temperature[27], there are multiple mechanisms that could drive such a relationship. Where low temperature presents a challenge, an increase in temperature may increase pre-emergence survival, and post-emergence it has been shown that cooler conditions can reduce feeding activity and increase mortality risk[33], thereby suggesting that increasing temperatures could increase the guild abundance and distribution height. However, colder temperatures can increase the starvation tolerance of caterpillars[34], meaning the phenological synchrony between caterpillars and their host may alter the effect of temperature on the distribution height. Within the caterpillar guild, the average phenological distribution may vary among species, as could the thermal sensitivity of mean timing[35], height and width. As such, the variation in thermal sensitivity among species comprising the guild, and any temperature driven turnover in guild composition or richness could also contribute to shifts in width and height of the guild-level phenological distribution.

Here we use data on temperature and caterpillar abundance throughout spring, collected at 44 sites across 8 years (Fig. 2), yielding 293 site by year combinations, to analyse the effect of temperature on the phenological distribution of 8,196 arboreal caterpillars sampled from 37,674 branch beatings. Of the 3,950 samples in which one or more caterpillars were present, 69% recorded one and 16% recorded 2, with a maximum abundance of 109. We present 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 (standard deviation) (Fig. 1).

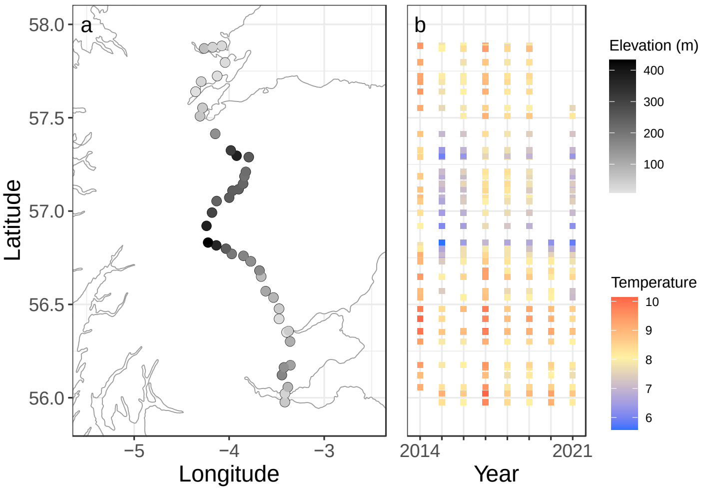

Figure 2: a) Map of site locations in Scotland with elevation above sea level indicated by a scale of grey to black, and b) shows the mean annual temperatures from mid-Feb to late June for each site in each year by latitude. Gaps in the temperature data reveal years when sites were not monitored.

To identify when in late winter/spring the mean air temperature has most effect on the phenological distribution, we used a sliding-window approach that simultaneously considered all three phenological parameters. We found 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, Fig. 3a), height was most sensitive to temperatures later in the spring (100-141, 9th April -20th May, Fig. 3a) and width to temperatures that spanned the spring (58-155, 27th February - 3rd June, Fig. 3a). For mean timing this period is similar to that identified as important in other European studies[26,36,37], whereas for width our time window is broader than identified in Visser et al[26], though we note a high degree of uncertainty in the position of the window for this phenological parameter (Fig. S1). We used the most sensitive windows (i.e. those returning the lowest AIC) in all subsequent analyses. The sliding window approach involves a very high-level of multiple testing (13231 window combinations in our case)[38], which inflates the type I

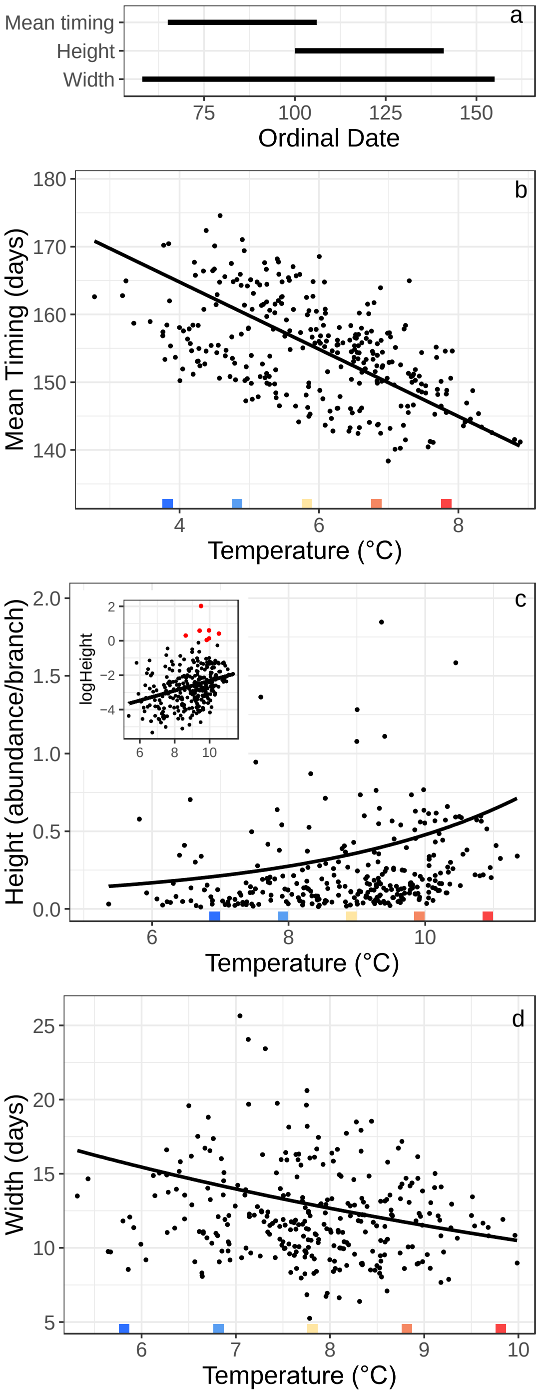

Figure 3: a) windows of time where spring temperature was identified as the best predictor of each parameter of the phenological distribution. b-d) show the model predictions (black points) for the mean timing, height and width of the caterpillar peak, as a function of temperature during the identified 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 +/- 1 and 2 degrees in blues/reds which correspond to the plots in Figure 4.

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.

Spring temperatures had a significant effect on all three phenological parameters, with the most profound effects being that the caterpillar phenological distribution is earlier and higher in warmer years (Fig. 3b-c, 4a). We found that mean timing shifted by -4.96 days ºC^{-1} (95% credible intervals [CIs]: -6.21 - -3.64 days ºC^{-1}, Fig. 3b), in keeping with results from previous studies[9,10,26]. When looking at the expected change in distribution height independently of the other parameters (see Methods), the maximum abundance increased by 34% ºC^{-1} (CIs: 5 - 61% ºC^{-1}, Fig. 3c), though we still find substantial variation in height among sites, years and site-years (Table S3). When we account for the uncertainty in all three parameters to attain the mean expectations of abundance on each day in spring (see Methods), we found the distribution height increased by 28% (CIs: 1 - 52%) when temperature increased by one degree above the mean (Fig. 4a). Here our findings agree with the suggested increase in mean daily biomass across a spatial temperature gradient in Austria[28], and appear to depart substantially from work in Poland that reported a lack of correlation between temporal temperature change and maximum biomass[27], though we cannot properly compare as they report no confidence interval. The width parameter decreased by 9% ºC^{-1} (CIs: 1 – 17% ºC^{-1}, Fig. 3d), indicating the shape of the distribution narrows as spring temperature increases.

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 (Fig. 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 the absence of a biological motivation the choice of abundance was arbitrary and these allowed comparison across a 4ºC range (blue to red lines in Fig 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°C range within out data (Fig. 4b; mean [CIs] difference between 2°C and -2°C at 0.1 = 19.45 days [-4.23 - 47.90]; at 0.05 = 9.42 days [-7.75 - 29.58]). Whilst 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 whilst 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 period of time where caterpillars are present above a particular abundance. We can also derive the thermal sensitivity of the area under the phenological distribution; and whilst the slope estimate of 1.21 times the area per °C suggests an increase in area with temperature, this effect was not significantly removed from 1 (CIs: 0.97 - 1.44, Fig. 4c).

Where suitably replicated spatiotemporal data have been collected, as in our study, this presents an opportunity 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[39,40]. Within the timescale of our study a difference in slopes could arise where different processes are operating in space and time, such as local adaptation or species turnover in space but not time, or if a third variable correlated with temperature also drives phenological processes[41]. We employed a within-site centring approach[42] to our temperature variables to separate the temporal effects (annual deviations from site mean temperatures) of temperature from the spatial (mean site temperatures) on the three phenological parameters. 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[40,43].

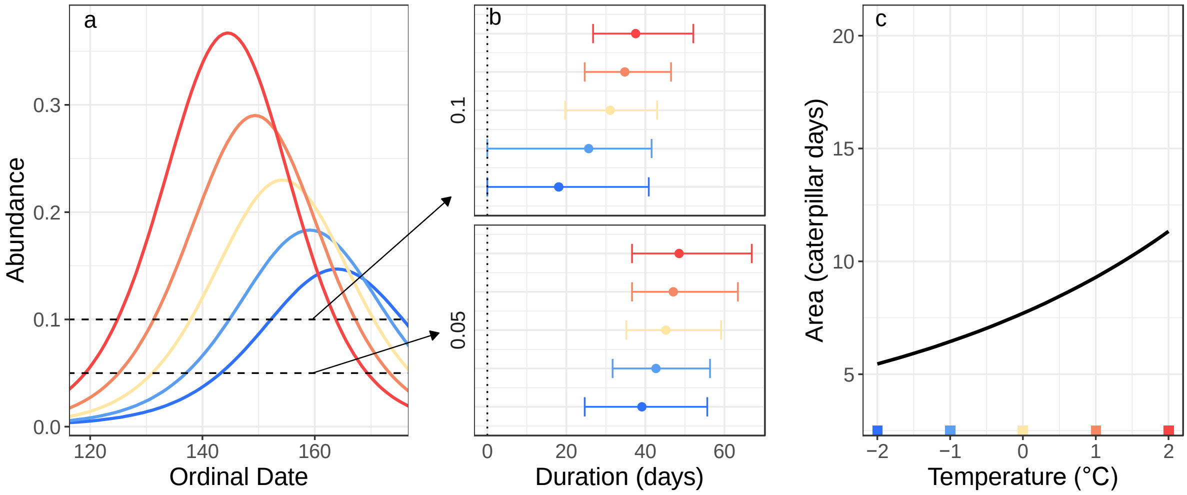

Figure 4: a) posterior mean expected abundance on the data scale of the full phenological distribution at different temperatures: the mean of each temperature window (mean timing = 5.85°C, height = 8.92°C, width = 7.81°C; yellow), +1°C (orange), +2°C (red), -1°C (light blue) and -2°C (dark blue); calculated from the posterior predictive distribution. b) shows 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; and c) shows 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.

We found that spatial and temporal slopes were generally in the same direction as the main spatio-temporal model (Table 1), except for the temporal width parameter slope, with no parameter yielding slopes that differed significantly in space versus time. For the mean timing parameter the estimates in space and time were not significantly different and the point estimates were in the same direction and removed from zero, suggesting temperature has a causal effect and consistent with plasticity being responsible for much of the spatiotemporal variation in mean timing[9,10,40]. Whilst 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, which may suggest some local adaptation or differing species turnover within the guild. Our estimates differ in magnitude to previous results from across eight localities in the UK , which reported a significant negative temporal slope in mean timing, but a shallow and non-significant negative slope in space[9]. For the thermal sensitivity of the distribution height, the spatial and temporal point estimates were both in the same direction and did not significantly differ, suggestive of a causal effect of temperature, and showed a co-gradient pattern; however neither effect was significant. While all point estimates are in the same direction, there is large uncertainty when this relationship is separated into spatial and temporal trends; therefore we suggest analyses with increased power through greater temporal replication would be of value in future work. 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, consistent with the findings of Smith et al[29]. This suggests the effect of temperature on distribution width in our main model may not be causal, alternatively driven by spatially correlative variables or differences in guild species composition. The effect of temperature on the area under the phenological distribution is similar in the main model and over space and time, all showing positive but non-significant effects; we therefore cannot conclude that there is any effect of temperature on the distribution area within our data set, though this presents an interesting avenue for future work.

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. Spatio-temporal 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 centering 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 slope estimate columns: red text indicates a negative effect, blue text indicates a positive effect and coloured CI text indicates the effect was significant. 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.

Parameter	Unit	Spatio-temporal slope	Spatial slope	Temporal slope	Difference (S-T)
Mean Timing	days $^{o}C^{-1}$	-4.96 (-6.21 - -3.64)	-5.77 (-7.39 - -4.18)	-3.39 (-5.49 - -1.46)	-2.37 (-4.77 - 0.17)
Height	prop. change $^{o}C^{-1}$	1.34 (1.05 - 1.61)	1.66 (0.97 - 2.63)	1.17 (0.81 - 1.49)	0.49 (-0.31 - 1.55)
Width	prop. change $^{o}C^{-1}$	0.91 (0.83 - 0.99)	0.85 (0.75 - 0.96)	1.05 (0.89 - 1.21)	-0.20 (-0.39 - -0.01)
Area	prop. change $^{o}C^{-1}$	1.21 (0.97 - 1.44)	1.40 (0.90 - 2.12)	1.22 (0.89 - 1.53)	0.18 (-0.41 - 0.95)

Our finding that the phenological distribution increases in height by 34% °C^{-1} differs from the lack of correlation reported by Nadolski et al[27]. Our study includes high replication of site by year combinations so the uncertainty in our estimates may be narrower than that of Nadolski et al. and the slopes estimated may not truly be different; whilst the confidence intervals of Nadolski et al. were not reported, they would likely be broad. Alternatively, this may suggest a differing effect of temperature on caterpillar abundance compared to biomass or a stronger effect of temperature in space than time (Table 1); the Nadolski et al. results were based on samples of biomass and entirely on temporal variation, whilst Schöll et al[28] tested biomass across a spatial temperature gradient and suggest a positive effect, yet this was also low powered and was not using an estimate of the phenological distribution height. Alternatively, there could be geographic differences between regions; our study is based further north, where temperature may be more of a constraint on the guild, causing temperature variation to have a greater effect. It is unclear how much of the increase in height with temperature is attribuatble to within species versus between species thermal responses, and this will require further investigation at the species level. Future investigation at the species rather than guild level would shed light on the relative importance of within-species shifts in abundance or between-species turnover in abundance.

The previously undocumented increase in peak height within the caterpillar guild 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. The increase in herbivory pressure at the mean timing of the herbivorous caterpillar guild may give rise to an indirect effect of temperature on the severity of tree defoliation[44–47]. Though 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[48,49]. 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.

Previous studies have suggested that caterpillars are maintaining synchrony with oak trees[8,9], and our spatiotemporal estimate of -4.96 days°C^{-1} is broadly consistent with European estimates for the thermal sensitivity of the timing of leaf out in oak trees and other deciduous species[41,50,51]. In contrast, our estimate of the temporal slope for mean timing is shallower than that of some dominant UK trees, e.g., *Quercus* sp leaf-out found to have sensitivity to forcing temperatures of -8.81 +/- 0.52 days °C^{-1} [50]. This means that increasing temperatures could alter the phenological (a)synchrony between caterpillars and deciduous trees. Increased asynchrony may impede the increase in the height of the caterpillar phenological distribution and prevent the most extreme detrimental effects for the trees[48], whilst greater synchrony could exacerbate the increase in herbivory pressure[48,49]; highlighting an important direction for future analyses.

A study of bird species in UK and Netherlands showed an average advance in lay date of 3.24 days °C^{-1} (SE = 0.4)[52], which is shallower than our spatio-temporal estimate for the shift in caterpillar mean timing, albeit with overlapping confidence/credible intervals. However, whilst our mean timing slopes over space and time did not differ significantly, our temporal estimate for the caterpillar timing is similar to this temporal estimate in birds, which may allow the average bird species to track the change in caterpillar phenology within the range of temperatures tested.

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 synchronous with the caterpillars. However, the relative abundance of food available to synchronous versus asynchronous consumers changes with temperature, with the reduction in peak width driving a steeper decline in abundance to either side of the mean timing under warmer conditions. These changes to the phenological distribution of the resource could alter the dynamics of the MMH for consumers as the relative fitness consequences of asynchrony within the population could change with temperature, potentially increasing the strength of selection on breeding phenology. Whilst the strength of selection within the bird population may increase, as the duration remains constant and the maximum height increases, late birds at increased temperatures will have access to more resource than at cooler temperatures, suggesting focus on asynchrony in mean timing alone may give an overly pessimistic view of the bird's ability to cope under a warming climate. Much of the previous work on effects of the MMH on consumer fitness has focused on the strength of selection on phenology attributed to asynchrony between consumers and mean resource timing[10,11]. Very few studies have examined the effects of the height or width of the resource distribution on fitness[16]; this presents an important direction for future work to fully understand the impact of climate-mediated mismatch on fitness.

We anticipate that our statistical approach offers great potential for modelling effects of climate on many phenological distributions. The approach is similar to the Gaussian model functions described in de Villemereuil et al.[53] and Dennis et al.[14], with the major difference being that we include a linear effect of temperature on the three parameters that control the position, shape and height of the phenological distribution. Whilst a GLM/GLMM with a Poisson response and quadratic date term has been used to estimate the effects of an environmental variable on mean timing[54,55], this forces an undesirable non-linear relationship between the environmental variable and height (see Extended Data for further details).

Using a novel method in phenology research 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 research systems and questions within phenology and the MMH, and we encourage more work to study 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.

Methods

Study System

Data were collected between 2014 and 2021 at 44 deciduous woodland sites along a 220km transect from Edinburgh (55°980 N, 3°400 W) to Dornoch (57°890 N, 4°080 W) in Scotland[13,56] (Fig. 2a). The sites vary in temperature and extend across two degrees of latitude and a 440m elevation range (Fig. 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 among years 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.

Caterpillar sampling used a branch beating method, recording the abundance of caterpillars on each branch monitored on different dates throughout spring[13,17]. 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[13] for 2014-20 details). An average of 14 trees (range: 10-17) were sampled at each site in each year from 2017-21, prior to that, 5 trees per site (range: 3-7) were sampled from 2014-16. One branch on each tree was marked for sampling and the species of trees at each site varied to represent the local habitat. Each site was visited every two days with half of the focal trees sampled on alternating visits, leaving four days between each branch beating to allow for recolonisation. The same branches were sampled across and within years unless damaged or dead.

Approximating the caterpillar peak using 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; Eq. 1) using the RStan package[57]. The Gaussian function (Eq. 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 (μ), height (A_{max}) and width (σ) (Fig. 1a):

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

Eq. 1 can be rearranged into Eq. 2 allowing the height and width parameters to be modelled on the log scale:

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

For our main analysis (spatio-temporal temperature model) we modelled $logA_{max}$, $log\sigma$ and μ (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 (Fig. 1b-d). 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 a sliding window approach;

see section below. 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, tree taxon sampled, unique tree identity, recorder of the sample and each observation were also fitted as random terms for $logA_{max}$ to account for other important sources of variance in caterpillar abundance[13], the latter term dealing with any over-dispersion with respect to the Poisson.

To test for any difference in the thermal sensitivity of the caterpillar phenological distribution in space and time we then included two fixed effect temperature slopes for each phenological parameter (space vs time temperature model): one using the site mean temperatures and another for the annual deviations from the mean of each site; employing within-site centering[42]. The site mean temperatures were attained from a linear mixed-model using the lme4 package[58] to estimate a mean site temperature which is not biased by the years in which each site has been monitored (Fig. 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 spatio-temporal temperature model.

Derived parameters and mean expectations on the arithmetic scale

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 (Fig. 1d). When the height parameter changes with a constant width this also alters the duration (Fig. 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 attained by rearranging the integral of the Gaussian function (Eq. 3) and Gaussian probability function (Eq. 4), for which the area is equal to one.

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

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

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

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

Eq. 5: $$T = A_{max}\sigma\sqrt{2\pi}$$

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

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 spatio-temporal temperature model and both components of the space vs time temperature model (Table 1).

Mean expectation 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. There are two forms of expectations on the arithmetic scale that we were interested in from the spatio-temporal temperature model: i) the average value of each phenological parameter at different temperatures, and ii) the average value of mean caterpillar abundance on each date throughout spring at different temperatures which depends on all phenological parameters. Both required marginalising random terms, but the method to do this differed.

(i) To estimate the height or width at different temperatures (Fig. 3c-d), half of the variance for each random term associated with each parameter was added to the estimate before exponentiating.

(ii) Since an analytical solution was not available, marginalisation was carried out by simulating from the posterior predictive distribution 10,000 times for each date:temperature combination and taking the average abundance. This allows visualisation of changes to the full phenological distribution with changing temperature (Fig. 4a). The duration was calculated for each temperature as the dates on which the average abundance exceeded the threshold (Fig. 4b), and the area was calculated as the sum of the average abundance across dates (Fig. 4c). Due to the uncertainty in the mean timing of the distribution the maximum average abundances reached are lower than those predicted from i).

Determination of temperature variable using sliding windows

It is feasible that the period during which temperature is most influential for the mean timing, height and width of the phenological distribution may differ among the parameters; therefore, we began our analyses by identifying the periods during which temperature best predicted the thermal sensitivity of each peak parameter using a sliding window approach. As the number of windows to consider was the product of the number of windows considered for each parameter, for efficiency we applied a frequentist meta-analytic approach (using the metafor package[59]) to the site by year estimates for the three parameters. This allowed us to compare sliding windows based on AIC.

To obtain estimates of the three phenological parameters for each site in each year we modelled the phenological distribution of at each site in each year using the same model composition as the spatio-temporal temperature model using RStan[57], but excluding the temperature fixed effects. From the model output the intercept and random intercepts for each site, year and site by year combination could be summed to obtain the estimate of each phenological parameter for each site in each year. The posterior mode (calculated using the MCMCglmm package[60] function) was used as our estimate of mean timing, height and width for each site by year combination for the response variable in metafor multivariate meta-analyses. The variance-covariance matrix of the posterior distributions for the three parameters in each site in each year were included as the sampling variance.

We modelled the effect of temperature on each distribution parameter under a sliding window framework, allowing each parameter to be predicted by different time windows of temperature. For mean timing the window start dates ranged from day 58 to day 100, shifting in 7 day increments. For the height and width the window start dates ranged from 58 to 128, shifting in 14 day increments. The incremental shifts in start date were slightly higher resolution and restricted to an earlier period of the year for the mean timing parameter due to stronger a priori predictions from previous studies[26]; whereas much less is known about the time windows that best predict the distribution height and width (see Visser et al.[26]) so we allowed larger increments to reduce the extent of multiple testing. All three parameters had windows ranging in duration from 28 to 98 days, increasing in duration in 14 day increments. This produced 30 window options for the mean timing variable and 21 for the height and width, resulting in 13231 models in total.

The metafor multivariate models included independent intercepts and temperature slopes for each of the response variable, as well as including year and each site in each year (site-year) as random terms for each response. As it is only possible to include two random terms that are independent for each response variable in the metafor package we selected year and site-year but not site. Random terms were estimated using an unstructured variance-covariance matrix. The models were fitted using maximum-likelihood rather than restricted maximum-likelihood to enable model comparison using AIC (see Extended Data for more detailed results). The mean daily temperature for each site by year combination during the identified windows were then used within the Gaussian function models described above.

All analyses used R version 4.0.2[61], and models including the Gaussian function used the RStan package[57]. Models were run using four chains with 2500 iterations after warmup with a thinning of 5; the spatio-temporal temperature model and space vs time model had a warm up 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 vs time temperature model had 3 divergent transitions after the warmup which was 0.15% of the 2000 iterations retained.

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Extended data

Part 1: Sliding window analysis

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.

Mean Timing		**Height**		**Width**	
Start	Duration	Start	Duration	Start	Duration
93	28	72	70	100	28
93	28	72	84	100	28
93	28	58	98	100	28
100	56	72	70	128	28
100	56	72	70	114	42
100	56	72	84	128	28
100	56	58	98	128	28

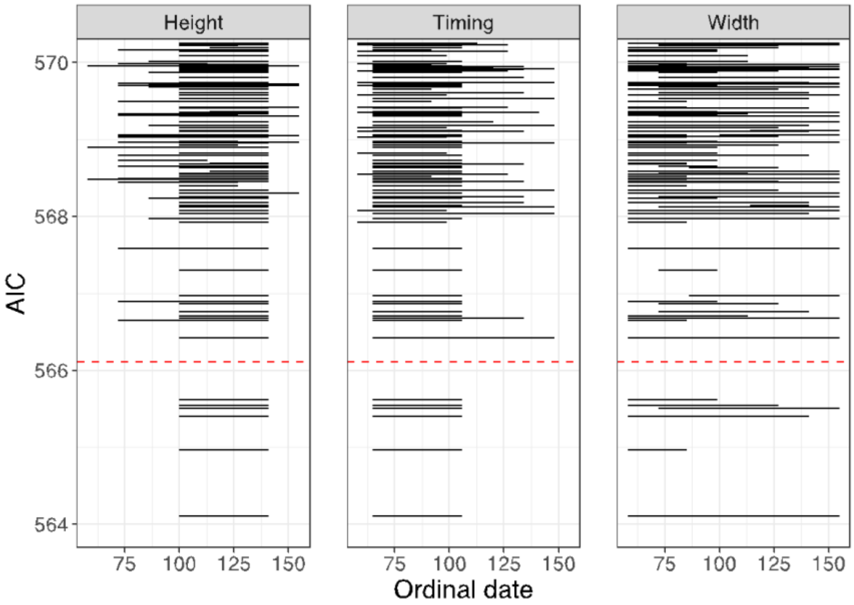

Figure S1: Plot of the AICs from models using different windows of temperature (horizontal black lines) as predictors of the three parameters describing the phenological distribution of caterpillar abundance. All lines beneath the red dashed line are within two AICs of the model with the lowest AIC value. Cropped Y axis, only showing subset of models with lower AICs.

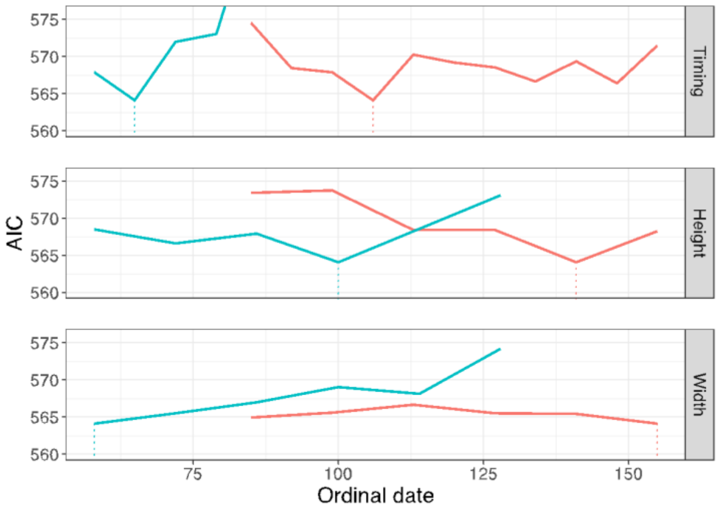

Figure S2: Plots of the minimum AIC from models using windows of temperature starting (blue) or ending (red) on each date for each parameter describing the phenological distribution of caterpillar abundance. Dashed vertical lines indicate the start and end dates with the lowest AICs.

Of the 13231 models run, 7 did not converge, the details of which can be found in Table S1.

As seen in Fig S1, all models with AIC's within 2 of the best fitting model for the mean timing and height parameters included the windows that were also in the best fitting model, however for the width parameter the windows used in models within 2 AICs of the best fitting were more varied, suggesting there is no particular time period between mid-Feb and late June during which temperature predicts the change in peak shape to a much greater extent. As the aim of this work was to identify the effect of spring temperatures on each metric of the caterpillar peak and not to identify the most influential time period of temperature throughout the year we proceeded using the windows of temperature identified in the best fitting model despite the lack of a clear optimal window for estimating the width parameter.

Temperature mean, standard deviation and range in the identified windows:

The mean temperature during the mean timing parameter window was 5.83°C, ranging from -3.05 to 3.06°C with a standard deviation (sd) of 1.22 after mean centring (spatial: -1.73 - 1.48°C; temporal: -2.13 - 1.57°C). The mean temperature during the width parameter window was 7.81°C , ranging from -2.50 to 2.17°C with a sd of 0.85 after mean centring (spatial: -1.58 - 1.16°C; temporal: -1.15 - 1.18°C). The mean temperature during the height parameter window was 8.92°C, ranging from -3.55 to 2.43°C with a sd of 1.20 after mean centring (spatial: -1.59 - 1.05°C; temporal: -2.40 - 2.01°C).

Correlation among temperatures in identified windows:

The temperatures that contribute to each of the three best windows (one for timing, height and width) are overlapping (Figure 3a, Table S2). Therefore one would expect the effect of a change in temperature to lead to a somewhat correlated response. When we estimate the pairwise correlations in temperatures between windows, we find that in space the correlations are very high (Table S2), whereas in time the correlation is weaker and there is no temporal correlation between the temperatures that predict timing and height. The stronger correlations between different windows in space (across sites) versus time (across years) is consistent with information about the position of the sliding windows stemming mainly from the temporal replication in the data[62].

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-year mean temperatures), spatial (using site means) and temporal (using annual deviations from site means) estimates.

Parameter pairs	**Prop. overlap**	**Spatiotemporal cor.**	**Spatial cor.**	**Temporal cor.**
MeanTiming:Height	0.08	0.31	0.94	-0.06
MeanTiming:Width	0.3	0.78	0.98	0.58
Height:Width	0.3	0.79	0.99	0.71

Part 2: Site, year and site-year variance in models

The variance in timing, height and width that is distributed among site, year and site-year quantify are captured by random terms in the model, and all terms are significantly removed from 0 (Table S3).

In the site by year model (i.e. a model without temperature predictors) we find substantial variation in timing among sites and years. When temperature is included in the model this leads to a substantial reduction in the among site variance.

The variation in height is greatest among sites, but also substantial among years and site-years and this variance is substantially reduced among years when temperature is included in the model (though credible intervals are broad). An implication of the substantial site-year variance is that the height of the caterpillar guild abundance peak may be quite idiosyncratic in space and time and not solely predictable on the basis of temperature.

For the width parameter the main difference seen was an increased variance among years when the temperature slope was included, supporting our finding from the space vs time model that temporal temperature variation does not affect the width of the phenological distribution.

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)

	Random term	Spatio-temporal temperature model	Site by year model
Timing	Site	0.043 (0.025 - 0.096)	0.145 (0.085 - 0.254)
	Year	0.142 (0.089 - 1.033)	0.119 (0.06 - 0.782)
	Site-year	0.012 (0.006 - 0.031)	0.019 (0.01 - 0.042)
Height	Site	0.744 (0.516 - 1.333)	0.860 (0.559 - 1.415)
	Year	0.134 (0.028 - 1.267)	0.397 (0.216 - 3.123)
	Site-year	0.459 (0.369 - 0.636)	0.462 (0.354 - 0.611)
Width	Site	0.029 (0.011 - 0.066)	0.029 (0.014 - 0.076)
	Year	0.055 (0.021 - 0.508)	0.020 (0.01 - 0.258)
	Site-year	0.034 (0.018 - 0.065)	0.037 (0.016 - 0.066)

Part 3: Why we have used the Gaussian function rather than the Poisson GLMM alternative

The non-linear Gaussian function used by our study has more often been modelled as the re-parameterised linear form in a Poisson GLMM (Eq. S1).

Eq. S1: $$y = \beta_0 + \beta_1 d + \beta_2 d^2$$

Previous work has suggested that by extending Eq. S1 to include an interaction between a temperature variable and the date parameter, d (Eq. S2) it is possible to estimate the change in mean timing with temperature[55,56].

Eq. S2: $$y = \beta_0 + \beta_1 d + \beta_2 d^2 + \beta_3 t + \beta_4 dt$$

The maximum height (H) of the distribution is reached at the mean timing (M), which can be simplified to $A + Bt$ (Eq. S3) where $A = -\frac{\beta_1}{2\beta_2}$ and B=$-\frac{\beta_4}{2\beta_2}$.

Eq. S3: $$\begin{aligned} M &= -\frac{(\beta_1 + \beta_4 t)}{2\beta_2} \\ &= -\frac{\beta_1}{2\beta_2} - \frac{\beta_4}{2\beta_2} t \\ &= A + Bt \end{aligned}$$

When quantifying the height of the phenological distribution ($d = M$) in Eq. S2, we found the composition of the model forces the height to be a quadratic function of temperature (Eq. S3).

Eq. S3: $$\begin{aligned} H &= \beta_0 + \beta_1 (A + Bt) + \beta_2 (A + Bt)^2 + \beta_3 t + \beta_4 (A + Bt) t \\ &= \beta_0 + \beta_1 A + \beta_1 Bt + \beta_2 A^2 + \beta_2 2ABt + \beta_2 B^2 t^2 + \beta_3 t + \beta_4 A + \beta_4 Bt^2 \\ &= \beta_0 + \beta_1 A + \beta_2 A^2 + \beta_4 A + (\beta_1 B + \beta_2 2AB + \beta_3) t + (\beta_2 B^2 + \beta_4 B) t^2 \end{aligned}$$

As our interest was modelling a change in the mean timing, height and width of the phenological distribution, this linear model composition has undesired properties. Therefore, we proceeded with the non-linear Gaussian function.

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