

Supplement to *Tree phenology responses to uneven warming temperatures*

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In this Supplement we first show that traditional degree-day models do not contain information on timing of onset of spring development. We then describe the continuous development model (CDM) and provide diagnostics.

*Appendix S1 -- Thermal effects in the degree day model*

Because degree-day models ignore the order of days, assumptions can be evaluated from a simple intensity function of daily temperatures  $q(T)$ . In other words, the number of days that fall within the temperature interval  $(T', T'+\Delta) \approx \Delta q(T')$ , where  $\Delta$  is a small time interval. Without loss of generality we can order daily temperatures from  $T'$  through the temperature  $U$  that corresponds to the date of the observed phenological event, e.g., budbreak. The number of intervening days from unknown  $T'$  to observed  $U$  is

$$Days(T', U) = \int_{T'}^U q(T) dT \quad S1$$

and the number of degree days is

$$DD(T', U) = \int_{T'}^U (T - T') q(T) dT \quad S2$$

If we are to estimate the parameter  $T'$  it must influence the calculation of degree days. From eqn S2 increasing  $T'$  by an amount  $\Delta$  has two effects. First, days falling in the temperature interval  $T \in (T', T' + \Delta)$  no longer contribute to degree days; they are now below the threshold. Second, the threshold weights the contribution of each day in the integrand. The question is, which contribution has impact on the calculated degree days?

Sensitivity to the threshold is given by the change in degree days that attends a change in threshold, a difference of integrals

$$\begin{aligned} \int_{T'+\Delta}^U (T - T' - \Delta) q(T) dT - \int_{T'}^U (T - T') q(T) dT \\ = -\Delta \int_{T'+\Delta}^U q(T) dT - \int_{T'}^{T'+\Delta} (T - T') q(T) dT \end{aligned} \quad S3$$

The first term is  $\Delta$  times the number of days above the new threshold (see eqn S1). The second term contains only contributions from days in the narrow interval between  $T'$  and  $T' + \Delta$ . Noting that this second term approaches  $\Delta^2 p(T' + \Delta)/2$ , eqn S3 gives sensitivity,

$$\frac{\partial DD}{\partial T'} = \lim_{\Delta \rightarrow 0} \left( \frac{DD(T' + \Delta) - DD(T')}{\Delta} \right) = \frac{1}{\Delta} \left[ -\Delta Days(T' + \Delta, U) - \Delta^2 q(T' + \Delta)/2 \right]$$

$$= -Days(T', U) - \Delta q(T')/2 \quad S4$$

$$= -(days\ above\ threshold + days\ lost\ at\ onset) \quad S5$$

$$= \text{chronic penalty} + \text{onset penalty}$$

Both penalties are now expressed in days. The chronic penalty (first term of S5) is overwhelming—for a degree increase in the threshold the calculated degree days declines by the number of days until budbreak. In three years of temperature data from Duke Forest the chronic penalty accounts for > 96 % of the effect of a  $\Delta = 3^\circ\text{C}$  increase in the threshold. Yet the motivation for and interpretation of the threshold comes largely from its implications for timing of onset.

The second term, the penalty for lost days at onset is incurred only for days having temperatures in the small interval between  $T'$  and  $T' + \Delta$ , and the few days that do occur in this interval contribute near zero (because temperature is only slightly above the threshold).

The small contribution of delayed onset means that we cannot identify when onset occurs, which is required in many models that attempt to estimate the relationship between chilling, then warming. Although a number of studies report estimates based on observations of budbreak dates, such estimates should be viewed cautiously.

Given the unrealistic assumption that the threshold imposes a chronic penalty, an alternative is to simply assume a reasonable value for  $T'$  as basis for the calculation of  $DD$ . A precise estimate of  $T'$  is not required in the CDM, because it is not based on degree days and there is no assumption that  $T'$  affects development after onset.

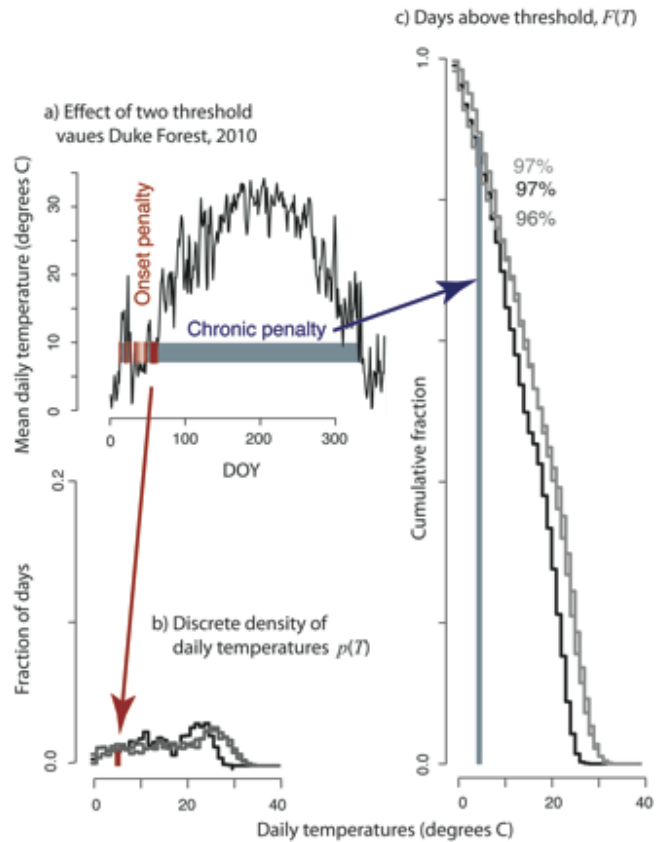


Figure S1. The two terms of eqn S5 showing how the thermal model is dominated by the assumption of a chronic penalty. a) A  $3^\circ\text{C}$  increase in threshold  $T'$  loses only a few days early in the season (brown), but the chronic penalty persists (blue). This loss is shown in the density in (b), less than 3% of the total penalty assumed in the thermal model. Over 3 yr, 96 to 97% of the penalty is chronic (c).

### Appendix S2 -- The Continuous Development Model of phenology

The observed discrete state  $S_{iy,t} \in \{1, \dots, K\}$  is observed for individual  $i = 1, \dots, n$  at times  $t$  in year  $y$ . The  $K = 6$  observed stages for our study, ranging from dormant to fully expanded leaves, are listed in Table 1. The underlying true stage is also discrete  $s_{iy,t} \in \{1, \dots, K\}$ , but it is assumed to exist at all times, not just when the individual is observed. There is multinomial observation error describing the probability that an individual is observed to be in stage  $S_{iy,t}$ , when its true stage is  $s_{iy,t}$ ,

$$p(S_{iy,t} | s_{iy,t} = k) \sim \text{multinom}(1, \pi_k) \quad \text{S6}$$

where  $\pi_k = [\pi_{k1}, \dots, \pi_{k6}]$  is the vector of probabilities that an individual in state  $k$  is recorded as any of  $K$  states. Observation error from eqn S6 allows for the fact that states are not precisely discrete, but are recorded as such. The  $K \times K$  matrix  $\pi$  is a concatenation of the six  $\pi_k$  vectors, each of length  $K$ .

The discrete stages  $s_{iy,t}$  arise as observable changes that result from development, which is unobserved and affected by the environment, genotype, and so forth. This latent continuous developmental state  $h_{iy}(t)$  is taken for discrete time as  $h_{iy,t}$ , where  $t$  is the time index of the model. For a given state  $h$  there are  $K = 6$  corresponding probabilities that the individual will be in each of the true states  $s_{iy,t}$ . The developmental state  $h_{iy,t}$  increases from 0 at onset to 100 at the time of bud break. The range of  $h_{iy,t}$  is not important, because we are ultimately interested in how environmental variation affects the probability of change in observable states--we marginalize over  $h_{iy,t}$  to move from environment to probability of observable states. In other words,  $h_{iy,t}$  is a device that allows for the fact that development is essentially continuous, responding instantaneously to the environment experienced by the individual, a vector of predictors  $\mathbf{x}_{iy,t}$ . We use the model

$$\begin{aligned} dh_{iy,t} &= \exp(x_{iy,t}\beta + \varepsilon_{iy,t}) \left(1 - h_{iy,t}/h_{\max}\right) dt \\ \varepsilon_{iy,t} &\sim N(0, \sigma^2) \end{aligned} \quad \text{S7}$$

where  $dt = 2$  days. This simple formulation is selected to have readily interpretable parameters and to capture the basic features of development toward a final state approached at asymptote  $h_{\max} = 100$ . We refer to eqn S7 as the process model with process variance  $\sigma^2$ . The form of eqn S7 means that incremental development is non-negative (it can approach zero, but not regress).

Covariates that accelerate development when positive are associated with positive values in  $\beta$ , and vice versa. Input variables occupy a design vector

$$\mathbf{x}_{iy,t} = \begin{bmatrix} 1 & T_{iy,t} & G_i & T_{iy,t} \times G_i & CU_{iy} \end{bmatrix} \quad \text{S8}$$

where  $T_{iy,t}$  is the average temperature for day  $t$  experienced by individual  $i$ ,  $G_i \in \{0, 1\}$  is a binary indicator for southern (0) vs northern (1) seed source,  $T_{iy,t} \times G_i$  is the interaction, and  $CU_{iy}$  are chilling units (eqn 2 of main text). Soil moisture and vapor pressure deficit were monitored, but

they do not explain spring phenology in our region, because soil moisture remains near field capacity throughout the time of spring development.

The discrete stages  $s_{iy,t}$  comprise an ordinal scale that is linked probabilistically to  $h_{iy,t}$ . As  $h_{iy,t}$  increases over time, individuals transition through the discrete states from  $s_{iy,t} = 1$  when dormant through  $s_{iy,t} = 6$  when leaves are fully expanded. The connection between  $h_{iy,t}$  and  $s_{iy,t}$  is established by a multinomial logit,

$$s_{iy,t} \sim \text{multinom}(1, \theta_{iy,t}) \quad \text{S9}$$

where  $\theta_{iy,t}$  the length- $K$  vector of elements

$$\theta_{iy,t,k} = P_{iy,t,k} - \sum_{j=1}^{k-1} P_{iy,t,j}$$

Here  $\theta_{iy,t,k}$  is the probability that individual  $i$  is in stage  $k$ , and  $P_{iy,t,k}$  is the probability that it has not progressed beyond  $k$  by day  $t$ . Probabilities are modeled as logits,

$$\ln\left(\frac{P_{iy,t,k}}{1 - P_{iy,t,k}}\right) = H_{iy,t,k} \quad \text{S10}$$

$$H_{iy,t,k} = c_{k0} + c_{k1} h_{iy,t}$$

There is a  $(K - 1) \times 2$  matrix of coefficients of intercepts  $c_{k0}$  and slopes  $c_{k1}$  on the logit scale that determine the transitions between states. The ordinal states imply  $(c_{k0} < c_{(k+1)0}, c_{k1} < c_{(k+1)1})$ . In other words stage 2 must follow stage 1, and so forth.

Prior distributions for the model are non-informative, with several exceptions. First, the observation errors are informative with prior

$$\pi_k \sim \text{Dirichlet}(r_k)$$

to admit departures from observations when there are reversals in observed states, i.e., an observation at one time implies an earlier stage than a previous time,  $S_{iy,t'} < S_{iy,t}$  for  $t' < t$ . All observational information enters through the  $S_{i,t}$ , so it is important priors informative and centered on observations. Organized as a matrix, the  $K = 6$  prior vectors are:

$$\begin{array}{c}
\text{True state:} \\
r_1 \quad r_2 \quad r_3 \quad r_4 \quad r_5 \quad r_6 \\
\text{Observed state:} \\
\begin{array}{c}
1 \\
2 \\
3 \\
4 \\
5 \\
6
\end{array}
\left[ \begin{array}{cccccc}
nJ & 0.1 & 10^{-4} & 10^{-4} & 10^{-4} & 10^{-4} \\
0.1 & nJ & 0.1 & 10^{-4} & 10^{-4} & 10^{-4} \\
10^{-4} & 0.1 & nJ & 0.1 & 10^{-4} & 10^{-4} \\
10^{-4} & 10^{-4} & 0.1 & nJ & 0.1 & 10^{-4} \\
10^{-4} & 10^{-4} & 10^{-4} & 0.1 & nJ & 0.1 \\
10^{-4} & 10^{-4} & 10^{-4} & 10^{-4} & 0.1 & nJ
\end{array} \right]
\end{array}$$

where  $J$  is the number of observation times. In other words the diagonal is heavily weighted.

The prior distribution on  $\beta$  is uniform.

The prior distribution for the process variance

$$\sigma^2 \sim IG(n, 2(n-1))$$

has mean value of 2, which is approximately the maximum change in  $h_{iy,t}$  for a time increment  $dt$ .

The prior distribution for the  $c$  parameters is informative for transitions from the first stage and into the last stage, but otherwise weak. We specify the prior on breakpoints where the  $P_k = 0.5$  and slopes, which determine steepness of transitions. The prior on breakpoints is flat over a specified interval

$$h_k^* \sim \text{unif}(h_k^{(1)}, h_k^{(2)})$$

where

$$\begin{bmatrix} h^{(1)} \\ h^{(2)} \end{bmatrix} = \begin{bmatrix} 10 & 20 & 30 & 55 & 85 \\ 15 & 30 & 55 & 80 & 90 \end{bmatrix}$$

In other words, the transition from stage two to stage three will fall in the interval (20, 30). The gradients at breakpoints  $k$  are largely determined by the slope parameters  $c_{1k}$ . Initial slopes  $c_{k1}$  together with breakpoints are used to initialize the matrix of  $c$  coefficients, with intercepts determined by slopes and breakpoints,

$$c_{k0} = -\ln\left(\frac{1}{0.5 + P_k} - 1\right) - c_{k1}h_k^*$$

$$P_k = \sum_{j=1}^{k-1} \theta_j(h_k^*)$$

i.e., the sum of class probabilities  $< k$  taken at the breakpoint  $k$ . Initial breakpoints and slopes determine a prior  $c$  matrix

$$c = \begin{bmatrix} 25 & -2.00 \\ 41 & -1.65 \\ 55 & -1.30 \\ 64 & -0.95 \\ 65 & -0.74 \end{bmatrix}$$

However, the prior is vague, with diagonal covariance matrix having 10 along the diagonal. Thus, the prior is truncated normal, with truncations on breakpoints rather than  $c$ 's, maintaining the ordering required for ordinal data.

### *Appendix S3 -- Diagnostics of the fitted model*

Predictive distributions of discrete states were compared with observations for all species analyzed. The predicted discrete states for individuals agree with the observations for those individuals (Fig. 5 of main text). These distributions are predicted from the estimated latent states  $h(t)$  (solid lines with dashed 95% CIs) marginalized over the full posterior. These predictions for individuals verify that the model estimating latent states that concur with observations. The broad scatter results from the fact that we are predicting the full time series of states initialized from the beginning of the year. Because errors accumulate we expect there to be scatter, particularly in the center of the sequence. However, the 1 sd predictive intervals span the line of agreement. Good predictive capacity for an entire season ahead is not a requirement for a useful fit, but provides one of the most rigorous ways to evaluate the model.

### *Appendix S4 -- From the development scale to discrete observations*

Here we discuss two types of sensitivity, the effect of an input on i) the rate of development, taken to be the probability of transition to a particular stage  $k$ , and ii) the timing of the transition to stage  $k$ . Sensitivity of development rate begins with the probability of being in at least stage  $k$  at time  $t$ , which changes at rate

$$\frac{\partial(1 - P_k)}{\partial t} = - \frac{\partial P_k}{\partial h} \frac{dh}{dt}$$

The density of  $h$  for stage  $k$  is logistic,

$$Q_k(h) = - \frac{\partial P_k}{\partial h} = \frac{-c_{(k-1)l} e^{c_{h,k-1}}}{(1 + e^{c_{h,k-1}})^2} \quad \text{S11}$$

For a benchmark comparable across species, we evaluate eqn S11 at the value of  $h$  where  $P_k = 1/2$ ,

$$Q_k(h)_{P_k=1/2} = \frac{-c_{(k-1)l}}{4}$$

The sensitivity to an input variable  $q$  (say, temperature) is expressed on this scale as a rate sensitivity,

$$\begin{aligned} \gamma_{k,q} &= \frac{\partial}{\partial x_q} \left( Q(h) \frac{dh}{dt} \right) \Big|_{P_k=1/2} = Q_k(h) \frac{\partial}{\partial x_q} \left( \frac{dh}{dt} \right) \Big|_{P_k=1/2} \\ &= \frac{-c_{(k-1)1}}{4} \left( \beta_q + \sum_{\{q'\}} x_{qq'} \beta_{qq'} \right) \frac{dh}{dt} \end{aligned} \quad \text{S12}$$

where  $q'$  is an input variable that interacts with  $q$ , and  $\{q'\}$  is the set of all interactions for  $q$ , and  $dh/dt$  is approximated by dividing the right-hand side of eqn S12 by  $dt = 2$  days.

### *Appendix S5 –From the development scale to event time*

Degree-day models often use regression to relate timing of an event, such as budbreak, to temperature. Note the inverse relationship between timing in degree-day models and development rate in our CDM. For the model comparisons in Figure 7 of the main text, we transform estimates from our CDM from an effect on rate to an effect on timing.

The rate of development is  $r = 1/h \, dh/dt$ , and the associated time scale (in days) is  $\tau = 1/r$ . Because the model is non-linear we select benchmark values for comparison with the regression approach, the mean values for predictor variables and the midpoint of development,  $h = h_m/2$ , where  $h_m = 100$  is full development. The predicted effect of a variable  $x'$  (DD or CU in °C) on timing is  $\partial\tau/\partial x' = -\beta' e^{-x\beta} h_m / dt$ , where  $\beta$  is the vector of estimated parameters for corresponding covariates in vector  $\mathbf{x}$ , and  $\beta'$  is the parameter associated with  $x'$ , either warming °C or CU. This is the advance in days represented by a one-degree increase in spring temperatures or a 1 unit increase in chilling.