Supporting information: A simple explanation for declining temperature sensitivity with warming

E. M. Wolkovich J. Auerbach, C. J. Chamberlain, D. M. Buonaiuto,
A. K. Ettinger, I. Morales-Castilla & A. Gelman

1   A first-hitting-time model of leafout

We use a simple model based on the general understanding of how warm temperatures (forcing) trigger leafout in temperate deciduous trees (Chuine, 2000): that leafout occurs after a certain thermal sum is met (see also Lindsey and Newman, 1956; Zohner et al., 2020). Though this model is very simple, we formalize it here to show its inherent non-linearity and some of its relevant statistical properties.

We use a first-hitting-time model, which describes the first time a random process hits a threshold, because of its broad applicability and conceptual simplicity. We define leafout day, n_β, as the day, n, that cumulative daily temperature, S^n, hits the threshold, β.

We derive the relationship between daily temperature and leafout in two common scenarios. In the first, we take the average daily temperature up until the leafout date. In the second, we take the average daily temperature over a fixed window, such as March 1st to April 30th. In both cases, we discretize time since, although many biological processes depend continuously on time, research typically measures time in discretized units, such as days, weeks, or months.

1.1   Scenario 1: Using average daily temperature until the leafout date

We use the following notation:

n = day since temperatures start to accumulate, $n = 0, 1, ..., N$

X_n = observed temperature on day n

$S_0^n = \sum_{i=0}^{n} X_i$, the cumulative daily temperature from day 0 to day n

$M_0^n = \dfrac{S_0^n}{n}$, the average daily temperature from day 0 to day n

β = the threshold of interest, $\beta > 0$, (thermal sum required for leafout)

$n_\beta = \underset{n}{\operatorname{argmin}} \, S_n > \beta$, the first day the cumulative daily temperature passes the threshold

(for example, day of year (doy) of leafout).

We model X_n as a Gaussian random walk, $X_n \overset{\text{i.i.d}}{\sim} \text{normal}\,(\alpha_0 + \alpha_1 n, \sigma)$, where $\alpha_0 > 0$ is the average temperature on day $n = 0$, $\alpha_1 > 0$ is the day-over-day increase in average temperatures, and σ is the standard deviation. This model differs from the traditional Gaussian random walk because of the factor n.

This model has two important consequences:

(1) Leafout time is inversely related to average temperature at leafout time.

Under this model, $M_0^{n_\beta}$ and n_β are inversely proportional. To see why, assume for the moment that the cumulative daily temperature hits the threshold exactly on leafout day. That is, $S_0^{n_\beta} = \beta$. Then

$$M_0^{n_\beta} = \frac{S_0^{n_\beta}}{n_\beta} = \frac{\beta}{n_\beta}$$

rearranging yields

$$n_\beta = \frac{\beta}{M_0^{n_\beta}}$$

Many global change biology studies use linear regression to quantify the relationship between n_β and $M_0^{n_\beta}$ (or similar metrics, see Wolkovich et al., 2012; Piao et al., 2017; Keenan et al., 2020, for examples). Regressing n_β on $M_0^{n_\beta}$ finds a best fit line to the inverse curve, $n_\beta = \frac{\beta}{M_0^{n_\beta}}$. The relationship is linearized with the logarithm transformation: $\log(n_\beta) = \log(\beta) - \log(M_0^{n_\beta})$. That is, $\log(n_\beta)$ is linear in log-average daily temperature with slope -1 and intercept $\log(\beta)$.

(2) The variance of the average temperature may decrease as temperatures rise.

Under the model, the mean and variance of M_0^n are $\text{E}(M_0^n | \alpha_0, \alpha_1) = \frac{1}{n} \sum_{i=0}^{n} (\alpha_0 + \alpha_1 i) = \alpha_0 + \alpha_1 \frac{(n+1)}{2}$ and $\text{Var}(M_0^n | \alpha_0, \alpha_1) = \frac{\sigma^2}{n}$.

By the law of total variance,

$$
\begin{aligned}
\text{Var}(M_0^n) &= \text{E}(\text{Var}(M_0^n | \alpha_0, \alpha_1)) + \text{Var}(\text{E}(M_0^n | \alpha_0, \alpha_1)) \\
&= \frac{\sigma^2}{n} + \text{Var}(\alpha_0 + \alpha_1 \frac{n+1}{2}) \\
&= \frac{\sigma^2}{n} + \text{Var}(\alpha_0) + \frac{(n+1)^2}{4} \text{Var}(\alpha_1) + (n+1)\text{Cov}(\alpha_0, \alpha_1)
\end{aligned}
$$

As temperatures rise and leafout date becomes earlier, the variance of the average temperature will decline—provided the variation in temperatures, σ^2, is sufficiently small.

1.2 Scenario 2: Using average daily temperature over a fixed window

We slightly modify the notation:

n = day since temperatures start to accumulate, $n = 0, \ldots, a, \ldots, b$

X_n = observed temperature on day n

$S_a^n = \sum_{i=a}^{n} X_i$, the cumulative daily temperature from day a to day n

$M_a^n = \dfrac{S_a^n}{n-a}$, the average daily temperature from day a to day n

β = the threshold of interest, $\beta > 0$, (thermal sum required for leafout)

$n_\beta = \underset{n}{\operatorname{argmin}}\ S_0^n > \beta$, the first day the cumulative daily temperature passes the threshold

(for example, day of year (doy) of leafout).

As before, we model X_n as a Gaussian random walk, $X_n \overset{\text{i.i.d}}{\sim} \text{normal}\,(\alpha_0 + \alpha_1 n, \sigma)$, where $\alpha_0 > 0$ is the average temperature on day $n = 0$, $\alpha_1 > 0$ is the day-over-day increase in average temperatures, and σ is the standard deviation. We make the additional assumption that $X_n \geq 0$ for all n and $a < n_\beta < b$. That is, the cumulative temperature acquired by the plant always increases.

Note that

$$S_a^b \sim \text{normal}\left(\alpha_0(b-a) + \tfrac{\alpha_1}{2}(b-a)(b+a+1), \sigma\sqrt{b-a}\right)$$

$$M_a^b \sim \text{normal}\left(\alpha_0 + \tfrac{\alpha_1}{2}(b+a+1), \tfrac{\sigma}{\sqrt{b-a}}\right)$$

$$S_n^b - S_a^b \sim \text{normal}\left(\alpha_0(b-a-n) + \tfrac{\alpha_1}{2}((b-n)(b+n+1) - a(a+1)), \sigma\sqrt{b+a-n}\right)$$

so that

$$
\begin{aligned}
Pr\left(n_\beta \leq n \mid M_a^b = m\right) &= Pr\left(n_\beta \leq n \mid S_a^b = (b-a)m\right) \\
&= Pr\left(S_0^n \geq \beta \mid S_a^b = (b-a)m\right) \\
&= Pr\left(S_n^b \leq (b-a)m + S_0^a - \beta\right) \\
&= Pr\left(S_n^b - S_0^a \leq (b-a)m - \beta\right) \\
&= \Phi\left(\frac{(b-a)m - \beta - [\alpha_0(b-a-n) + \tfrac{\alpha_1}{2}((b-n)(b+n+1) - a(a+1))]}{\sigma\sqrt{b+a-n}}\right)
\end{aligned}
$$

The distribution of M_a^b shows that consequence (2) above still holds with this model. Consequence (1) no longer holds directly, but will in many situations where average daily temperature until an event correlates strongly with average daily temperature because the window is chosen based, in part, on the expected hitting time (Figs. S3-S4). We note two additional consequences:

(3) The conditional median is quadratic in n:

$$\frac{1}{2} \stackrel{\text{set}}{=} Pr\left(n_\beta \le n \mid M_a^b = m\right)$$

$$\Rightarrow 0 = (b-a)m - \beta - \left[\alpha_0(b-a-n) + \frac{\alpha_1}{2}((b-n)(b+n+1) - a(a+1))\right]$$

$$\Rightarrow m = \frac{1}{(a-b)}\left[-\beta - \alpha_0(b-a-n) - \frac{\alpha_1}{2}((b-n)(b+n+1) - a(a+1))\right]$$

$$= \frac{1}{(a-b)}\left[-\beta - \alpha_0(b-a) - \frac{\alpha_1}{2}(b-a)(b+a+1)\right] + \frac{\alpha_0 + \frac{\alpha_1}{2}}{(a-b)}n + \frac{\frac{\alpha_1}{2}}{(a-b)}n^2$$

$$:= \gamma_0 + \gamma_1 n + \gamma_2 n^2$$

(4) The conditional mean and variance are sums of negative sigmoids, according to the following identities

$$E\left(n_\beta \mid M_a^b = m\right) = \sum_{n=0}^{\infty} Pr\left(n_\beta \ge n \mid M_a^b = m\right)$$

$$E\left(n_\beta^2 \mid M_a^b = m\right) = \sum_{n=0}^{\infty} n\, Pr\left(n_\beta \ge n \mid M_a^b = m\right)$$

2   Simulations of common hypotheses for declining sensitivity

2.1   Effect of increasing thermal sum on sensitivity

Many biological hypotheses explain the observed decline in plant sensitivity as a consequence of declines in over-winter chilling or short photoperiods (Fu et al., 2015; Zohner et al., 2016; Fu et al., 2019). These forces generally increase the thermal sum required for leafout each year (Polgar et al., 2014; Zohner et al., 2017; Flynn and Wolkovich, 2018), hypothesized to weaken the linear relationship between biological responses and temperature.

An increase in the thermal sum required for leafout (β in our first hitting-time model in section 1.1 above) yields a larger in magnitude regression coefficient (when regressing leafout date on spring-time temperature). Thus, if climate change drives higher thermal thresholds, we should see increasing—not declining—sensitivity (Fig. S5). This happens due to a decreasing (in magnitude) variance in temperature alongside an increasing in magnitude covariance between temperature and leafout day. Similar results are seen given the model in section 1.2, though due mainly to increasing covariance between temperature and leafout day. Previous work has highlighted how shifting temperature variance (over space and/or time) could lead to shifting estimates of temperature sensitivities (Keenan et al., 2020), but these results stress that shifting variance in temperature is likely only part of a larger story driven by the non-linearity of temperature response.

2.2 Effects of chilling and daylength

We extended simulations from our first hitting-time model to examine two common biological hypotheses for declining sensitivities in spring plant phenology to understand how discernible biological shifts would be from the shifts present when using linear models to estimate sensitivities for non-linear temperature responses.

First, we simulated the most often cited hypothesis (e.g., Fu et al., 2015; Piao et al., 2017): an increasing thermal sum threshold given declines in over-winter chilling with warming. In a model where increased thermal sums are driven by declines in overwinter chilling with warming sensitivities from log-transformed data first increase and then decrease (as winter warming delays leafout day and spring warming advances leafout day) in step with biological shifts in cues (Fig. S6a, c), while for estimates from the linear model changes in sensitivity occur throughout warming, despite no major change in cues before 4 °C (Fig. S6a, c). The ultimate effect with warming depends on exact parameter values (e.g., how much thermal cues shift with declines in warming) and on the covariation of X and β, highlighting how difficult teasing apart relationships in observational spring phenology may be given correlations across multiple predictors (correlations that are likely exacerbated by climate change).

Second, we simulated an alternative hypothesis where warming causes the thermal sum to be reached before a required daylength threshold and plants then leaf out on the first day the daylength threshold is met (Zohner et al., 2016; Fu et al., 2019). At its extreme this model produces the same leafout day (the day when the required daylength is met) across different temperatures and thus produces smaller in magnitude estimated sensitivities in both linear and logged models. Estimated sensitivities, however, from a linear model do not necessarily decline depending on exact parameter values (see Fig. S6b, d). Again this shift appears more visible when using sensitivities that include the non-linear nature of plants temperature response compared to linear estimates (see Fig. S6b, d).

Annotated code for these simulations are available via github to allow testing of alternative parameter values or versions of these hypotheses.

3 Additional methods & results from long-term empirical data

We draw on three empirical data sources: (1) data from a controlled experiment across a wide temperature range (Charrier et al., 2011) (selected as it is the only study with multiple observations across a wide range of forcing temperatures in fully controlled settings from a recent meta-analysis of all published spring phenology controlled environment studies, OSPREE) and long-term phenology data from two major sources—(2) PEP 725 phenological data and (3) winegrape harvest records from two main regions in France. We selected these datasets because the are relatively long-term, complete, public, have been widely used in the past and have paired climate data (see Data & Code Availability). Code for these analyses are available via github (https://github.com/temporalecologylab/labgit/tree/master/projects/decsenspost).

To examine how estimated sensitivities of leafout shift over time, we selected sites of two common European tree species (silver birch, *Betula pendula*, and European beech, *Fagus sylvatica*) that have long-term observational data of leafout, through the Pan European Phenology Project (PEP725, Templ et al., 2018). We selected these two species given that they were best represented for consistent data at the same sites over our study years for an early-leafout (*Betula pendula*) and a late-leafout (*Fagus sylvatica*) species (e.g., *Betula pendula* had 17 sites with leafout data from 1950-1960 and 2000-2010, while the next best option for an early-leafout species, *Alnus glutinosa*, had data for only five sites). We used sites with complete leafout data across both our 10-year (and 20-year) windows to avoid possible confounding effects of shifting sites over time (see Tables S1-S2 for numbers of sites per species-window combination). We calculated temperature sensitivities as a simple linear regression of leafout day of year versus the mean daily temperature, using a European-wide gridded climate dataset (E-OBS, *Cornes et al., 2018*) to calculate average temperature from 1 March to 30 April (60 d).

Estimated sensitivities for the empirical data (PEP725) using logged variables are far lower than the value obtained in our simulations (-1). This likely results from a contrast between our simulations—where we can accurately define the temperature plants experience and the temporal window that drives leafout—and our empirical data, where we do not know how measured temperatures translate into the temperatures that plants accumulate and where we have no clear method to define the relevant temporal window.

To examine how estimated sensitivities of harvest shift over time, we used data from Cook and Wolkovich (2016), which combines data from Daux et al. (2012) and various paleoclimate and instrumental climate metrics. We used the instrumental temperature seasonal record from the paper and split the data after 1950 at 1979/1980 to provide a nearly even complete set of data for each period (29 and 28 years).

Our results highlight how the acceleration of biological time with warming requires caution in linking observed patterns to mechanisms. We have shown that patterns of lower sensitivities with higher temperatures should be expected, and not used alone as strong evidence of shifting biology. Indeed, when our model holds, declining sensitivity with rising temperatures should be the null hypothesis of any analysis of temperature sensitivity based on linear regression or similar methods. In addition to improving null expectations across both biological and calendar time, researchers need to develop and test logical predictions for how their results may scale across space, time and temperature (e.g., while Keenan et al. (2020) suggest results in Wolkovich et al. (2012) are due to using annual temperatures for observational studies, Wolkovich et al. (2012) showed results were robust to using annual temperatures versus three-month temperature windows, and found no relationship between temperature sensitivity and degree of warming), consider the complexity of both correlated climate variables (which may be difficult to uncouple even in some experiments, Ettinger et al., 2019) and correlated biotic variables, which may themselves lead to altered estimates of temperature sensitivity (Yuste et al., 2004).

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4 Tables

Table S1: Climate and phenology statistics for two species (*Betula pendula, Fagus sylvatica*, across 45 and 47 sites respectively) from the PEP725 data across all sites with continuous data from 1950-1960 and 2000-2010. ST is spring temperature (°C) from 1 March to 30 April, ST.lo is temperature 31 days before leafout, and GDD is growing degree 31 days before leafout (with a base temperature of 0°C). Slope represents the estimated sensitivity using untransformed leafout and ST, while log-slope represents the estimated sensitivity using log(leafout) and log(ST). We calculated all metrics for each species x site x 10 year period before taking mean or variance estimates.

years	species	mean (ST)	mean ST.lo	var (ST)	var (lo)	GDD	slope	log-slope
1950-1960	*Betula pendula*	5.6	7.0	3.4	110.51	71.71	-4.28	-0.17
2000-2010	*Betula pendula*	6.6	6.8	1.2	46.96	64.63	-3.61	-0.22
1950-1960	*Fagus sylvatica*	5.6	7.5	3.3	71.89	83.81	-2.85	-0.11
2000-2010	*Fagus sylvatica*	6.7	7.7	1.2	38.29	86.69	-3.43	-0.20

Table S2: Climate and phenology statistics for two species (*Betula pendula, Fagus sylvatica*, across 17 and 24 sites respectively) from the PEP725 data across all sites with continuous data from 1950-2010. ST is spring temperature (°C) from 1 March to 30 April, ST.lo is temperature 31 days before leafout, and GDD is growing degree 31 days before leafout (with a base temperature of 0°C). Slope represents the estimated sensitivity using untransformed leafout and ST, while log-slope represents the estimated sensitivity using log(leafout) and log(ST). We calculated all metrics for each species x site x 10 year period before taking mean or variance estimates.

| years	species	mean (ST)	mean ST.lo	var (ST)	var (lo)	GDD	slope	log-slope
1950-1970	*Betula pendula*	5.8	7.1	2.6	79.89	72.48	-4.34	-0.19
1970-1990	*Betula pendula*	5.9	7.2	1.3	104.83	72.15	-6.11	-0.33
1990-2010	*Betula pendula*	6.8	6.7	0.9	36.22	60.03	-3.35	-0.21
1950-1970	*Fagus sylvatica*	5.6	7.6	2.7	63.35	86.02	-3.08	-0.12
1970-1990	*Fagus sylvatica*	5.6	7.5	1.3	56.19	81.31	-2.51	-0.16
1990-2010	*Fagus sylvatica*	6.7	7.5	1.0	32.82	79.92	-2.76	-0.15

5 Figures
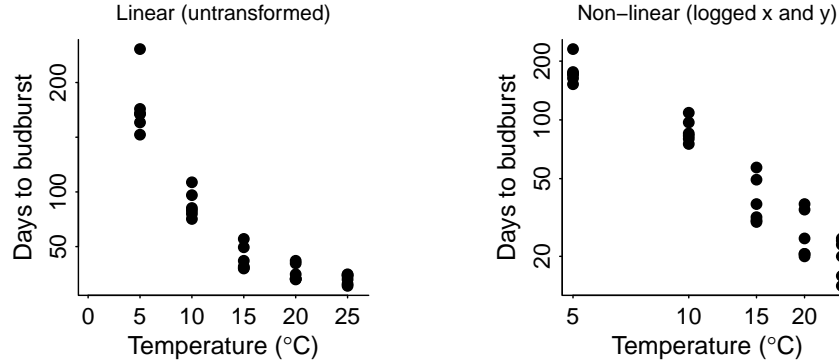
Figure S1: **Controlled experiments across a wide temperature range show a non-linear response to temperature.** Here we use data from Charrier et al. (2011), one of the few studies covering a wide range of temperatures in a fully controlled experiment. Data are from a growth chamber experiment of tree branch cuttings of walnut trees (*Juglans regia*), taken from the field on 29 January 2009 and exposed to five different temperatures with a 16 hour photoperiod.
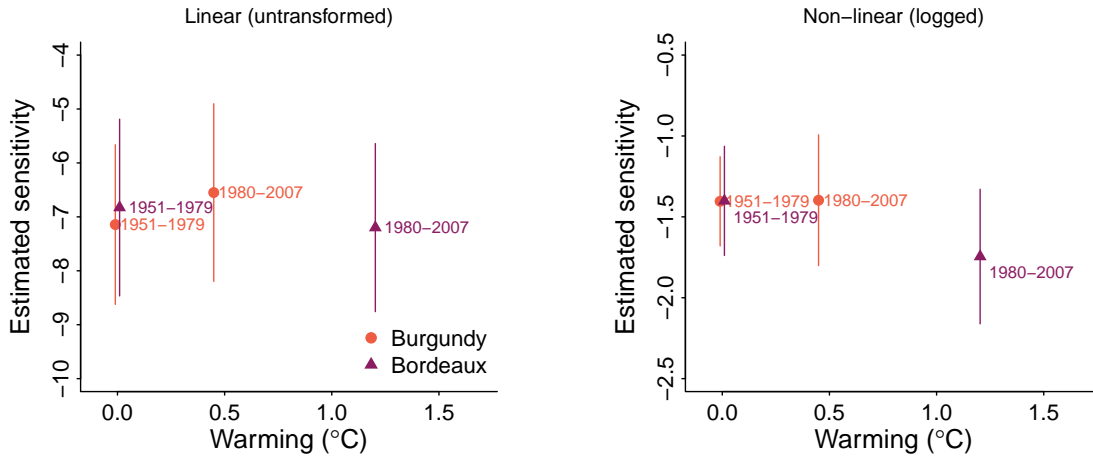

Figure S2: **Estimates of temperature sensitivities (response per °C) using linear (left) and non-linear (right) models of long-term harvest data from two major French winegrowing regions.** Temperature sensitivity of data from Burgundy declines with warming when estimated with linear regression (left). This decline disappears when performing the regression on logged predictor and response variables, and increases the relative magnitude of an increase in sensitivity estimated from data from Bordeaux (right). Harvest and temperature data from Cook and Wolkovich (2016).
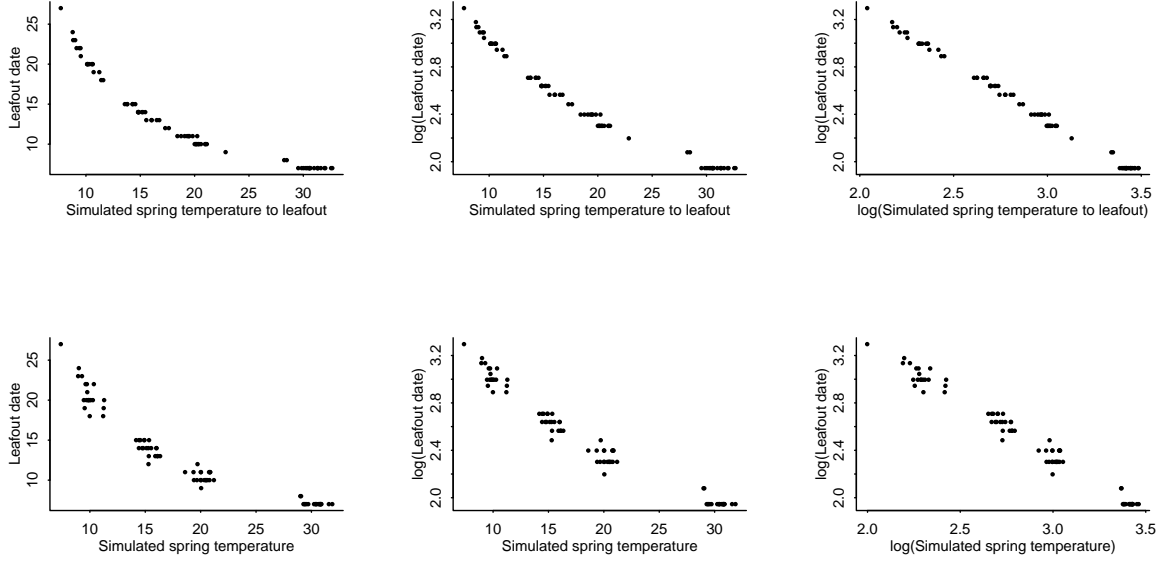
Figure S3: **Simulated leafout as a function of temperature across different temperatures highlights non-linearity of process.** Here we simulated sets of data where leafout constantly occurs at 200 growing degree days (thermal sum of mean daily temperatures with 0°C as base temperature) across mean temperatures of 10, 15, 20 and 30°C (constant SD of 4), we calculated estimated mean temperature until leafout date (top row) or across a fixed window (bottom row, similar to estimates of 'spring temperature'). While within any small temperature range the relationship may appear linear, its non-linear relationship becomes clear across the greater range shown here (left). Taking the log of both leafout and temperature (right) linearizes the relationship.
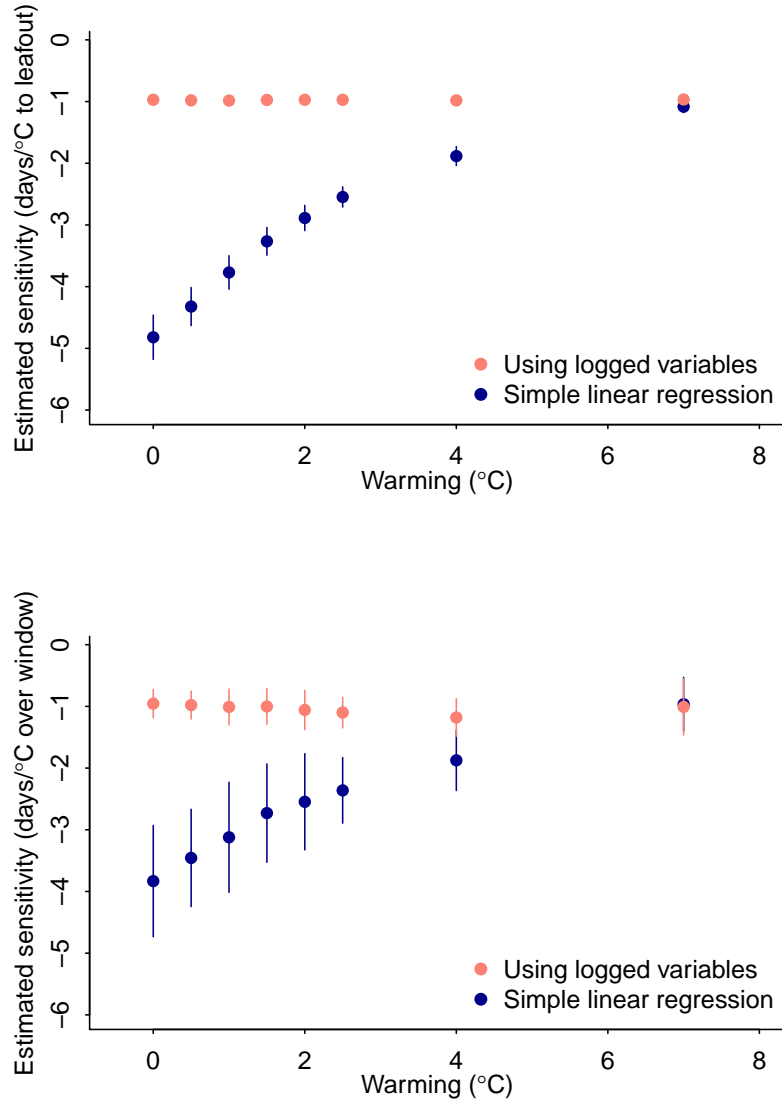
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Figure S4: **A simple model generates declining sensitivities with warming.** We show declines in estimated sensitivities with warming from simulations (top: using average temperature until leafout, bottom: using a fixed window; dots and lines represent means ± standard deviation) with no underlying change in the biological process when sensitivities were estimated with simple linear regression ("Simple linear regression"). This decline disappears using regression on logged predictor and response variables ("Using logged variables").
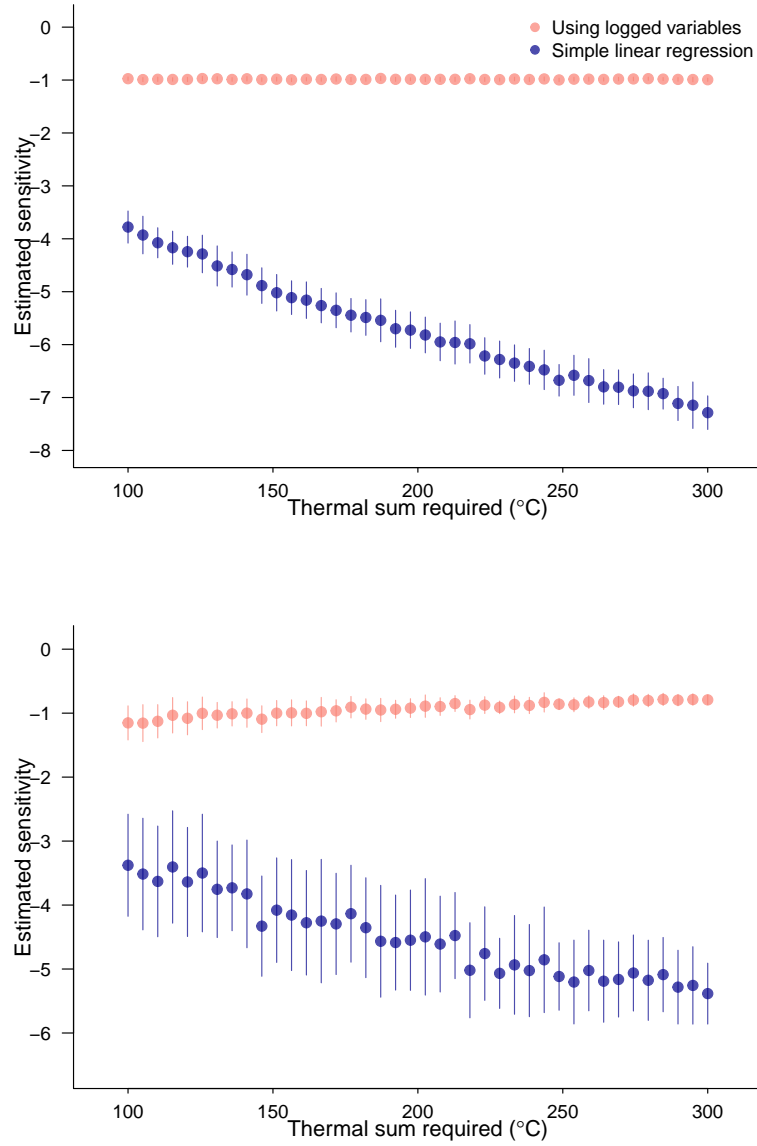
Figure S5: **Simulated leafout as a function of required thermal sum for leafout.** Here we simulated sets of data where leafout occurs at varying thermal sums (sum of mean daily temperatures with 0°C as base temperature) and estimated sensitivities using mean temperature until leafout date (top) or across a fixed window (bottom) with simple linear regression ("Simple linear regression"), and using regression on logged predictor and response variables ("Using logged variables"). Dots and lines represent means ± standard deviation.
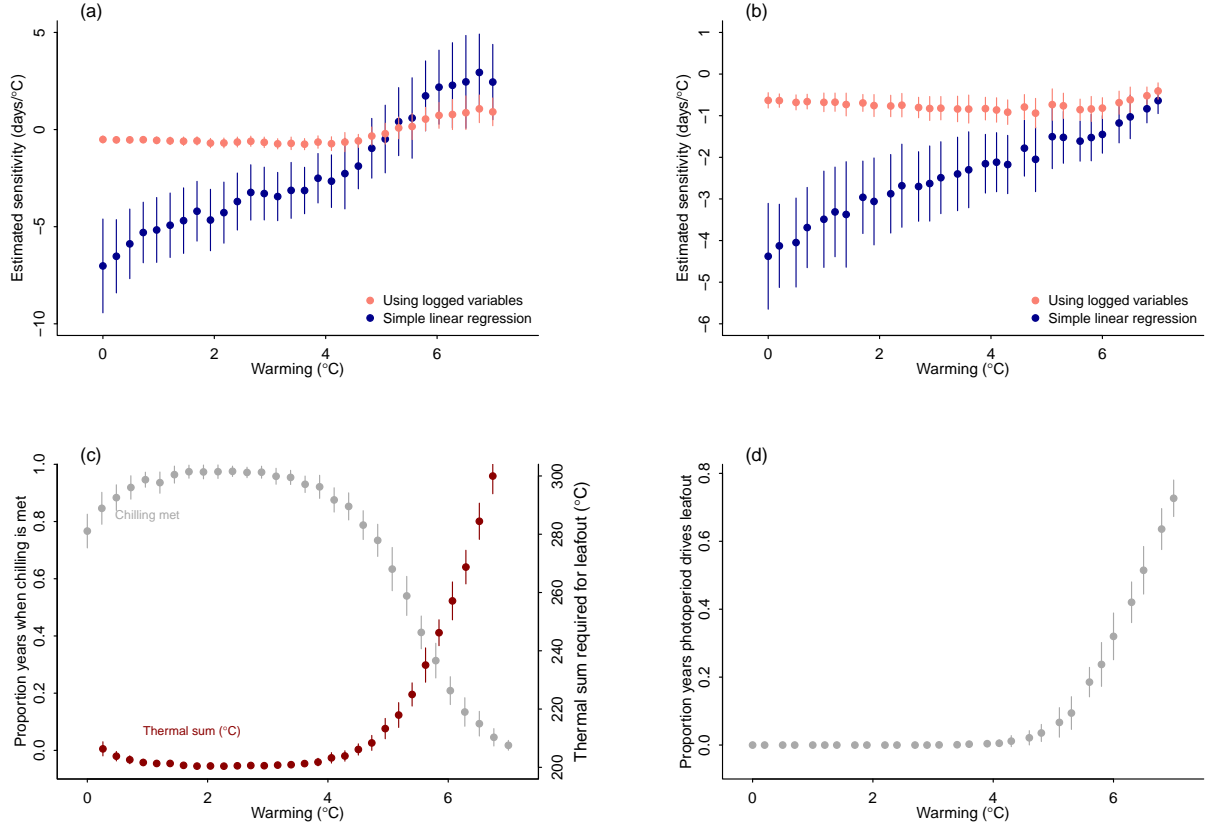
Figure S6: **Simulated leafout as a function of temperature across different levels of warming with shifts in underlying biology through lower chilling (a, c) and photoperiod thresholds (b, d).** We show estimated sensitivities in the top panels (a-b), and the shifting cues in the bottom panels (c-d). Here we simulated sets of data where leafout occurs at a thermal sum of 200 (sum of mean daily temperatures with 0°C as base temperature) when chilling and photoperiod requirements are met, and requires a higher thermal sum when chilling is not met (a, c, required chilling set at 110 units summing temperatures between 0-5°C over 120 d winter period, increasing the thermal sum by 3 units per unmet chilling unit) or where leafout occurs at a thermal sum of 200 as long as the daylength of that day is ≥ 12 hours (at 45 N, estimated from R's geosphere package); otherwise leafout occurs on the first day when daylength is 12 hours (b, d). In all simulations the daily increase in spring temperatures was 0.1°C, the variance in daily temperatures was 4°C, in the chilling simulations winter temperatures were centered at 1°C and spring temperatures at 2°C; in the photoperiod simulations spring temperatures were centered at 4°C. Dots and lines represent means ± standard deviation.