# Supplemental materials: A simple explanation for declining temperature sensitivity with warming

the lab & friends

## 1 Model of leafout timing

Following a general understanding of how warm temperatures (forcing) triggers leafout in temperate deciduous trees (Chuine, 2000), we define leafout day, $n_\beta$, as the day, $n$, that cumulative daily temperature, $S_0^n$, hits the threshold, $\beta$. Here we assume that we know the day temperatures start to accumulate, $n = 0$ (below we extend to the case there is fixed window of temperatures).

### 1.1 Random walk model

We use the following notation:

$$
\begin{aligned}
n &= \text{day since temperatures start to accumulate, } n = 0, 1, ..., N \\
X_n &= \text{observed temperature on day } n \\
S_0^n &= \sum_{i=0}^{n} X_i, \text{the cumulative daily temperature from day 0 to day } n \\
M_0^n &= \frac{S_0^n}{n}, \text{the average daily temperature from day 0 to day } n \\
\beta &= \text{the threshold of interest, } \beta > 0, \text{ (for example, F* or required GDD)} \\
n_\beta &= \underset{n}{\operatorname{argmin}}\ S_n > \beta, \text{the first day the cumulative daily temperature passes the threshold} \\
&\quad \text{(for example, day of year (doy) of budburst).}
\end{aligned}
$$

We model $X_n$ as a Gaussian random walk, $X_n \overset{\text{i.i.d}}{\sim} \mathcal{N}(n\Delta, \sigma)$, where $\Delta > 0$ is the day-over-day increase in average temperatures and $\sigma$ is the standard deviation. Note that this model differs from the typical Gaussian random walk because of the factor $n$.

This model yields two important points:

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

Under this model, $M_0^{n_\beta}$ and $n_\beta$ 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

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

Much research uses linear regression to quantify the relationship between $n_\beta$ and $M_0^{n_\beta}$. Regressing $n_\beta$ on $M_0^{n_\beta}$ finds a best fit line to the inverse curve, $n_\beta = \frac{\beta}{M_0^{n_\beta}}$. The relationship can be approximately linearized with a 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 $\log(\beta)$ (e.g., in simulations in Fig. 1 is -1, and intercept is $\log(200) = 5.3$). In this example, where we stop accumulating $X$ based on $n_\beta$, an inverse would be more appropriate, and would be especially important if results are extrapolated (see Fig. S2).

(2) Declining sensitivity is explained by the declining variance of the average temperature (which, given the relationship between leafout time and average temperature also leads to declining variance in leafout date).

Under the model, the mean and variance of $M_0^n$ is $\mathrm{E}(M_0^n) = \frac{1}{n}\sum_{i=0}^{n} i\Delta = \frac{(n+1)}{2}\Delta$ and $\mathrm{Var}(M_0^n) = \frac{\sigma^2}{n}$.

Consider two years, $A$ and $B$, where $A_0^n$ denotes the average temperature in year $A$ by day $n$ with increase $\Delta_A$ and $B_0^n$ the average temperature in year $B$ with increase $\Delta_B$. Suppose year $B$ is warmer than year $A$, $\Delta_A < \Delta_B$, so that $A_0^n$ typically gets to $\beta$ in $n_A$ steps and $B_0^n$ gets to $\beta$ in $n_B$ steps, $n_A > n_B$.

Then $\mathrm{Var}(A_0^{n_A}) = \frac{\sigma^2}{n_A} < \frac{\sigma^2}{n_B} = \mathrm{Var}(B_0^{n_B})$.

## 1.2 Adjusted random walk model for a temporal window of measured temperature

Here we consider a scenario where there is a chosen a window of temperatures, for example March 1 to April 30. Let:

$$\begin{aligned}
n &= \text{day since temperatures start to accumulate, } n = 0, \ldots, a, \ldots, b \\
X_n &= \text{observed temperature on day } n \\
S_a^n &= \sum_{i=a}^{n} X_i, \text{the cumulative daily temperature from day } a \text{ to day } n \\
M_a^n &= \frac{S_a^n}{n-a}, \text{the average daily temperature from day } a \text{ to day } n \\
\beta &= \text{the threshold of interest, } \beta > 0, \text{ (for example, F* or required GDD)} \\
n_\beta &= \underset{n}{\operatorname{argmin}}\ S_0^n > \beta, \text{the first day the cumulative daily temperature passes the threshold} \\
&\qquad \text{(for example, day of year (doy) of budburst).}
\end{aligned}$$

We model $X_n$ as a Gaussian random walk, $X_n \overset{\text{i.i.d}}{\sim} \mathcal{N}(\alpha_0 + \alpha_1 n, \sigma)$. We assume $X_n > 0$ for all

$n$ and $a < n_\beta < b$.

Then

$S_a^b \sim \mathcal{N}\left(\alpha_0(b-a) + \frac{\alpha_1}{2}(b-a)(b+a+1), \sigma\sqrt{b-a}\right)$

$M_a^b \sim \mathcal{N}\left(\alpha_0 + \frac{\alpha_1}{2}(b+a+1), \frac{\sigma}{\sqrt{b-a}}\right)$

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

and

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

The mean and variance can be found from the identities

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

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

In this scenario, leafout time is no longer directly inversely related to average temperature at leafout time, but the relationship is sigmoidal rather than linear, thus issues will remain in using linear regression or forecasting from correlation analysis using linearity assumptions. Transformations, such as log, can lessen these issues, however, as noted above, they will not remove the problem entirely and will provide poor forecasts.

## 2 Results using long-term empirical data from PEP725

To examine how estimated sensitivities 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 used a European-wide gridded climate dataset *(*E-OBS*, Cornes et al., 2018)* to extract daily minimum and maximum temperature for the grid cells where observations of leafout for these two species were available. We used sites with leafout across our full temporal windows to avoid possible confounding effects of shifting sites over time (see Tables S1-S2 for numbers of sites per species x window).

Our estimates of temperature sensitivity from a linear model using untransformed variables shows a decline in sensitivity with recent warming for *Betula pendula* over 10 and 20-year windows, but no decline for *Fagus sylvatica*; using logged variables estimates appeared more similar over time or sometimes suggested an increase sensitivity (see Figs. S5-S6, Tables S1-S2). This shift in estimated sensitivity when regressing with untransformed versus logged variables suggests these declining estimates from untransformed variables may not be caused by biological shifts and driven instead by using linear regression for a non-linear process. This hypothesis is supported further by large declines in variance of leafout in recent decades.

Shifts in variance provide another hurdle to robust estimates of temperature sensitivity. 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 our results stress that variance in both leafout and temperature are shifting. If both shift in step, estimates would not be impacted by changes in temperature variance, but our results suggest variance in temperature—for these data—has declined more than variance in leafout, though both have declined substantially in recent decades (Tables S1-S2).

*References*

Chuine, I. 2000. A unified model for budburst of trees. Journal of Theoretical Biology 207:337–347.

Cornes, R. C., G. van der Schrier, E. J. van den Besselaar, and P. D. Jones. 2018. An ensemble version of the E-OBS temperature and precipitation data sets. Journal of Geophysical Research: Atmospheres 123:9391–9409.

Keenan, T. F., A. D. Richardson, and K. Hufkens. 2020. On quantifying the apparent temperature sensitivity of plant phenology. New Phytologist 225:1033–1040.

Templ, B., E. Koch, K. Bolmgren, M. Ungersböck, A. Paul, H. Scheifinger, T. Rutishauser, M. Busto, F.-M. Chmielewski, L. Hájková, S. Hodzić, F. Kaspar, B. Pietragalla, R. Romero-Fresneda, A. Tolvanen, V. Vučetič, K. Zimmermann, and A. Zust. 2018. Pan European Phenological database (PEP725): a single point of access for European data. International Journal of Biometeorology 62:1109–1113.

## 3 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 from March 1 to April 30, ST.leafout is temperature 30 days before leafout, and GDD is growing degree days 30 days before leafout. 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 for each species x site x 10 year period before taking mean or variance estimates. See also Fig. S5.

| | | mean(ST) | mean(ST.leafout) | var(ST) | var(leafout) | mean(GDD) | slope | log-slope |
|---|---|---|---|---|---|---|---|---|
| 1950-1960 | *Betula pendula* | 5.6 | 7.0 | 3.4 | 110.5 | 71.7 | -4.3 | -0.17 |
| 2000-2010 | *Betula pendula* | 6.6 | 6.8 | 1.2 | 47.0 | 64.6 | -3.6 | -0.22 |
| 1950-1960 | *Fagus sylvatica* | 5.6 | 7.5 | 3.3 | 71.9 | 83.8 | -2.8 | -0.11 |
| 2000-2010 | *Fagus sylvatica* | 6.7 | 7.7 | 1.2 | 38.3 | 86.7 | -3.4 | -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 from March 1 to April 30, ST.leafout is temperature 30 days before leafout, and GDD is growing degree days 30 days before leafout. 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 for each species x site x 20 year period before taking mean or variance estimates. See also Fig. S6.

| | | mean(ST) | mean(ST.leafout) | var(ST) | var(leafout) | mean(GDD) | slope | log-slope |
|---|---|---|---|---|---|---|---|---|
| 1950-1970 | *Betula pendula* | 5.8 | 7.1 | 2.6 | 79.9 | 72.5 | -4.3 | -0.19 |
| 1970-1990 | *Betula pendula* | 5.9 | 7.2 | 1.3 | 104.8 | 72.2 | -6.1 | -0.33 |
| 1990-2010 | *Betula pendula* | 6.8 | 6.7 | 0.9 | 36.2 | 60.0 | -3.3 | -0.21 |
| 1950-1970 | *Fagus sylvatica* | 5.6 | 7.6 | 2.7 | 63.4 | 86.0 | -3.1 | -0.12 |
| 1970-1990 | *Fagus sylvatica* | 5.6 | 7.5 | 1.3 | 56.2 | 81.3 | -2.5 | -0.12 |
| 1990-2010 | *Fagus sylvatica* | 6.7 | 7.3 | 1.2 | 31.4 | 76.0 | -3.4 | -0.19 |

# 4 Figures

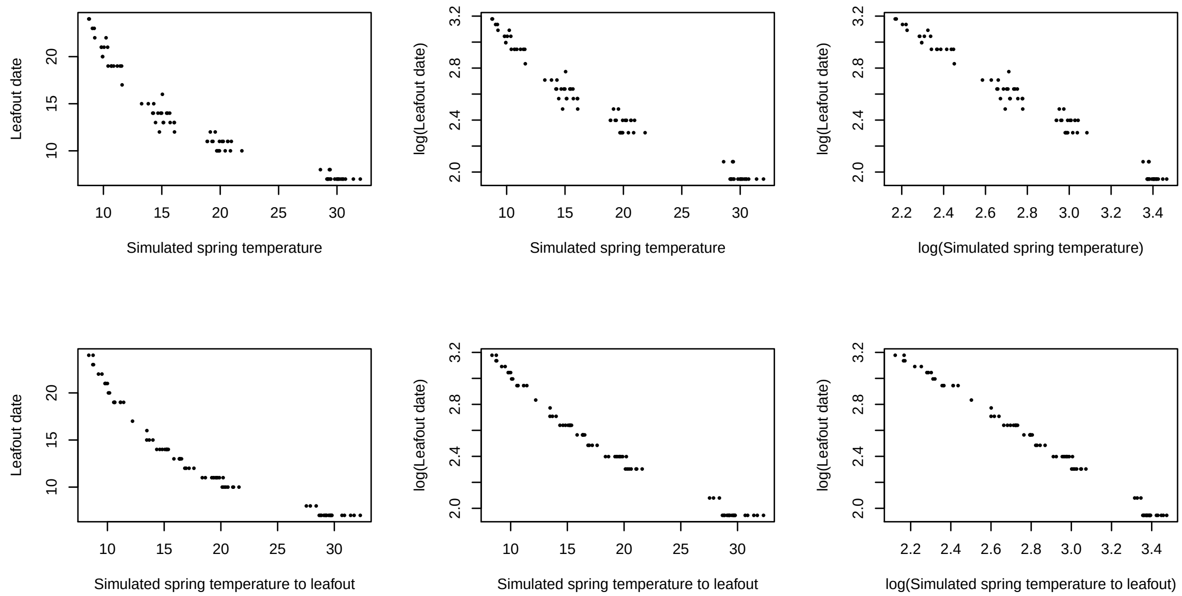


Figure S1: **Simulated leafout as a function of temperature across different temperatures highlights non-linearity of process.** Here we simulated sets of data where leafout constantly occurs at 200 growing degree days across mean temperatures of 0, 5, 10 and 20C (constant SD of 4), we calculated estimated mean temperature across a fixed window (top row, similar to estimates of 'spring temperature') or until leafout date (bottom row). 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 leafout (middle) reduces this some, but taking the log of both leafout and temperature (right) further linearizes the relationship.

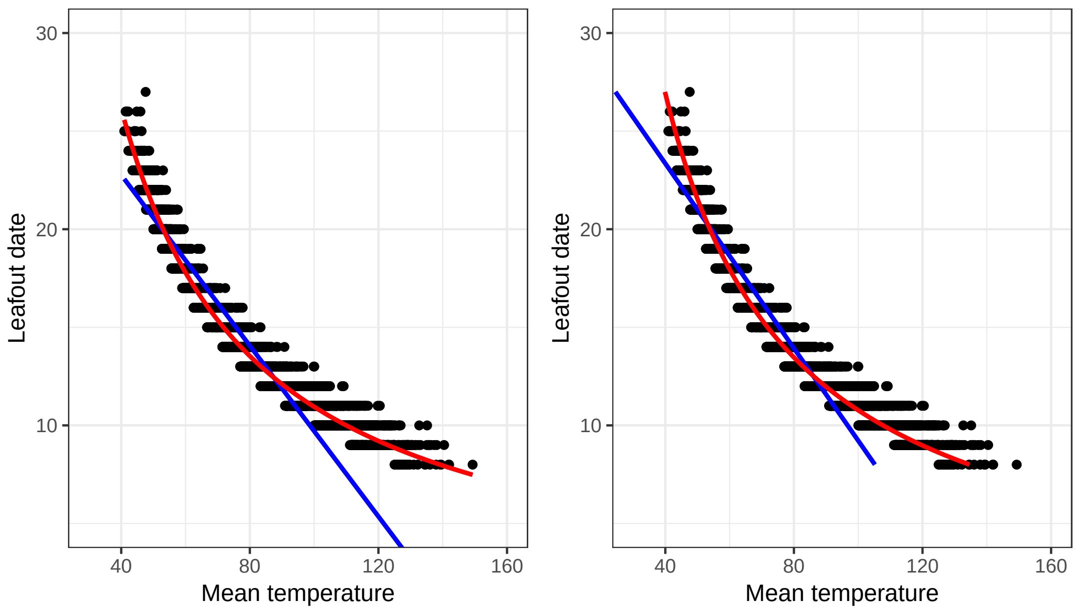


Figure S2: **Extrapolation of regression from simulated data given models of leafout day versus average daily temperature** where leafout day is regressed against log(average daily temperature), shown on left, gives poorer predictions than when modeling the inverse (log(leafout day) against mean average daily temperature), shown on right.

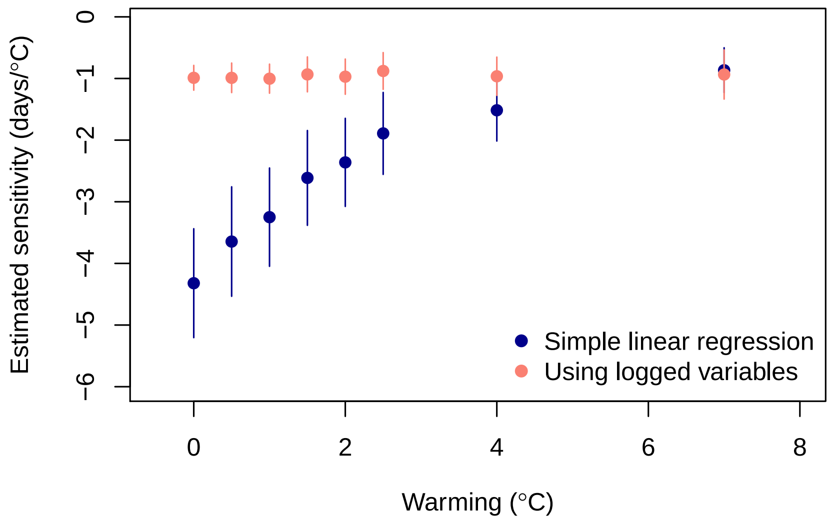


Figure S3: **A simple model generates declining sensitivities with warming.** We found declines in estimated sensitivities with warming from simulations with no underlying change in the biological process when sensitivities were estimated with simple linear regression ("Simple linear regressions"). This decline disappears using regression on logged predictor and response variables ("Using logged variables").

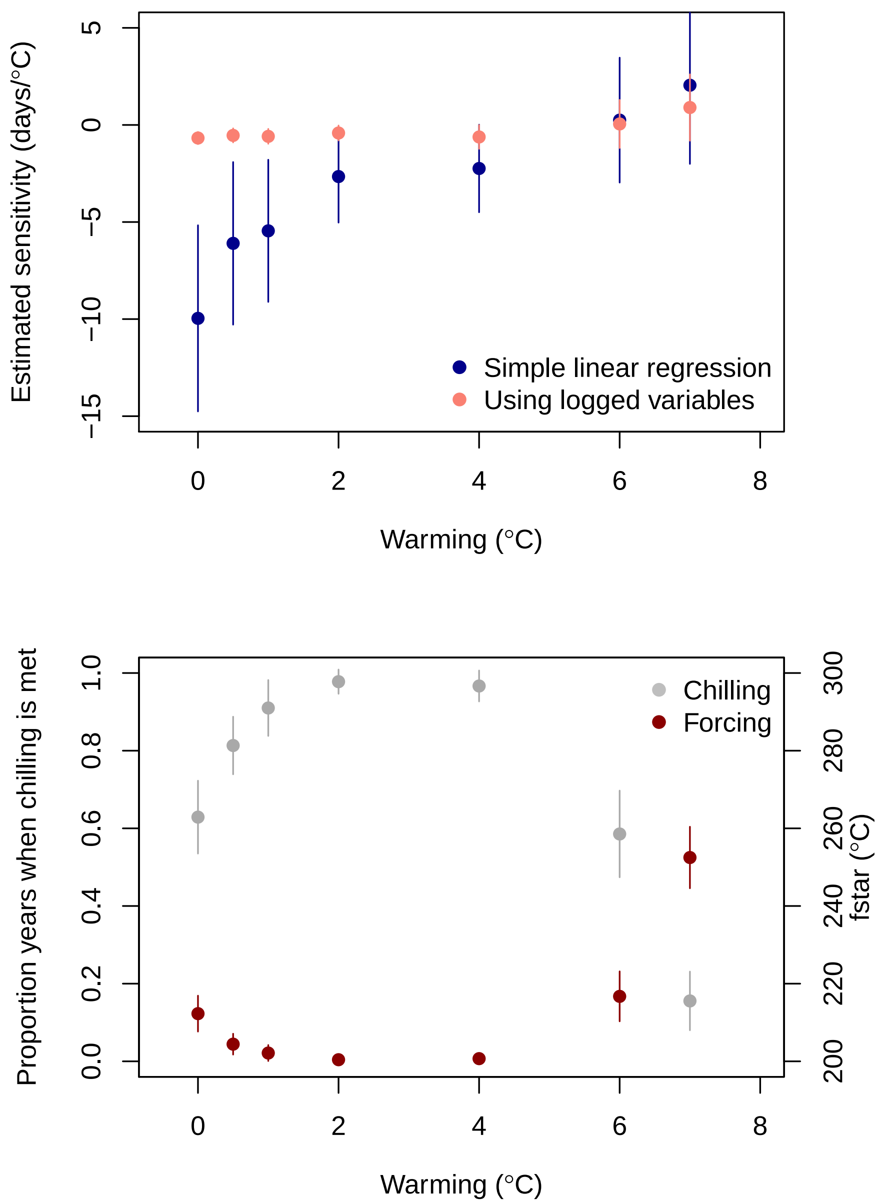


Figure S4: **Simulated leafout as a function of temperature across different temperatures with shifts in underlying cues.** Here we simulated sets of data where leafout occurs at 200 growing degree days ('fstar') when chilling is met, and requires additional growing degree days when chilling is not met. We show estimates sensitivities in the top panel, and the shifting cues on the bottom panel. Note that this model is non-identifiable as the same response data could come from a forcing-only model or a chilling and forcing model.

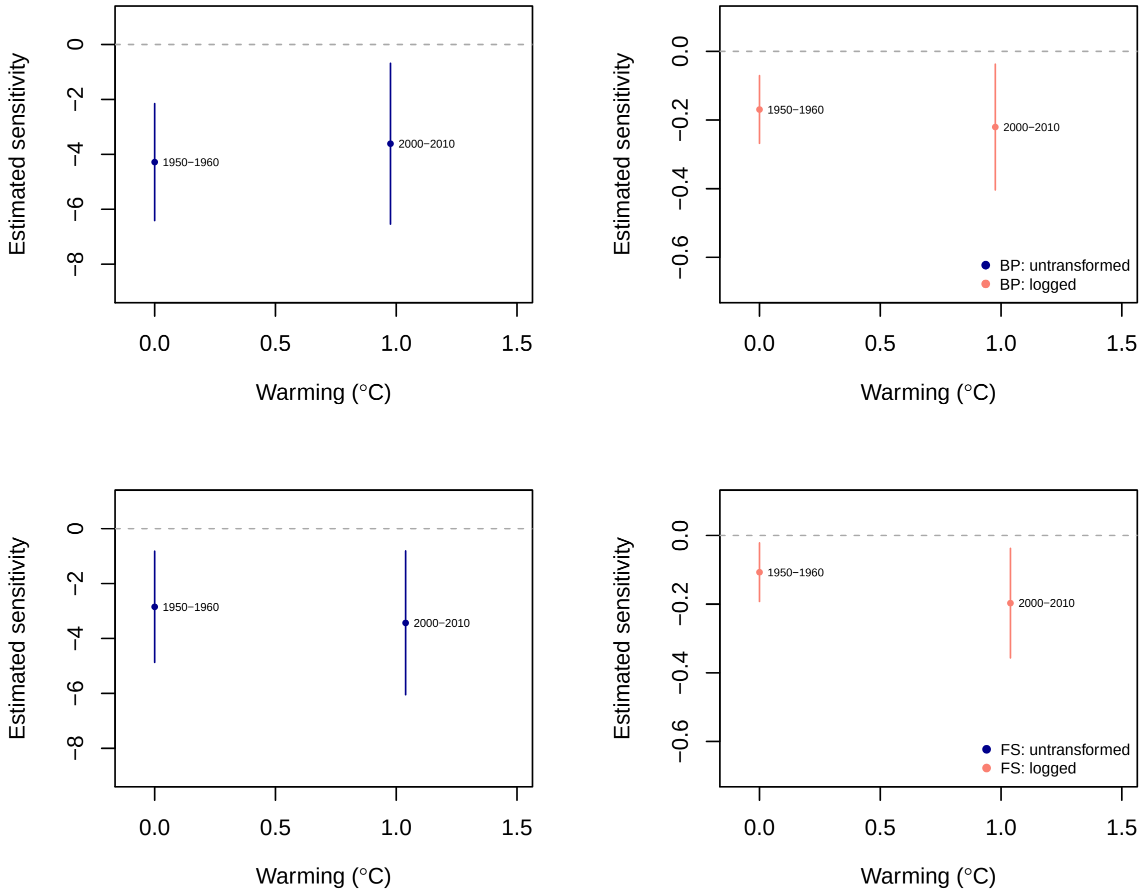


Figure S5: **Sensitivities from PEP725 data using 10 year windows of data** for two species (top – *Betula pendula*, bottom – *Fagus sylvatica*; all lines show 78% confidence intervals from linear regressions). Amounts of warming are calculated relative to 1950-1960 and we used only sites with leafout data in all years shown here. Both approaches show variation in sensitivity across time. See Table S1 for further details.

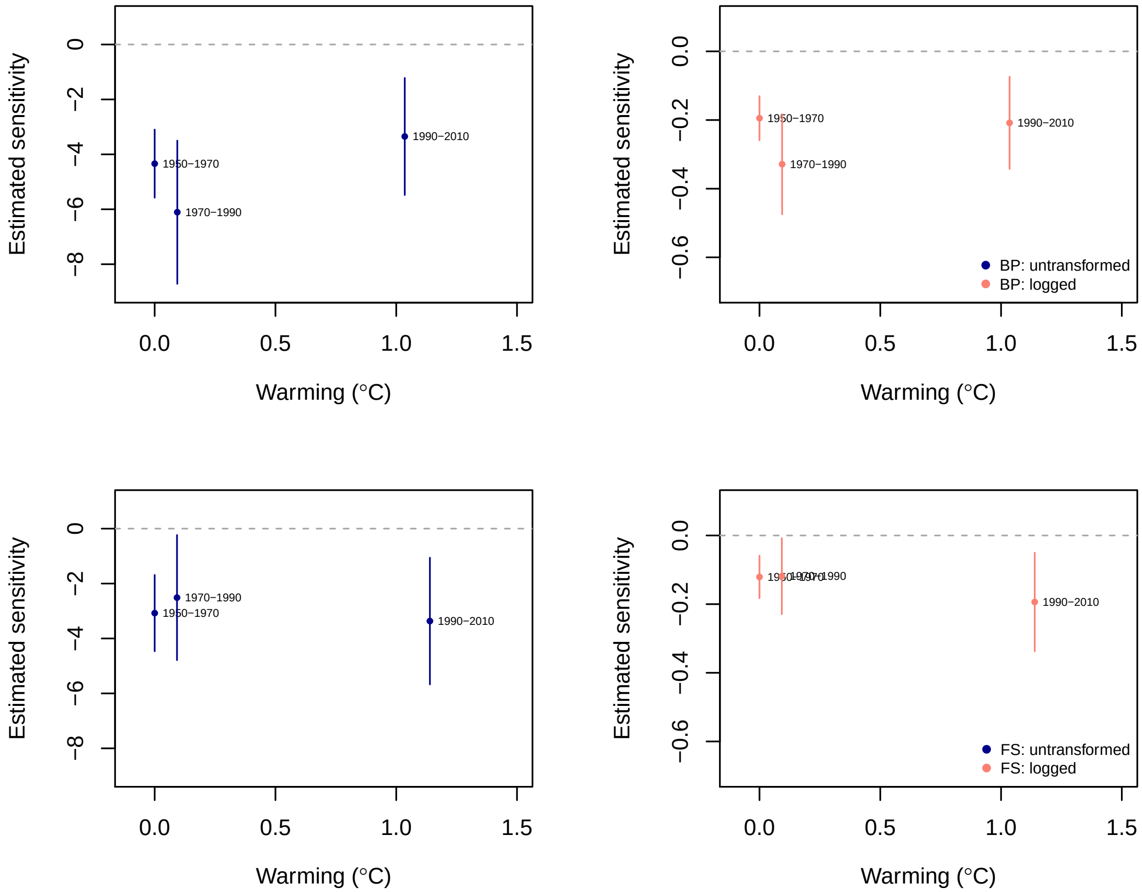


Figure S6: **Sensitivities from PEP725 data using 20 year windows of data** for two species (top – *Betula pendula*, bottom – *Fagus sylvatica*; all lines show 78% confidence intervals from linear regressions). Amounts of warming are calculated relative to 1950-1970 and we used only sites with leafout data in all years shown here. Both approaches show variation in sensitivity across time. See Table S2 for further details.