

# A simple explanation for declining temperature sensitivity with warming

E. M. Wolkovich<sup>1,a</sup>, J. L. Auerbach<sup>2</sup>, C. J. Chamberlain<sup>3</sup>, D. M. Buonaiuto<sup>3</sup>,  
A. K. Ettinger<sup>4</sup>, I. Morales-Castilla<sup>5</sup> & A. Gelman<sup>2</sup>

<sup>1</sup>Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada

<sup>2</sup>Department of Statistics, Columbia University, New York, NY 10027, USA

<sup>3</sup>Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

<sup>4</sup>TNC, USA

<sup>5</sup>Department of Life Sciences, University of Alcalà CTRA N-II, KM., 33,600, 28802, Alcalà de Henares, Spain

<sup>a</sup>Corresponding author (ORCID: 0000-0001-7653-893X)

*Article type:* Report

*Short title:* Declining temperature sensitivity

*One sentence summary:* Declines in temperature sensitivity may mean warming is changing biology, or they are simply the outcome of current methods.

## Abstract

Temperature sensitivity—the magnitude of a biological response per  $^{\circ}\text{C}$ —is a fundamental concept across scientific disciplines, especially biology, where temperature determines the rate of many plant, animal and ecosystem processes. Recently, a growing body of literature in global change biology has found temperature sensitivities decline as temperatures rise (1; 2; 3; 4). Such observations have been used to suggest climate change is reshaping biological processes, with major implications for forecasts of future change. Here we present a simple alternative explanation for observed declining sensitivities: the use of linear models to estimate non-linear temperature responses. Corrections for the non-linearity of temperature response in simulated data and long-term phenological data from Europe remove the apparent decline. Our results show that rising temperatures combined with linear estimates based on calendar time are expected to produce observations of declining sensitivity—without any shift in the underlying biology.

# 1 Main text

Climate change has reshaped biological processes around the globe, with shifts in the timing of major life history events (phenology), carbon dynamics and other ecosystem processes (5). With rising temperatures, a growing body of literature has documented changes in temperature sensitivity—the magnitude of a biological response scaled per °C. Many studies have found declining responses to temperature in recent decades (1; 2; 3; 4), and some have reported more uniform sensitivities across elevation (6), or lower sensitivities in warmer, urban areas (7).

Most studies attribute changes in temperature sensitivity to shifts in underlying biological processes. For example, researchers have suggested weaker temperature sensitivities are evidence of increased light limitation in the tundra (3), or a decline in the relative importance of warm spring temperatures for spring phenological events (e.g., leafout, insect emergence) in the temperate zone (1; 7), as other environmental triggers (e.g., winter temperatures that determine ‘chilling’) play a larger role. Yet, despite an increase in studies reporting declining or shifting temperature sensitivities, none have provided strong evidence of the biological mechanisms underlying these changes (e.g., 1; 7). The missing mechanisms may be hidden in the data: environmental factors moderate biological processes in complex ways (8; 2), are strongly correlated in nature (e.g., 1), and temperature variance shifts over time and space (9).

Here we propose a simpler alternative explanation: the use of linear models for non-linear responses to temperature. Researchers generally use methods with assumptions of linearity to calculate temperature sensitivities, often relying on some form of linear regression to compute a change in a quantity—days to leafout or carbon sequestered over a fixed time, for example—per °C, thus ignoring that many biological responses to temperature are non-linear. We show, theoretically then with simulated and empirical data, how the use of linear methods for non-linear processes can produce an illusion that the mechanisms underlying biological processes are changing.

Many observed biological events are the result of continuous non-linear processes that depend

on temperature, which are discretized into temporal units for measurement. For example, a biological response, such as leafout, occurs when a certain thermal sum is reached, and plants will reach this threshold more quickly—in calendar time—when average daily temperatures are warmer. Biologically, however, the plants may require the same temperature sum. Indeed any process observed or measured as the time until reaching a threshold is inversely proportional to the speed at which that threshold is approached. Temperature determines the speed of many biological processes. Thus, at very low temperatures plants would never leaf out and at higher temperatures they could leaf out in only a matter of days—yet sensitivities estimated from linear regression at higher (warmer) temperatures would appear much lower than those observed at lower temperatures. Warming acts to step on the biological accelerator, and thus may produce declining sensitivities without any change in the underlying process.

We show this by deriving the relationship between a biological response and temperature using a simple stochastic model, which describes the first time a random process hits a threshold (see ‘A first-hitting-time model of leafout’ in Supplementary Materials). Our model holds the temperature threshold for leafout constant. Even though the mechanism by which temperature leads to leafout does not change, the model produces declining sensitivity—as measured in days per °C—with warming. Indeed, under this model constant temperature sensitivity would be evidence that the temperature threshold is not constant and the mechanisms underlying the leafout process have changed.

Simulations show that correcting for non-linearity removes apparent declines in temperature sensitivity (Fig. 1, S2, code link). Assuming a model where warming increases the required thermal sum for a biological event—a common hypothesis for declining sensitivities in spring phenological events—yields declining sensitivities that remain after correcting for non-linearity (Fig. S3).

Further, after correcting for non-linearity in long-term leafout data from Europe, we find little evidence for declining sensitivities with warming (Figs. 1, S4, S5). An apparent decline in sensitivity for silver birch (*Betula pendula*) from -4.3 days/°C to -3.6 days/°C from 1950-1960 compared to 2000-2010 disappears using a log-log regression (-0.17 versus -0.22). We see similar

corrections using 20-year windows, and a potential increase in sensitivity for European beech (*Fagus sylvatica*, see Tables S1-S2). Moreover, the variance of the leafout dates of both species declines as temperatures rise—(declines of roughly 50%, see Tables S1-S2), which is expected under our model as warming accelerates towards the thermal threshold that triggers leafout (and in contrast to predictions from changing mechanisms, see 10).

Our theoretical model and empirical results show that rising temperatures are sufficient to explain declining temperature sensitivity. It is not necessary to invoke changes to the mechanisms that underlie the biological processes themselves.

Inferring biological processes from statistical artifacts is not a new problem (e.g., 11), but climate change provides a new challenge in discerning mechanism from measurements because it affects biological time, while researchers continue to use calendar time. Other fields focused on temperature sensitivity often use approaches that acknowledge the non-linearity of responses (e.g., 12). Researchers have called for greater use of process-based models (9), which often include non-linear responses to temperature, but rely themselves on exploratory methods and descriptive analyses for progress (8). The challenge, then, is to interrogate the implicit and explicit models we use to interpret data summaries, and to develop null expectations that apply across biological and calendar time.

## References

- [1] Fu, Y. S. H. *et al.* Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107 (2015).
- [2] Güsewell, S., Furrer, R., Gehrig, R. & Pietragalla, B. Changes in temperature sensitivity of spring phenology with recent climate warming in switzerland are related to shifts of the preseason. *Global Change Biology* **23**, 5189–5202 (2017).
- [3] Piao, S. *et al.* Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nature Climate Change* **7**, 359 (2017).

- [4] Dai, W. J., Jin, H. Y., Zhang, Y. H., Liu, T. & Zhou, Z. Q. Detecting temporal changes in the temperature sensitivity of spring phenology with global warming: Application of machine learning in phenological model. *Agricultural and Forest Meteorology* **279** (2019).
- [5] IPCC. *Climate Change 2014: Impacts, Adaptation, and Vulnerability* (Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2014).
- [6] Vitasse, Y., Signarbieux, C. & Fu, Y. H. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences* **115**, 1004–1008 (2018).
- [7] Meng, L. *et al.* Urban warming advances spring phenology but reduces the response of phenology to temperature in the conterminous united states. *Proceedings of the National Academy of Sciences* **117**, 4228 (2020).
- [8] Chuine, I. *et al.* Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology* **22**, 3444–3460 (2016).
- [9] Keenan, T. F., Richardson, A. D. & Hufkens, K. On quantifying the apparent temperature sensitivity of plant phenology. *New Phytologist* **225**, 1033–1040 (2020).
- [10] Ford, K. R., Harrington, C. A., Bansal, S., Gould, J., Peter & St. Clair, J. B. Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas-fir. *Global Change Biology* **22**, 3712–3723 (2016).
- [11] Nee, S., Colegrave, N., West, S. A. & Grafen, A. The illusion of invariant quantities in life histories. *Science* **309**, 1236–1239 (2005).
- [12] Yuste, J., Janssens, I. A., Carrara, A. & Ceulemans, R. Annual  $Q_{10}$  of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* **10**, 161–169 (2004).

*Acknowledgements:* Thanks to TJ Davies, TM Giants, D. Lipson and C. Rollinson.

*List of Supplementary materials:*

A first-hitting-time model of leafout

Results using long-term empirical data from PEP725

Table S1-S2

Fig S1-S5

## Figures

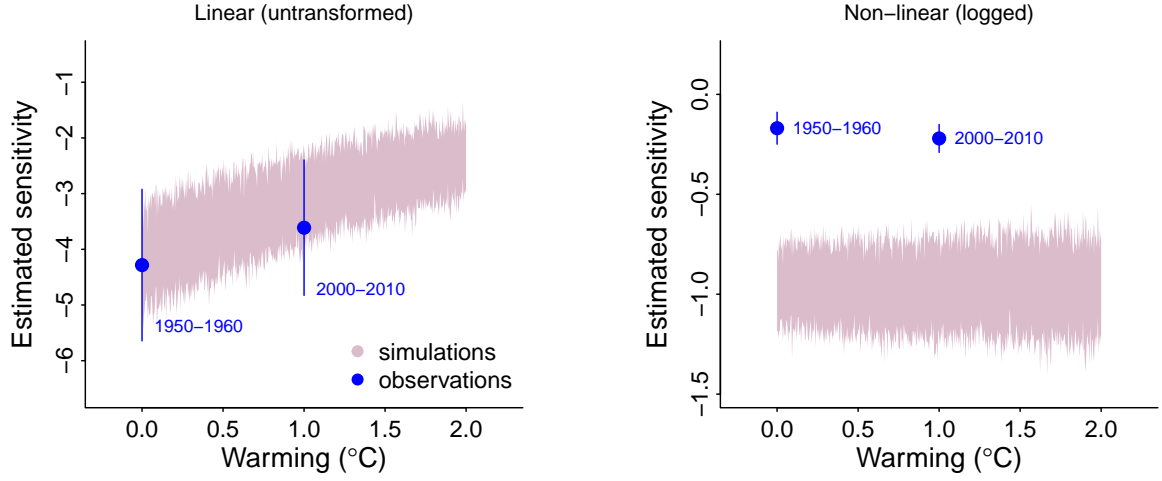


Figure 1: **Shifts in temperature sensitivities with warming occur when using linear models for non-linear processes.** Estimated sensitivities decline with warming in simulations (left) with no underlying change in the biological process when sensitivities were estimated with linear regression (estimated across 45 sites with a base temperature of  $\text{normal}(6,4)$ ). This decline disappears when performing the regression on logged predictor and response variables (right). Such issues may underlie declining sensitivities calculated from observational data, including long-term observations of leafout across Europe (‘observations,’ using data for *Betula pendula* from PEP725 from for the 45 sites that had complete data for 1950-1960 and 2000-2010), which show a lower sensitivity with warming when calculated on raw data, but no change in sensitivity using logged data. Shading, symbols and lines represent means  $\pm$  standard deviations of regressions across sites. See Supplementary Materials for a discussion of why estimated sensitivities are -1 or lower in non-linear models.