

A simple explanation for declining temperature sensitivity with warming

E. M. Wolkovich^{1,a}, J. L. Auerbach², C. J. Chamberlain³, D. M. Buonaiuto³,
A. K. Ettinger⁴, I. Morales-Castilla⁵ & A. Gelman²

¹Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, British Columbia, Canada

²Department of Statistics, Columbia University, New York, NY 10027, USA

³Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

⁴The Nature Conservancy in Washington, 74 Wall Street, Seattle, WA, USA

⁵GloCEE – Global Change Ecology and Evolution Group, Department of Life Sciences, University of Alcalà CTRA N-II, KM., 33,600, 28802, Alcalà de Henares, Spain

^aCorresponding author (ORCID: 0000-0001-7653-893X)

Article type: Opinion

Abstract

Recently, multiple studies have reported declining phenological sensitivities (Δ days per $^{\circ}\text{C}$) with higher temperatures. Such observations have been used to suggest climate change is reshaping biological processes, with major implications for forecasts of future change. Here we show that these results may simply be the outcome of using linear models to estimate non-linear temperature responses, specifically for events that occur after a cumulative thermal threshold is met—a common model for many biological events. Corrections for the non-linearity of temperature responses consistently remove the apparent decline. Our results show that rising temperatures combined with linear estimates based on calendar time produce observations of declining sensitivity—without any shift in the underlying biology. Current methods may thus undermine efforts to identify when and how warming will reshape biological processes.

1 Main text

2 Climate change has reshaped biological processes around the globe, with shifts in the timing of
3 major life history events (phenology), carbon dynamics and other ecosystem processes (IPCC,
4 2014). With rising temperatures, a growing body of literature has documented changes in tem-
5 perature sensitivity—the magnitude of a biological response scaled per °C. Many studies have
6 found declining responses to temperature in recent decades (Fu et al., 2015; Güsewell et al.,
7 2017; Piao et al., 2017; Dai et al., 2019) or lower sensitivities in warmer, urban areas (Meng
8 et al., 2020).

9
10 Most studies attribute changes in temperature sensitivity to shifts in underlying biological pro-
11 cesses. Researchers have suggested weaker temperature sensitivities are evidence of increased
12 light limitation in the tundra (Piao et al., 2017), or a decline in the relative importance of warm
13 spring temperatures for spring phenological events (e.g., leafout, insect emergence) in the tem-
14 perate zone (Fu et al., 2015; Meng et al., 2020), as other environmental triggers (e.g., winter
15 temperatures that determine ‘chilling’) play a larger role. Yet, despite an increase in studies
16 reporting declining or shifting temperature sensitivities, none have provided strong evidence of
17 the biological mechanisms underlying these changes (e.g., Fu et al., 2015; Meng et al., 2020).
18 The missing mechanisms may be hidden in the data: environmental factors moderate biological
19 processes in complex ways (Chuine et al., 2016; Güsewell et al., 2017), are strongly correlated
20 in nature (e.g., Fu et al., 2015), and temperature variance shifts over time and space (Keenan
21 et al., 2020).

22
23 Here we propose a simpler alternative explanation: the use of linear models for non-linear re-
24 sponses to temperature. Researchers generally use methods with assumptions of linearity to
25 calculate temperature sensitivities, often relying on some form of linear regression to compute a
26 change in a quantity—days to leafout or carbon sequestered over a fixed time, for example—per
27 °C, thus ignoring that many biological responses to temperature, especially events, are non-
28 linear (Fig. S1).

Many observed biological responses 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 (Dijkhuis, 1956; Lindsey and Newman, 1956), and plants will reach this threshold more quickly—in calendar time—when average daily temperatures are warmer (Fig. S1, Kramer, 2012). Biologically, however, the plants require the same temperature sum to trigger leafout at high and low average temperatures. 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 (Bonan and Sirois, 1992; Hofmann and Todgham, 2010). 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. Using a simple model where leafout occurs after a thermal sum is met we can hold the temperature threshold for leafout constant (Hunter and Lechowicz, 1992; Zohner et al., 2020) and examine how estimated sensitivities (measured in days per °C using linear regression) shift with warming. In this simple thermal sum model (which we argue is the null model for studies of biological events across different temperatures, Fig. S1 and Dijkhuis, 1956; Lindsey and Newman, 1956; Zohner et al., 2020) we find declining sensitivities with warming (Fig S3; see ‘A first-hitting-time model of leafout’ in Supplementary Information for a full derivation of the statistical properties). 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.

Correcting for non-linearity using the transformation for an inverse relationship (log transformation) removes apparent declines in temperature sensitivity in long-term leafout and harvest data (Fig. 1-2, S3, code link). In empirical long-term tree leafout data from Europe, correcting for non-linearity in responses produces little evidence for declining sensitivities with warming (Figs. 1). 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 ver-

60 sus -0.22). Moreover, the variance of the leafout dates declines as temperatures rise—(declines
61 of roughly 50%, see Tables S1-S2), which is expected under our model as warming accelerates
62 towards the thermal threshold that triggers leafout (and in contrast to predictions from chang-
63 ing mechanisms, see Ford et al., 2016). A similar apparent decline in winegrape harvest data in
64 Burgundy disappears with a log transformation (estimates of -7.1 days/°C to -6.5 days/°C from
65 1951-1979 compared to 1980-2007 are both estimated as -1.4 using log-log regression), and an
66 increase in sensitivity in Bordeaux, which has warmed substantially, becomes larger in relative
67 magnitude (-6.8 days/°C from 1951-1979 compared to -7.2 from 1980-2007 become -1.4 and -1.7,
68 respectively, using log-log regression).

69
70 Fundamentally rising temperature should alter many biological processes, making robust meth-
71 ods for identifying these changes critical. In spring plant phenology, where declining sensitivities
72 are often reported (Fu et al., 2015; Piao et al., 2017; Dai et al., 2019), warming may increase the
73 role of ‘chilling’ (determined mainly by winter temperatures) and daylength (Laube et al., 2014;
74 Zohner et al., 2016)—potentially increasing the thermal sum required for leafout at lower values
75 of these cues (Polgar et al., 2014; Zohner et al., 2017). Adjusting our simulations to match this
76 model yielded shifts in sensitivities with warming. After correcting for non-linearity, the shifts
77 in sensitivities remained and they occurred in step with the biological change (Fig. S5a, c).
78 In contrast, sensitivities estimated from a linear model showed shifts across the entire range of
79 warming, well before the simulated biological change (Fig. S5a, c). Further, we found that an
80 increase in the thermal sum required for leafout should yield larger in magnitude temperature
81 sensitivities, not smaller, as is often expected (e.g., Fu et al., 2015). These results highlight the
82 complexity of identifying what trends to expect in sensitivities with warming, and suggest that
83 without useful null models we may misinterpret when biological change occurs.

84 85 *Conclusion*

86 Inferring biological processes from statistical artifacts is not a new problem (e.g., Nee et al.,
87 2005), but climate change provides a new challenge in discerning mechanism from measurements
88 because it affects biological time, while researchers continue to use calendar time. Other fields
89 focused on temperature sensitivity often use approaches that acknowledge the non-linearity of re-

sponses (e.g., Yuste et al., 2004). Researchers have called for greater use of process-based models (Keenan et al., 2020), which often include non-linear responses to temperature, but process-based models themselves rely on exploratory methods and descriptive analyses for progress (Chuine et al., 2016). 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

- Bonan, G. B., and L. Sirois. 1992. Air-temperature, tree growth, and the northern and southern range limits to *Picea-mariana*. *Journal of Vegetation Science* 3:495–506.
- Charrier, G., M. Bonhomme, A. Lacointe, and T. Améglio. 2011. Are budburst dates, dormancy and cold acclimation in walnut trees (*Juglans regia* L.) under mainly genotypic or environmental control? *International journal of biometeorology* 55:763–774.
- Chuine, I., M. Bonhomme, J.-M. Legave, I. García de Cortázar-Atauri, G. Charrier, A. Lacointe, and T. Améglio. 2016. Can phenological models predict tree phenology accurately in the future? The unrevealed hurdle of endodormancy break. *Global Change Biology* 22:3444–3460.
- Cook, B. I., and E. M. Wolkovich. 2016. Climate change decouples drought from early wine grape harvests in France. *Nature Climate Change* 6:715–719.
- Dai, W. J., H. Y. Jin, Y. H. Zhang, T. Liu, and Z. Q. Zhou. 2019. 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.
- Dijkhuis, F. J. 1956. Computation of heat unit accumulations in maize for practical application. *Euphytica* 5:267–275.
- Ford, K. R., C. A. Harrington, S. Bansal, J. Gould, Peter, and J. B. St. Clair. 2016. Will changes

in phenology track climate change? A study of growth initiation timing in coast Douglas-fir.
Global Change Biology 22:3712–3723.

Fu, Y. S. H., H. F. Zhao, S. L. Piao, M. Peaucelle, S. S. Peng, G. Y. Zhou, P. Ciais, M. T. Huang,
A. Menzel, J. P. Uelas, Y. Song, Y. Vitasse, Z. Z. Zeng, and I. A. Janssens. 2015. Declining
global warming effects on the phenology of spring leaf unfolding. Nature 526:104–107.

Güsewell, S., R. Furrer, R. Gehrig, and B. Pietragalla. 2017. 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.

Hofmann, G. E., and A. E. Todgham. 2010. Living in the now: Physiological mechanisms to
tolerate a rapidly changing environment. Annual Review of Physiology 72:127–145.

Hunter, A. F., and M. J. Lechowicz. 1992. Predicting the timing of budburst in temperate trees.
Journal of Applied Ecology 29:597–604.

IPCC. 2014. Climate Change 2014: Impacts, Adaptation, and Vulnerability. Cambridge Uni-
versity Press, Cambridge, United Kingdom and New York, NY, USA.

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

Kramer, P. 2012. Physiology of woody plants. Elsevier, New York.

Laube, J., T. H. Sparks, N. Estrella, J. Höfler, D. P. Ankerst, and A. Menzel. 2014. Chilling
outweighs photoperiod in preventing precocious spring development. Global Change Biology
20:170–182.

Lindsey, A. A., and J. E. Newman. 1956. Use of official weather data in spring time - temperature
analysis of an Indiana phenological record. Ecology 37:812–823.

Meng, L., J. Mao, Y. Zhou, A. D. Richardson, X. Lee, P. E. Thornton, D. M. Ricciuto, X. Li,
Y. Dai, X. Shi, and G. Jia. 2020. 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.

- Nee, S., N. Colegrave, S. A. West, and A. Grafen. 2005. The illusion of invariant quantities in life histories. *Science* 309:1236–1239.
- Piao, S., Z. Liu, T. Wang, S. Peng, P. Ciais, M. Huang, A. Ahlstrom, J. F. Burkhart, F. Chevalier, I. A. Janssens, et al. 2017. Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nature Climate Change* 7:359.
- Polgar, C., A. Gallinat, and R. B. Primack. 2014. Drivers of leaf-out phenology and their implications for species invasions: insights from Thoreau’s Concord. *New Phytologist* 202:106–15.
- Yuste, J., I. A. Janssens, A. Carrara, and R. Ceulemans. 2004. Annual Q_{10} of soil respiration reflects plant phenological patterns as well as temperature sensitivity. *Global Change Biology* 10:161–169.
- Zohner, C. M., B. M. Benito, J. D. Fridley, J. C. Svenning, and S. S. Renner. 2017. Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe and East Asia. *Ecology Letters* 20:452–460.
- Zohner, C. M., B. M. Benito, J. C. Svenning, and S. S. Renner. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* 6:1120–1123.
- Zohner, C. M., L. D. Mo, T. A. M. Pugh, J. F. Bastin, and T. W. Crowther. 2020. Interactive climate factors restrict future increases in spring productivity of temperate and boreal trees. *Global Change Biology* 26:4042–4055.

Acknowledgements: Thanks to TJ Davies, TM Giants, Y. Fu, D. Lipson, C. Rollinson, Y. Vitasse for comments that improved the manuscript. IM-C acknowledges funding from the Spanish Ministry for Science and Innovation. NSERC (grant no. RGPIN05038 to EMW), Canada Research Chair in Temporal Ecology (EMW) and the Spanish Ministry for Science and Innovation (grant no. PID2019/109711RJ-I00 to IM-C) provided funding.

167 *Data & Code Availability:* Code for simulations, empirical analysis, and plots is provided here.
168 For empirical examples, we extracted data from Charrier et al. (2011) which is available through
169 the OSPREE database, used PEP 725 phenological data, E-OBS climate data and data from
170 Cook and Wolkovich (2016), which is available through the NOAA Paleoclimate Archive. All
171 data are freely available via the links.

172

173 *Author contributions:* All authors contributed to idea development and editing the manuscript.
174 In addition, EMW wrote the manuscript, developed the simulations, and made the figures; JLA
175 formalized the first-hitting time model and its derivations, CJC did much of the PEP725 analysis.

176

177 *List of Supplementary Information:*

178 A first-hitting-time model of leafout

179 Simulations of common hypotheses for declining sensitivity

180 Additional methods & results from long-term empirical data

181 Table S1-S2

182 Fig S1-S4

183

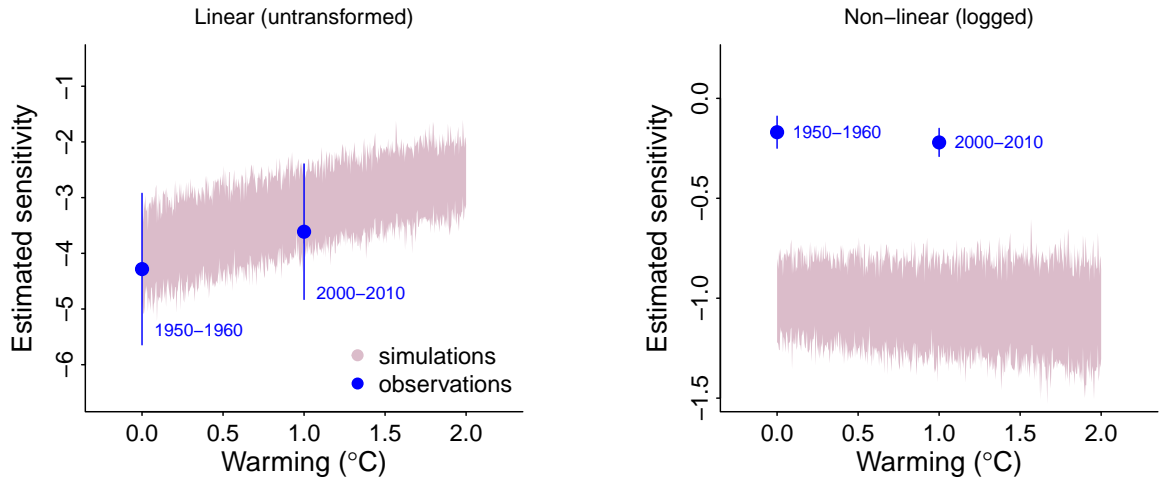


Figure 1: **Shifts in temperature sensitivities (response per °C) with warming occur when using linear models for non-linear processes.** Estimated sensitivities decline (in magnitude) with warming in simulations (shading, we simulated leafout for 45 sites as occurring after a certain thermal sum is met, simulating spring temperatures using draws from a normal(6,4) where daily temperatures increase over time, variation comes from fluctuation in the Monte Carlo simulations) with no underlying change in the biological process when sensitivities were estimated with linear regression (left). 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 (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 Information for a discussion of why estimated sensitivities are -1 in simulations in non-linear models.

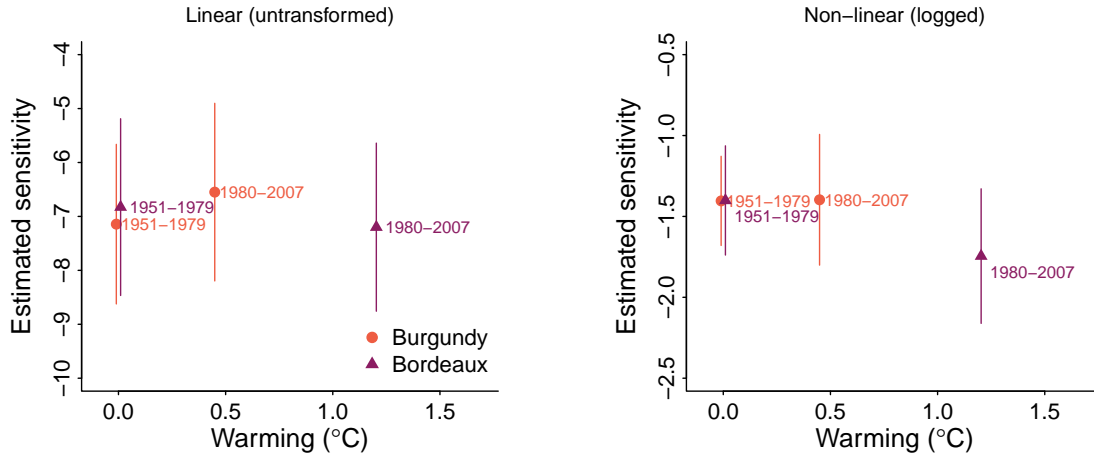


Figure 2: **Estimates of temperature sensitivities (response per °C) using linear (left) and non-linear (right) models of long-term harvest data from two major French winegrowing regions.** Temperature sensitivity of data from Burgundy declines with warming when estimated with linear regression (left). 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).