

The illusion of declining temperature sensitivity with warming

OR A simple explanation for declining temperature sensitivity with warming

E. M. Wolkovich^{1,a}, C. J. Chamberlain², D. M. Buonaiuto²,
A. K. Ettinger³, I. Morales-Castilla⁴ [Auerbach & Gelman]

January 10, 2020

**Authorship order is not set.

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

²Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, Massachusetts, USA

³TNC, USA

⁴Department of Life Sciences, University of Alcalà CTRA N-II, KM., 33,600, 28802, Alcalà de Henares, Spain

^aCorresponding author.

1 Main text

Abstract

The concept of temperature sensitivity is fundamental to many disciplines, especially in biology, where temperature determines the rate of diverse plant, animal and ecosystem processes. Recently, a growing body of literature has found declining temperature sensitivities with global warming (Fu et al., 2015; Güsewell et al., 2017; Dai et al., 2019). Such declines are predicted if warming causes fundamental shifts in underlying biological processes, but to date researchers have not conclusively documented changes in the underlying biology. Here we show a far more simple explanation for observed declining sensitivities: the use of linear methods to describe non-linear temperature responses. Simple corrections for the non-linearity of temperature response in simulated (and probably real—working on that) data remove the apparent decline. By accelerating biological time climate change thus makes methods and approaches that may work in stationary systems problematic for inferring mechanism from measurements today.

Climate change has already reshaped biological processes around the globe, with shifts in the timing of major life history events (phenology), in carbon dynamics and other ecosystem processes (IPCC, 2014). With increasing warming, a growing body of literature has documented a suite of changes in temperature sensitivity—the magnitude of a response scaled per °C—including apparently declining responses to temperature in recent decades (Fu et al., 2015; Güsewell et al.,

2017; Piao et al., 2017; Dai et al., 2019), and more uniform sensitivities across elevation (Vitasse et al., 2018). Researchers generally suggest these shifts in temperature sensitivity are driven by fundamental shifts in underlying biological processes. For example, fundamental science suggests that warm temperatures (‘forcing’) are the main controller on many temperate phenological events (e.g., leafout, insect emergence), but cool temperatures (referred to often as ‘chilling’ and generally associated with dormancy processes) or photoperiod can also play a role, especially given warmer winters. Thus, observed declines in the temperature sensitivity of temperate plant phenology with warming are generally attributed to the increasing role of photoperiod or chilling (e.g., Fu et al., 2015; Gauzere et al., 2019). Yet, providing strong evidence of this mechanistic link is difficult given that the underlying model of exactly how these other factors control phenological events is unknown (Chuine et al., 2016), and that the cues are generally correlated in nature given long-term trends in warming (e.g., Fu et al., 2015).

Given the difficulty of providing strong evidence that shifting biology underlies shifting temperature sensitivities, a small but increasing number of studies have focused on potential statistical issues with commonly used metrics of temperature sensitivity. Studies to date have shown how shifts in temperature variance and related complexities in defining relevant temporal windows (Clark et al., 2014; Güsewell et al., 2017; Keenan et al.) can influence estimated sensitivities, but have not explained observed shifts. Importantly, all have examined sensitivities through methods based on assumptions of linearity, ignoring that many biological processes to temperature are non-linear.

Metrics of temperature sensitivity focused on shifting responses generally rely on some form of linear regression to compute a change in a quantity—days to leafout or carbon sequestered, for example—per °C. Many observed biological events, however, are the result of continuous processes that depend on temperature which are discretized into temporal units for measurement. Leafout, for example, is generally observable only after a certain thermal sum is reached, and plants will reach this threshold more quickly—in calendar time—when average daily temperatures are, for example, 15°C compared to when they are 10°C. Biologically, however, the plants require the exact same temperature sum and have not shifted their sensitivity to temperature. 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. Thus, at very low temperatures plants would never leaf out and at higher temperatures they could leaf out in only a matter of days—and sensitivities estimated from simple linear regression at these higher temperatures would appear much lower than those observed at lower temperatures (given the low variance possible for response variable). Warming acts to step on the biological accelerator, and makes the use of classic calendar time precarious.

Simple simulations of biological events observed after a certain thermal sum show that sensitivities estimated from simple linear regression will always appear to decline with warming (Fig. 1, code link). Examining the same responses using proportional change or logged variables removes the apparent decline, and yields a constant sensitivity of 1 (the expected slope given that these sensitivities are effectively include temperature as both the predictor and response variable, Nee

et al., 2005). Using alternative simulations where warming increases the required thermal sum for a biological event—a common hypothesis for declining sensitivities in spring phenological events—show declining sensitivities that cannot be corrected by adjusting response variables using proportions or logs (Fig. 2)

[Here we add what we see with the PEP 725 data.]

Inferring biological processes from statistical artifacts is not a new problem (e.g., Nee et al., 2005), but climate change provides a new challenge in discerning mechanism from measurements because it accelerates biological time over years and reshapes the spatial landscape of temperature. Before anthropogenic climate change, the use of sensitivities calculated from linear models may have been less prone to yielding notable temporal patterns. With warming declining sensitivities with higher warming should be the null model for analyses using simple linear regressions, and highlights how the nonstationarity of climate change upends methods and approaches that may work in stationary systems (Milly et al., 2008; Wolkovich et al., 2014). Attempts to use sensitivities to identify shifting biological process across space has always required caution (e.g., Phillimore et al., 2012; Tansey et al., 2017), but climate change adds further complexity.

Research inferring biological processes from differing temperature sensitivities across space and time must look beyond shifting sensitivities with warming as strong evidence. Other fields, focused on temperature sensitivity generally use approaches that avoid the issue we have outlined here, such as the use of Q_{10} in soil science. Researchers have called for more use of process-based models (Keenan et al.), which is also beneficial. But many fields, still lack the underlying mechanistic understanding to robustly develop and fit process-based models, and thus many parameters and exact model specification are still unknown (Chuine et al., 2016). Thus using more exploratory methods will remain necessary to advance science, but findings from such methods must be interrogated vigorously, confronted with multiple diverse methods of calculating similar metrics, and tested for logical outcomes. Greater use of data simulation and null models is can highlight issues and force greater focus on mechanisms.

References

- 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.
- Clark, J. S., J. Melillo, J. Mohan, and C. Salk. 2014. The seasonal timing of warming that controls onset of the growing season. *Global Change Biology* 20:1136–1145.
- 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.

- 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.
- Gauzere, J., C. Lucas, O. Ronce, H. Davi, and I. Chuine. 2019. Sensitivity analysis of tree phenology models reveals increasing sensitivity of their predictions to winter chilling temperature and photoperiod with warming climate. *Ecological Modelling* 441:108805.
- 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.
- IPCC. 2014. *Climate Change 2014: Impacts, Adaptation, and Vulnerability*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.
- Keenan, T. F., A. D. Richardson, and K. Hufkens. 2017. On quantifying the apparent temperature sensitivity of plant phenology. *New Phytologist* .
- Milly, P. C. D., J. Betancourt, M. Falkenmark, R. M. Hirsch, Z. W. Kundzewicz, D. P. Lettenmaier, and R. J. Stouffer. 2008. Climate change - stationarity is dead: Whither water management? *Science* 319:573–574.
- Nee, S., N. Colegrave, S. A. West, and A. Grafen. 2005. The illusion of invariant quantities in life histories. *Science* 309:1236–1239.
- Phillimore, A. B., S. Stalhandske, R. J. Smithers, and R. Bernard. 2012. Dissecting the contributions of plasticity and local adaptation to the phenology of a butterfly and its host plants. *AMERICAN NATURALIST* 180:655–670. Phillimore, Albert B. Stalhandske, Sandra Smithers, Richard J. Bernard, Rodolphe.
- 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.
- Tansey, C. J., J. D. Hadfield, and A. B. Phillimore. 2017. Estimating the ability of plants to plastically track temperature-mediated shifts in the spring phenological optimum. *Global Change Biology* 23:3321–3334.
- Vitasse, Y., C. Signarbieux, and Y. H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences* 115:1004–1008.
- Wolkovich, E. M., B. I. Cook, K. K. McLauchlan, and T. J. Davies. 2014. Temporal ecology in the anthropocene. *Ecology Letters* 17:1365–1379. Cook, Benjamin/H-2265-2012.

2 Outline & notes

Need to work on this, notes to date on here.

Meeting with Jonathan Auerbach & Andrew Gelman on 18 December 2019:

Fundamental issue is that we have a non-linear relationship ($y = 1/x$) being described by a linear function ($y = x$), where x is the mean temp and 1 could be the GDD. The time until you reach a threshold is inversely proportional to the speed you go at. So, at very low temperatures plants would (theoretically) never leaf out and at 200 C days it would take one day.

The classic algebra example (they tell me) is how long does it take to drive 200 miles? It depends on your miles per hour. (Side note by Lizzie while typing up these notes: the speed analogy is sort of nice, climate change is stepping on the accelerator, making this algebra problem relevant.)

- The artifact comes from the mean getting larger while the variance goes down (I think, I may have this noted wrong, but it's about the mean relative to the variance, not just the variance or the mean). If you make the variance scale with the mean you will see the issue go away (though Andrew pointed out this should be done on the SD scale, not the var).
- “The statistical artifact is that fitting a linear regression requires linearity” said Jonathan Auerbach.
- If this was all simple, we could fix it two ways: percent scale (decline relative to some base C temp) or log both axes. (Note from Lizzie: but we don't know when to start accumulating so not sure how this works, though Jonathan seemed to have insight into this.)
- An example of inferring process from an artifact is regression to the mean, though Andrew pointed out regression to the mean is more complicated compared to this as regression to the mean is a statistical issue and this is just a deterministic reality.
- Convexity in economics has had similar problems to this.

3 Tasks, milestones etc.

- Finish minimal analyses we think we need:
 - Produce simulated data where chilling is not met (Lizzie has notes on this below `enddocument` command ... (bucket model).
 - Do sliding windows for ... BETPEN (done) and FAGSYL from PEP725 and for simulated data.
- Chat with Rob Guy for foundational papers that many events like leafout are based on temperature accumulations.
- Review the literature

- Cat did some of this: see `ospree/analyses/bb_analysis/pep_sims/pepsimslitreview.txt`
- Review beyond phenology?
- Outline the paper
- Decide on targeted journals
- Write the paper
- Submit the paper

4 Literature notes

Sagarin 2001: False estimates of the advance of spring (leap year issues).

I noticed as you go back to 2014 and before in my ISI searches, you get a lot of soil respiration lit. And in that literature they use Q_{10} for temperature sensitivities, “[t]he temperature sensitivity of soil respiration is often expressed as the Q_{10} value; that is, the factor by which soil respiration increases by a 10C increase in temperature (e.g., Kirschbaum, 1995; Van’t Hoff, 1898),” which would avoid a good dose of the issue we’re seeing.

Shen et al. 2014 shows earlier-season vegetation more temperature-sensitive, which is the same artifact. Do we want to work this in?

Figures

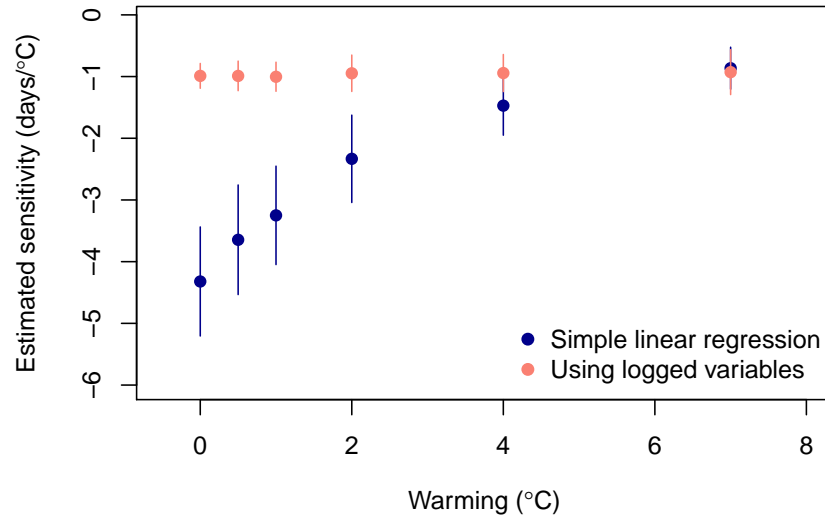


Figure 1: **Declining sensitivities with warming explained by using linear regression for non-linear processes.** We found declines in estimated sensitivities with warming from simulations with no underlying change in the biological process when sensitivities were estimated with simple linear regression (“Simple linear regressions”). This spurious decline can be removed by performing the regression on logged predictor and response variables (“Using logged variables”).

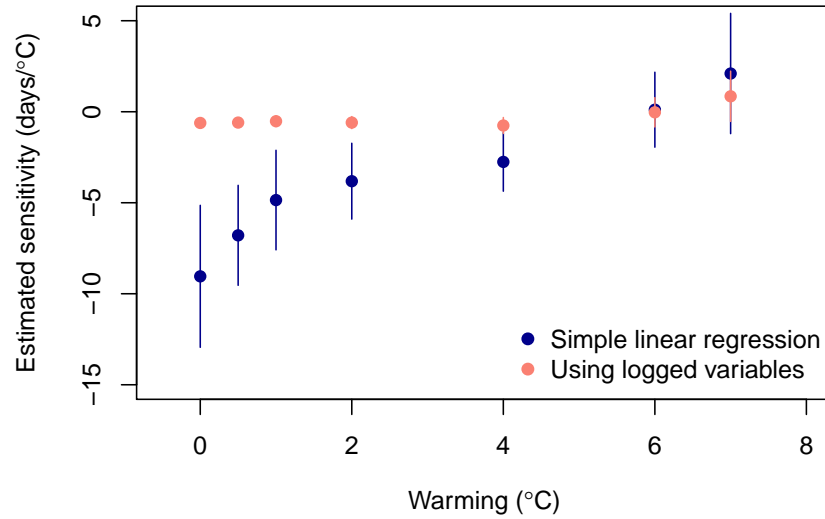


Figure 2: **Truly declining sensitivities remain even after correction.** Here we used simulations where the biological process shifts at moderate warming levels (basically I made the GDD increase when chilling was low, see the code).