The illusion of declining temperature sensitivity with warming OR A simple explanation for declining temperature sensitivity with warming

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Abstract

The concept of temperature sensitivity is fundamental across scientific disciplines, especially in biology, where temperature determines the rate of many 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 present a simpler 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 data, and long-term phenological data from Europe, remove the apparent decline. By accelerating biological time climate change makes methods and approaches that may suffice in stationary systems problematic for inferring mechanism from measurements today.

1 Main text

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 often suggest these changes in temperature sensitivity are driven by important 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., 2020) can influence estimated sensitivities, but have not explained observed shifts. Importantly, all have examined sensitivities through methods based on assumptions of linearity, generally relying on some form of linear regression to compute a change in a quantity—days to leafout or carbon sequestered, for example—per °C—thus ignoring that many biological processes to temperature are non-linear.

Many observed biological events 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 warmer. 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 of the 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, S2, 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, see 'Model of leafout timing' in SI and 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—yields declining sensitivities that remain after adjusting response variables using proportions or logs (Fig. S3).

Comparing these simulation results with long-term leafout data from Europe, we find little evidence for declining sensitivities with warming (Figs. 1, S4, S5). A 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). Across both species, there are large declines in the variance of leafout dates—(declines of roughly 50%, see Tables S1-S2), as expected if warming accelerates towards a thermal threshold that triggers leafout (and in contrast to predictions from shifting biology, see Ford et al., 2016).

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., 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 Q_{10} in soil science. Researchers have called for more use of process-based models (Keenan et al., 2020), which is also beneficial. But many fields, still lack the underlying mechanistic understanding to robustly develop and fit process-based models, with many parameters and aspects of the model specification unknown (Chuine et al., 2016). Thus using more exploratory methods will remain necessary to advance science, but findings from such methods must be interrogated, confronted with multiple diverse methods of calculating similar metrics, and tested for logical outcomes. Greater use of data simulation and null models can highlight issues and bring greater focus on mechanisms.

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2 Tasks, milestones etc.

- Turn this into Sweave and add in-text refs for the sensitivities.
- Dan, please help check refs (did I use the correct Dai one? They seem very different!)

Figures

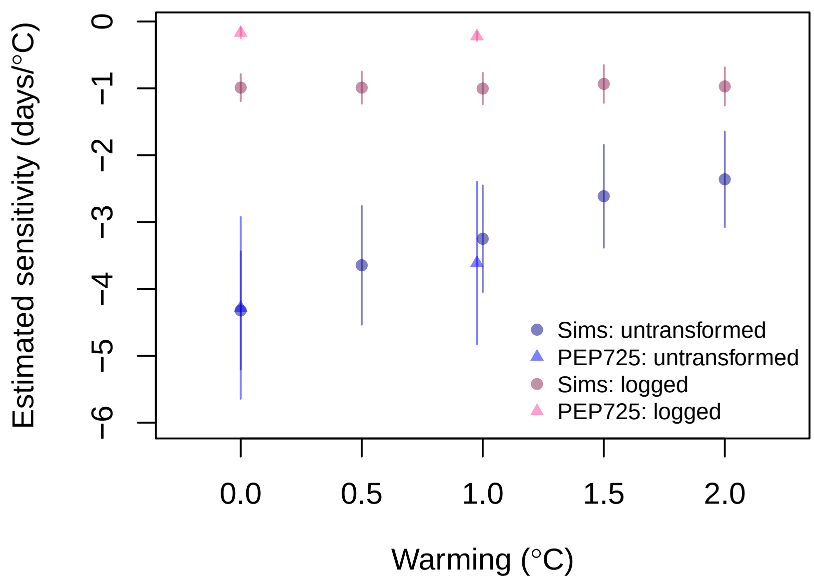

Figure 1: **Sensitivities with warming occur when using linear regression for a non-linear process.** We found declines in estimated sensitivities with warming from simulations with no underlying change in the biological process when sensitivities were estimated with simple linear regression ('Sims: untransformed,' estimated across 45 sites with a base temperature of $\mathcal{N}(6, 4)$). This decline disappears when performing the regression on logged predictor and response variables ('Sims: logged'). Such issues may underlie declining sensitivities calculated from long-term phenological data, such as from PEP725 observations. 'PEP: untransformed' shows a declining sensitivity with warming, while 'PEP725: logged' shows a similar sensitivity with warming. Estimates of sensitivities from logged variables were generally much lower than -1, suggesting other factors or a better metric of temperature underlie leafout dates. We used sites with leafout data for *Betula pendula* from PEP725 from 1950-1960 versus 2000-2010 (45 sites). We show means ± standard deviations of regressions across sites for all points.