

A simple explanation for declining temperature sensitivity with warming

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Abstract

Temperature sensitivity—the magnitude of a biological response per °C—is fundamental across scientific disciplines, especially biology, where temperature determines the rate of many plant, animal and ecosystem processes. Recently, a growing body of literature has found temperature sensitivities decline as temperatures rise with global warming (Fu et al., 2015; Güsewell et al., 2017; Piao et al., 2017; Dai et al., 2019). These declines are generally attributed to fundamental shifts in underlying biological processes caused by warming, yet to date there is no clear evidence of biological changes. Here we present a simple explanation for observed declining sensitivities: the use of linear models to estimate 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. Our results show that rising temperatures combined with linear models based on calendar time are sufficient to explain 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), in carbon dynamics and other ecosystem processes (IPCC, 2014). With rising temperatures, a growing body of literature has documented changes in temperature sensitivity—the magnitude of a biological response scaled per $^{\circ}\text{C}$ —including declining responses to temperature over time (Fu et al., 2015; Güsewell et al., 2017; Piao et al., 2017; Dai et al., 2019), more uniform sensitivities across elevation (Vitasse et al., 2018), and lower sensitivities in warmer, urban areas (Meng et al., 2020).

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 (Piao et al., 2017), or a relative decline the importance of warm spring temperatures for spring phenological events (e.g., leafout, insect emergence) in the temperate zone, as other environmental triggers (e.g., winter temperatures that determine ‘chilling’ or photoperiod) play a larger role (Fu et al., 2015; Meng et al., 2020). Yet, despite an increase in studies document declining or shifting temperature sensitivities, none have provided strong evidence of the biological mechanisms underlying these changes (e.g., Fu et al., 2015; Meng et al., 2020).

Alongside efforts to identify the biology that may underlie shifting temperature sensitivities, a small but increasing number of studies have focused on potential statistical issues in common metrics of temperature sensitivity. These studies have highlighted important complexities that can influence estimated sensitivities (Clark et al., 2014; Güsewell et al., 2017; Keenan et al., 2020). They have generally not, however, explained observed shifts. And 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 $^{\circ}\text{C}$ —thus ignoring that many biological responses 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 may require the same temperature sum and have not fundamentally 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—yet sensitivities estimated from simple linear regression at higher (warmer) 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, S3, 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 effectively include temperature as both the predictor and response variable, see ‘Model of leafout timing’ in SI). 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. S4).

Comparing these simulation results with long-term leafout data from Europe, we find little evidence for declining sensitivities with warming (Figs. 1, S5, S6). 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). 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 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 must look beyond shifting sensitivities with warming as strong evidence. Other fields focused on temperature sensitivity often use approaches that acknowledge the non-linearity of responses (e.g., Yuste et al., 2004). Researchers have called for greater use of process-based models (Keenan et al., 2020), which are beneficial, but rely themselves on exploratory methods and descriptive analyses for progress (Chuine et al., 2016). The challenge then is to interrogate the implicit and explicit models used to interpret data summaries across differing temperature regimes, including developing null expectations based on biological time.

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Figures

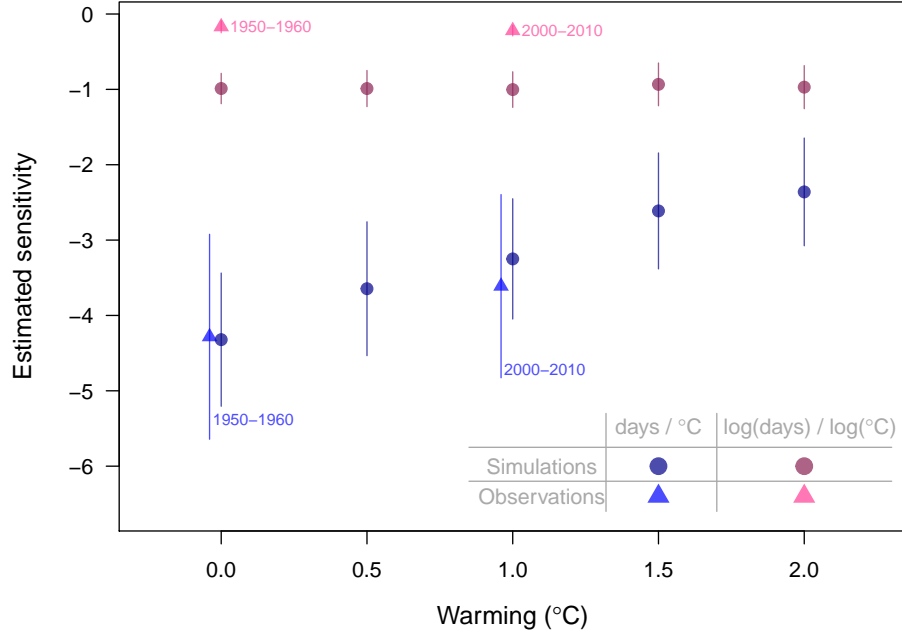


Figure 1: **Shifts in temperature sensitivities with warming occur when using linear models for non-linear processes.** Estimated sensitivities decline with warming in simulations with no underlying change in the biological process when sensitivities were estimated with simple linear regression (estimated 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. 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. Symbols and lines represent means \pm standard deviations of regressions across sites.