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 °C. Many studies have found declining responses to temperature in recent decades (Fu et al., 2015; Güsewell et al., 2017; Piao et al., 2017; Dai et al., 2019), and some have reported 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 decline in the relative importance of warm spring temperatures for spring phenological events (e.g., leafout, insect emergence) in the temperate zone, as other evironmental triggers (e.g., winter temperatures that determine 'chilling') play a larger role (Fu et al., 2015; Meng et al., 2020). Yet, despite an increase in studies reporting declining or shifting temperature sensitivites, none have provided strong evidence of the biological mechanisms underlying these changes (e.g., Fu et al., 2015; Meng et al., 2020). The missing mechanisms may be hidden in the data: environmental factors moderate biological processes in complex ways (Chuine et al., 2016; Güsewell et al., 2017), are strongly correlated in nature (e.g., Fu et al., 2015), and temperature variance shifts over time and space (Keenan et al., 2020).

Here, we suggest a simpler alternative expanation: incorrect modeling of how biological processes respond 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 and with simulated and empirical data, how the use of linear methods for non-linear processes can easily 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. Leafout, for example, generally occurs 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. 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 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 makes the use of classic calendar time precarious.

We derive the exact relationship between daily temperature and leafout theoretically using a first-hitting-time model, which describes the first time a random process hits a threshold (see 'A first-hitting-time model of leafout' in SI). Our model holds the temperature threshold for leafout constant, thus the mechanism by which temperature produces leaves does not change. Despite the fact that the underlying model does not change mechansitically, it shows 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 the correction for non-linearity completely explains the decline in temperature sensitivity (Fig. 1, S2, code link). 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 correcting for non-linearity (Fig. S3).

Comparing these results with 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 Ford et al., 2016).

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. In fact, when our model holds, declining sensitivity with rising temperatures should be the null hypothesis of any analysis of temperature sensitivity based on linear regression or similar methods.

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 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., 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 we use to interpret data summaries, and to develop null expectations for both biological and calendar time.

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Figures

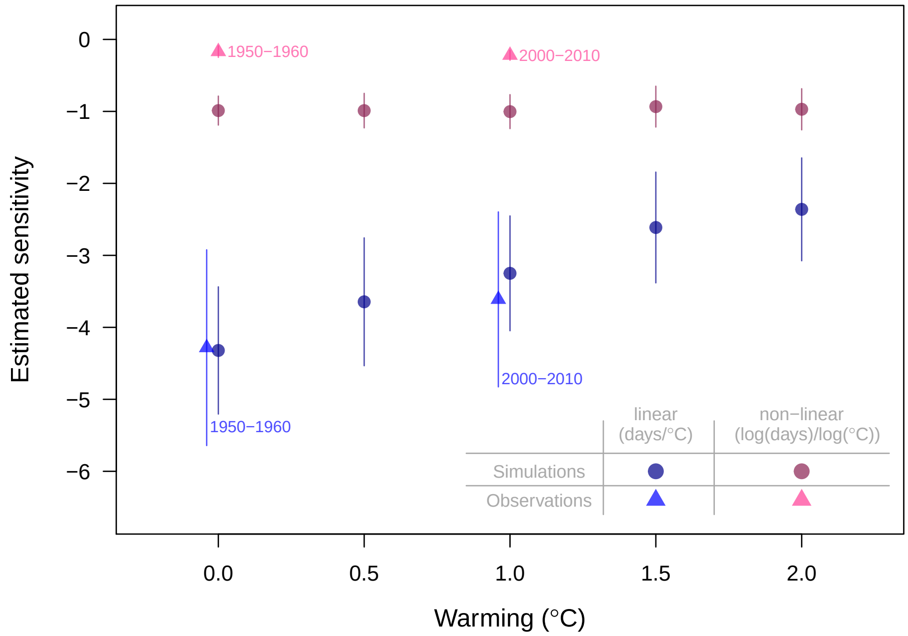

Figure 1: **Shifts in temperature sensitivities with warming occur when using linear models for non-linear processes.** Estimated sensitivities decline with warming in simulations with no underlying change in the biological process when sensitivities were estimated with linear regression (estimated across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