

A simple explanation for declining temperature sensitivity with warming

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Abstract

Recently a growing body of literature has reported declining phenological sensitivities (Δ days per $^{\circ}\text{C}$) with higher temperatures. Such results suggest that climate change is already reshaping fundamental biological processes. 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 response consistently remove the apparent decline. Our results suggest that current methods may undermine efforts to identify when and how warming will reshape biological processes.

1 Main text

Climate change has reshaped biological processes around the globe, with shifts in the timing of major life history events (phenology), 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) or lower sensitivities in warmer, urban areas (Meng et al., 2020).

Most studies attribute changes in temperature sensitivity to shifts in underlying biological processes. 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 (Fu et al., 2015; Meng et al., 2020), as other environmental triggers (e.g., winter temperatures that determine ‘chilling’) play a larger role. Yet, despite an increase in studies reporting 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). 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 propose a simpler alternative explanation: the use of linear models for non-linear responses 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, especially events, are non-linear (Fig. 1).

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 (Valentine, 1983; Lechowicz, 1984; Kramer, 2012). 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.

Temperature determines the speed of many biological processes (Bonan and Sirois, 1992; Hinrichsen, 2009; 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. Warming acts to step on the biological accelerator, producing shifts in estimates when non-linear responses are modeled as linear. Using a simple model where leafout occurs after a thermal sum is met we hold the temperature threshold for leafout constant (Hunter and Lechowicz, 1992; Zohner et al., 2020) and find declining sensitivities as measured in days per °C—with warming (see ‘A first-hitting-time model of leafout’ in Supplementary Information for a full derivation of the statistical properties of this simple stochastic model). 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. We argue that this simple thermal sum model should be the null model for studies of biological events across different temperatures.

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. 2-3, ??, 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. 2, ??, ??). 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

60 regression (-0.17 versus -0.22). Moreover, the variance of the leafout dates declines as temper-
61 atures rise—(declines of roughly 50%, see Tables ??-??), which is expected under our model
62 as warming accelerates towards the thermal threshold that triggers leafout (and in contrast to
63 predictions from changing mechanisms, see Ford et al., 2016).

64
65 Fundamentally rising temperature should alter many biological processes, making robust meth-
66 ods for identifying these changes critical. In spring plant phenology, where declining sensitivities
67 are often reported (Fu et al., 2015; Piao et al., 2017; Dai et al., 2019), warming may increase
68 the role of ‘chilling’ (determined mainly by winter temperatures) and daylength (Laube et al.,
69 2014; Zohner et al., 2016)—potentially increasing the thermal sum required for leafout at lower
70 values of these cues (Polgar et al., 2014; Zohner et al., 2017; Flynn and Wolkovich, 2018). Ad-
71 justing our simulations to match this model yielded shifts in sensitivities with warming. Unlike
72 a model with no underlying biological change, however, after correcting for non-linearity, the
73 shifts in sensitivities remained and they occurred in step with the biological change (Fig. ??a,
74 c). In contrast, sensitivities estimated from a linear model showed shifts across the entire range
75 of warming, well before the simulated biological change (Fig. ??a, c). Further, we found that
76 an increase in the thermal sum required for leafout should yield larger in magnitude tempera-
77 ture sensitivities, not smaller, as is often expected (e.g., Fu et al., 2015), thus highlighting the
78 complexity of identifying what trends to expect in sensitivities with warming (see ‘Simulations
79 of common hypotheses for declining sensitivity’ in Supplementary Information for an extended
80 discussion).

81
82 Our results show that rising temperatures are sufficient to explain declining temperature sen-
83 sitivity. It is not necessary to invoke changes to the mechanisms that underlie the biological
84 processes themselves. Our results provide a simpler explanation for observations of declining
85 temperature sensitivities, but do not rule out that important changes in biological processes may
86 underlie such declines. Instead, our results highlight how the use of linear models may make
87 identifying when—and why—warming alters underlying biology far more difficult.

88
89 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 often include non-linear responses to temperature, 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 that apply across biological and calendar time.

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

List of Supplementary Information:

A first-hitting-time model of leafout

Simulations of common hypotheses for declining sensitivity

Methods & results using long-term empirical data (PEP725)

Table S1-S2

Fig S1-S7

Figures

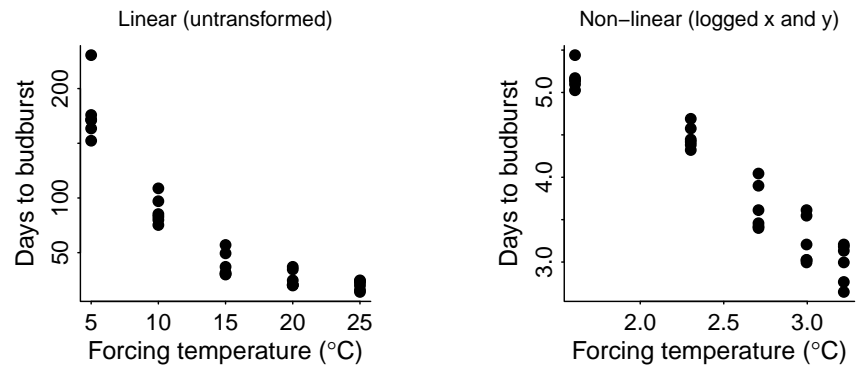


Figure 1: **Controlled experiments show non-linear response to temperature** from walnut trees *Juglans regia*, single-node cuttings at 16 hour photoperiod sampled on 29 November 2008 Charrier et al. (2011)

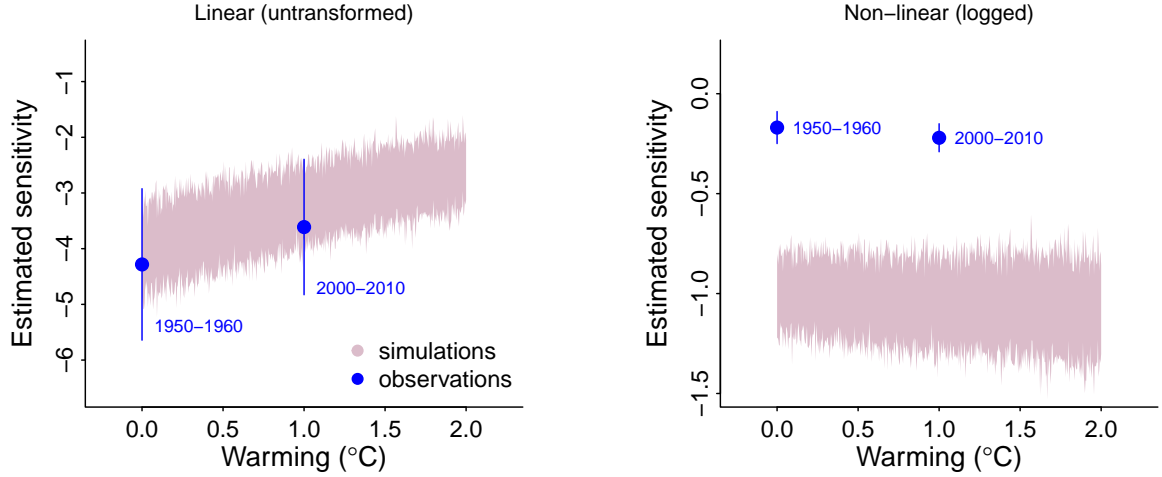


Figure 2: **Shifts in temperature sensitivities (response per °C) with warming occur when using linear models for non-linear processes.** Estimated sensitivities decline (in magnitude) with warming in simulations (shading, estimated across 45 sites with a base temperature of normal(6,4), variation comes 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 or lower in non-linear models.

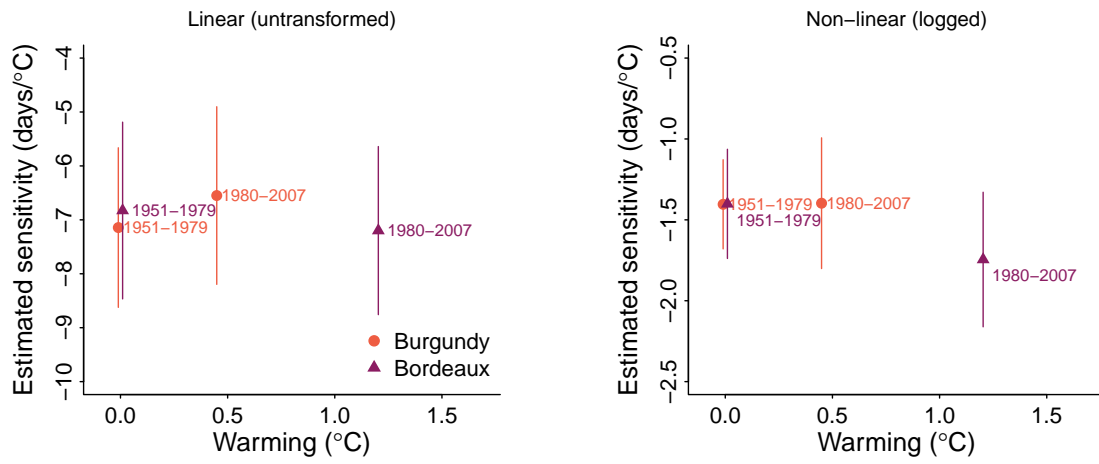


Figure 3: Estimates of temperature sensitivities (response per °C) using linear (left) and non-linear (right) models from long-term harvest data from two major French winegrowing regions. Data from ?