

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 responses 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 (Fig. 1, Kramer, 2012). Biologically, however, the plants require the same temperature sum to trigger leafout at high and low average temperatures. 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; 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. Using a simple model where leafout occurs after a thermal sum is met we can hold the temperature threshold for leafout constant (Hunter and Lechowicz, 1992; Zohner et al., 2020) and examine how estimated sensitivities (measured in days per °C using linear regression) shift with warming. In this simple thermal sum model (which we argue is the null model for studies of biological events across different temperatures, Fig. 1 and Dijkhuis, 1956; Lindsey and Newman, 1956; Zohner et al., 2020) we find declining sensitivities with warming (Fig S2; see ‘A first-hitting-time model of leafout’ in Supplementary Information for a full derivation of the statistical properties). 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.

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, S2, 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 regression (-0.17 ver-

60 sus -0.22). Moreover, the variance of the leafout dates declines as temperatures rise—(declines
61 of roughly 50%, see Tables S1-S2), which is expected under our model as warming accelerates
62 towards the thermal threshold that triggers leafout (and in contrast to predictions from chang-
63 ing mechanisms, see Ford et al., 2016). A similar apparent decline in winegrape harvest data in
64 Burgundy disappears with a log transformation (estimates of -7.1 days/°C to -6.5 days/°C from
65 1951-1979 compared to 1980-2007 are both estimated as -1.4 using log-log regression), and an
66 increase in sensitivity in Bordeaux, which has warmed substantially, becomes larger in relative
67 magnitude (-6.8 days/°C from 1951-1979 compared to -7.2 from 1980-2007 become -1.4 and -1.7,
68 respectively, using log-log regression).

69
70 Fundamentally rising temperature should alter many biological processes, making robust meth-
71 ods for identifying these changes critical. In spring plant phenology, where declining sensitivities
72 are often reported (Fu et al., 2015; Piao et al., 2017; Dai et al., 2019), warming may increase the
73 role of ‘chilling’ (determined mainly by winter temperatures) and daylength (Laube et al., 2014;
74 Zohner et al., 2016)—potentially increasing the thermal sum required for leafout at lower values
75 of these cues (Polgar et al., 2014; Zohner et al., 2017). Adjusting our simulations to match this
76 model yielded shifts in sensitivities with warming. After correcting for non-linearity, the shifts
77 in sensitivities remained and they occurred in step with the biological change (Fig. S4a, c).
78 In contrast, sensitivities estimated from a linear model showed shifts across the entire range of
79 warming, well before the simulated biological change (Fig. S4a, c). Further, we found that an
80 increase in the thermal sum required for leafout should yield larger in magnitude temperature
81 sensitivities, not smaller, as is often expected (e.g., Fu et al., 2015). These results highlight the
82 complexity of identifying what trends to expect in sensitivities with warming (see ‘Simulations
83 of common hypotheses for declining sensitivity’ in Supplementary Information for an extended
84 discussion), and suggest that without useful null models we may misinterpret when biological
85 change occurs.

86
87 Inferring biological processes from statistical artifacts is not a new problem (e.g., Nee et al.,
88 2005), but climate change provides a new challenge in discerning mechanism from measurements
89 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 process-based model themselves rely 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 Cook and Wolkovich (2016), which is available through the NOAA Paleoclimate Archive. All data are freely available via the links.

Methods:

We simulate leafout as occurring after a certain thermal sum is met (simulating spring temperatures using draws from a normal distribution where daily temperatures increase over time)—a first-hitting-time model (see ‘A first-hitting-time model of leafout’ in Supplementary Information for a full derivation of the statistical properties of this simple model). Across Fig. 2 and in the supplement (Fig. S1-S4) we show a variety of different thermal sums and underlying temperatures, all yielding the non-linear relationship in estimated sensitivity with warming.

We draw on three empirical data sources: (1) data from a controlled experiment across a wide temperature range (Charrier et al., 2011) (selected as it is the only study with multiple observations across a wide range of forcing temperatures in fully controlled settings from a recent meta-analysis of all published spring phenology controlled environment studies, OSPREE) and long-term phenology data from two major sources, (2) PEP 725 phenological data and (3) long-term records of winegrape harvests from two main regions in France. We selected these datasets because they are relatively long-term, complete, public, have been widely used in the past and have paired climate data (see Data & Code Availability). For both datasets we estimated the sensitivity as a simple linear regression of leafout or harvest day of year versus the mean daily temperature over a temperature window (see ‘Additional methods & results from long-term empirical data’ for further details), or a simple linear regression using logged versions of these predictors. Code for these analyses are available via github (<https://github.com/temporalecologylab/labgit/tree/master/projects/decsenspost>).

List of Supplementary Information:

A first-hitting-time model of leafout

198 Simulations of common hypotheses for declining sensitivity
199 Additional methods & results from long-term empirical data
200 Table S1-S2
201 Fig S1-S4
202

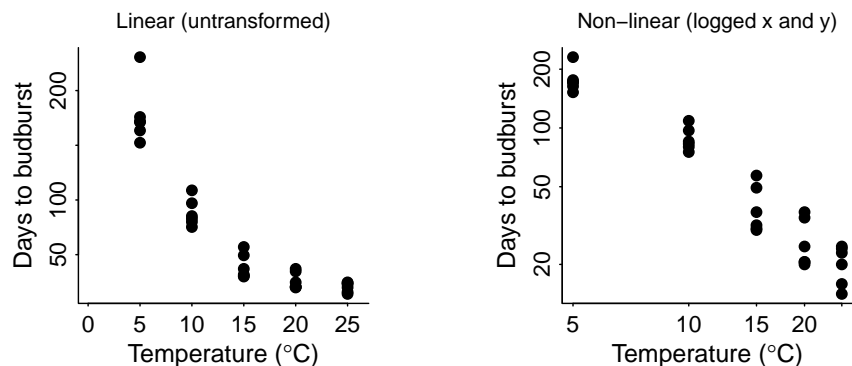


Figure 1: **Controlled experiments across a wide temperature range show a non-linear response to temperature.** Here we use data from Charrier et al. (2011), one of the few studies covering a wide range of temperatures in a fully controlled experiment. Data are from a growth chamber experiment of tree branch cuttings of walnut trees (*Juglans regia*), taken from the field on 29 January 2009 and exposed to five different temperatures with a 16 hour photoperiod.

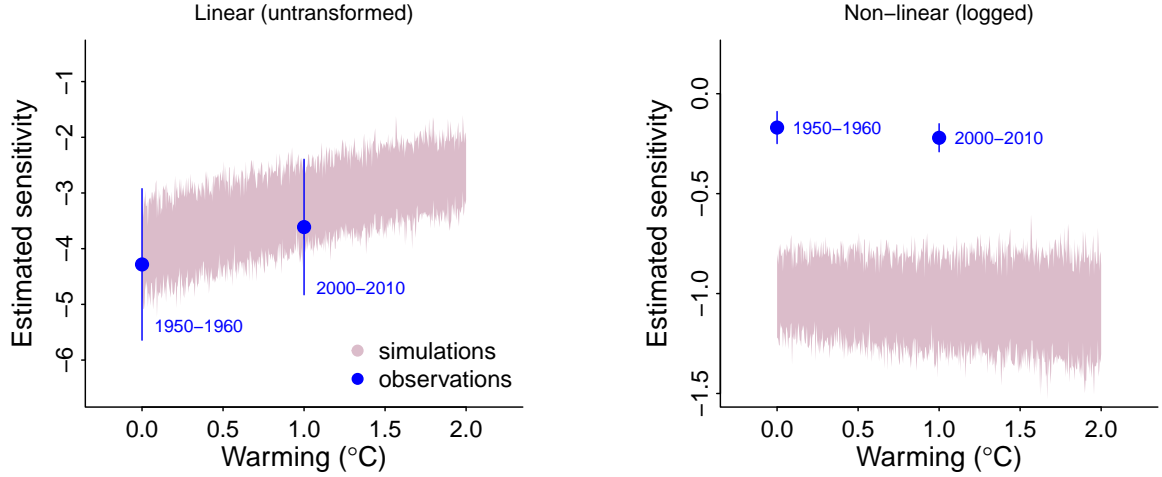


Figure 2: **Shifts in temperature sensitivities (response per °C) with warming occur when using linear models for non-linear processes.** Estimated sensitivities decline (in magnitude) with warming in simulations (shading, estimated across 45 sites with a base temperature of normal(6,4), variation comes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

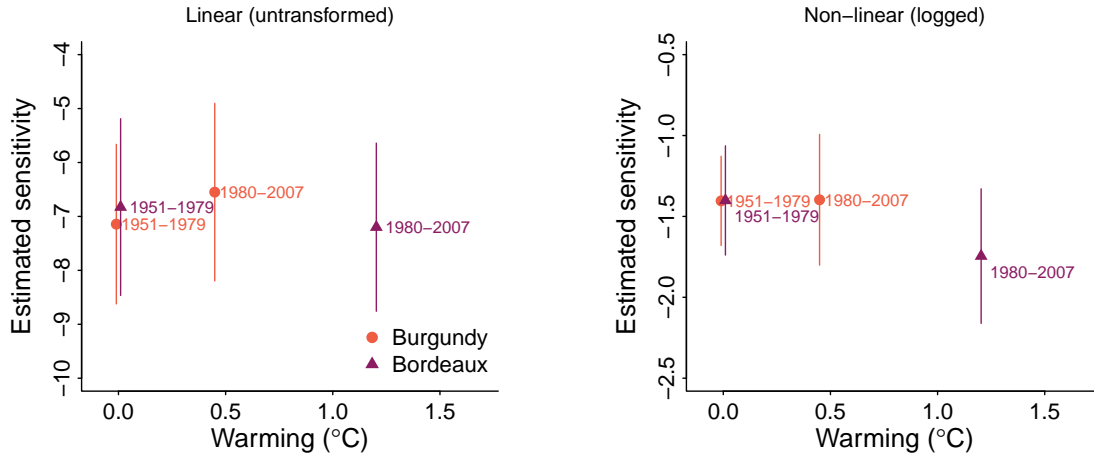


Figure 3: **Estimates of temperature sensitivities (response per °C) using linear (left) and non-linear (right) models from long-term harvest data from two major French winegrowing regions.** Temperature sensitivity of data from Burgunday declines with warming when estimated with linear regression (left). This decline disappears when performing the regression on logged predictor and response variables, and increases the relative magnitude of an increase in sensitivity estimated from data from Bordeaux (right). Harvest and temperature data from Cook and Wolkovich (2016).