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PERSPECTIVE

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A simple explanation for declining temperature sensitivity with warming

Abstract

Recently, multiple studies have reported declining phenological sensitivities (Δ days per ℃) with higher temperatures. Such observations have been used to suggest climate change is reshaping biological processes, with major implications for forecasts of future change. Here, we show that these results may simply be the outcome of using linear models to estimate nonlinear temperature responses, specifically for events that occur after a cumulative thermal threshold is met—a common model for many biological events. Corrections for the nonlinearity of temperature responses consistently remove the apparent decline. Our results show that rising temperatures combined with linear estimates based on calendar time produce the observations of declining sensitivity—without any shift in the underlying biology. Current methods may thus undermine efforts to identify when and how warming will reshape biological processes.

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. With rising temperatures, a growing body of literature has documented changes in temperature sensitivity—the magnitude of a biological response scaled per ℃. Many studies have found declining responses to temperature in recent decades (Fu et al., 2015; Piao et al., 2017) 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 that 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), 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 nonlinear 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 ℃, thus ignoring that many biological responses to temperature, especially events, are nonlinear (Figure S1).

Many observed biological responses are the result of continuous nonlinear 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, and plants will reach this threshold more quickly—in calendar time—when average daily temperatures are warmer (Figure S1, 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. 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 (Zohner et al., 2020) and examine how estimated sensitivities (measured in days per ℃ 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, Figure S1 and Kramer, 2012; Zohner et al., 2020), we find declining sensitivities with warming (Figure S4; see "A first-hitting-time model of leafout" in Supporting 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 nonlinearity using the transformation for an inverse relationship (log transformation) removes apparent declines in temperature sensitivity in long-term leafout and harvest data (Figure 1; Figures S2 and S4, code link). In empirical long-term tree leafout data from Europe, correcting for nonlinearity in responses produces little evidence for declining sensitivities with warming (Figure 1). An apparent decline in sensitivity for silver birch (*Betula pendula*) from −4.3 days/℃ to −3.6 days/℃ from 1950 to 1960 compared to 2000–2010 disappears using a log–log regression (−0.17 vs. −0.22). Moreover, the variance of the leafout dates declines as temperatures rise—(declines of roughly 50%, see Tables S1–S2), which is expected under our model as warming accelerates toward the thermal threshold that triggers leafout (and in contrast to predictions from changing mechanisms, see Ford et al., 2016). A similar apparent decline in winegrape harvest data in Burgundy disappears with a log transformation (estimates of −7.1 days/℃ to −6.5 days/℃ from 1951 to 1979 compared to 1980–2007 are both estimated as −1.4 using log–log regression), and an increase in sensitivity in Bordeaux, which has warmed substantially, becomes larger in relative magnitude (−6.8 days/℃ from 1951 to 1979 compared to −7.2 from 1980 to 2007 become −1.4 and −1.7, respectively, using log–log regression).

Fundamentally rising temperatures should alter many biological processes, making robust methods for identifying these changes critical. In spring plant phenology, where declining sensitivities are often reported (Fu et al., 2015; Piao et al., 2017), warming may increase the role of "chilling" (determined mainly by winter temperatures) and daylength—potentially increasing the thermal sum required for leafout at lower values of these cues (Laube et al., 2014). Adjusting our simulations to match this model yielded shifts in sensitivities with warming. After correcting for nonlinearity, the shifts in sensitivities remained and they occurred in step with the biological change (Figure S6a,c). In contrast, sensitivities estimated from a linear model showed shifts across the entire range of warming, well before the simulated biological change (Figure S6a,c). Furthermore, we found that an increase in the thermal sum required for leafout should yield larger in magnitude temperature sensitivities, not smaller, as is often expected (e.g., Fu et al., 2015). These results highlight the complexity of identifying what trends to expect in sensitivities with warming, and suggest that without useful null models, we may misinterpret when biological change occurs.

1 | CONCLUSION

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 nonlinearity of responses (e.g., Q_{10}). Researchers have called for greater use of process-based models (Keenan et al., 2020), which often include nonlinear responses to temperature, but process-based models 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.

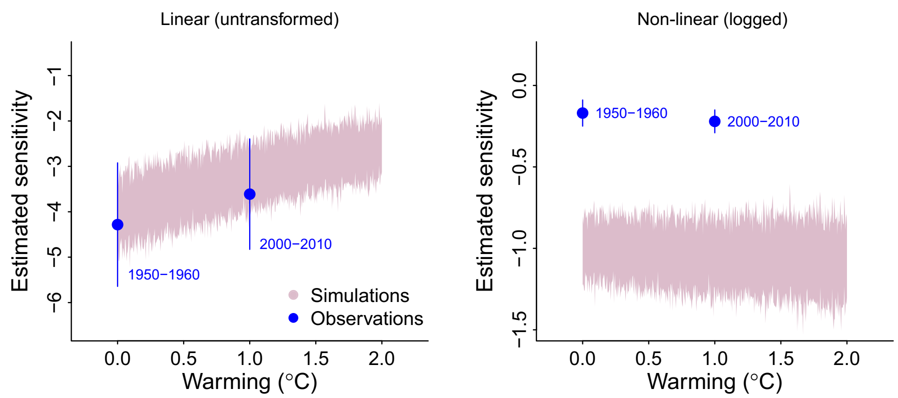

FIGURE 1 Shifts in temperature sensitivities (response per ℃) with warming occur when using linear models for nonlinear processes. Estimated sensitivities decline (in magnitude) with warming in simulations (shading) with no underlying change in the biological process when sensitivities were estimated with linear regression (left; we simulated leafout for 45 sites as occurring after a certain thermal sum is met, simulating spring temperatures using draws from a normal (6,4), variation comes from fluctuation in the Monte Carlo simulations). 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 for the 45 sites that had complete data from 1950 to 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 ± standard deviations of regressions across sites. See Data S1 for a discussion of why estimated sensitivities are −1 in simulations in nonlinear models

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DATA AVAILABILITY STATEMENT

Code for simulations, empirical analysis, and plots is provided here: https://github.com/temporalecologylab/labgit/tree/master/projects/decsenspost. For empirical examples, data are available through the OSPREE database (https://knb.ecoinformatics.org), PEP 725 phenological data (http://www.pep725.eu/data.php), E-OBS climate data (https://surfobs.climate.copernicus.eu/dataaccess/access_eobs.php), and NOAA Paleoclimate Archive (https://www.ncdc.noaa.gov/data-access/paleoclimatology-data/datasets). All data are freely available via the links.

AUTHOR CONTRIBUTIONS

All authors contributed to idea development and editing the manuscript. In addition, EMW wrote the manuscript, developed the simulations, and made the figures; JA formalized the first-hitting time model and its derivations, CJC did much of the PEP725 analysis.

E. M. Wolkovich[1]
J. Auerbach[2]
C. J. Chamberlain[3]
D. M. Buonaiuto[3]
A. K. Ettinger[4]
I. Morales-Castilla[5]
A. Gelman[2]

[1]*Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada*
[2]*Department of Statistics, Columbia University, New York, NY, USA*
[3]*Department of Organismic and Evolutionary Biology, Harvard University, Cambridge, MA, USA*
[4]*The Nature Conservancy in Washington, Seattle, WA, USA*
[5]*Global Change Ecology and Evolution Group-GloCEE, Department of Life Sciences, University of Alcalá, Madrid, Spain*

Correspondence
E. M. Wolkovich, Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, Vancouver, BC, Canada.
Email: e.wolkovich@ubc.ca

ORCID

E. M. Wolkovich https://orcid.org/0000-0001-7653-893X
C. J. Chamberlain https://orcid.org/0000-0001-5495-3219
D. M. Buonaiuto https://orcid.org/0000-0003-4022-2591
A. K. Ettinger https://orcid.org/0000-0002-6228-6732

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.