July 9, 2019

Dear Dr. Sudgen:

Please consider our paper, entitled "Winter temperatures dominate spring phenological responses to warming" for publication as a "Report" in *Science*.

The timing of spring phenology (e.g., budburst, leafout) in woody plants is critical to plant fitness, shapes plant and animal communities, and affects wide-ranging ecosystem services from crop productivity to carbon sequestration. Advances in budburst are some of the most reported—and tangible—biological impacts of climate change, garnering great research and public interest.

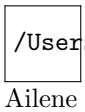
Recent warming has ignited debate over the fundamental drivers that determine spring phenology, with far-reaching implications for which environmental cues will dominate future trends (*1-4*). Although most temperate species show responses to spring warming (forcing), the prevalence and relative strengths of responses to chilling (associated with cool winter temperatures) and photoperiod (daylength) could slow or stall advances in spring phenology with continued warming. Indeed, recent work suggests chilling or daylength cues may underlie observed declines in the 'temperature sensitivity' of leafout in Europe (*5-6*).

We address this controversy by synthesizing four decades of controlled environment experiments to estimate overall chilling, forcing and photoperiod responses across 66 studies and 203 species from around the globe. We find most species respond strongly to all three cues, with chilling being the strongest cue—nearly four times greater than forcing. Yet, when we applied our results to areas with reported declining phenological responses to warming (*5*), we find few sites where chilling or daylength cues would constrain leafout advances under current or near-term warming. Instead, we suggest observed declines may be due in part to a statistical artifact: we show that temperature sensitivities (measured in days per °C) calculated without correcting for warmer daily temperatures will always predict a decline with warming—even with no change in chilling, forcing or photoperiod responses. Our results thus resolve several major debates in plant phenology by showing that most species respond to all cues strongly in experimental conditions, but forcing appears to determine responses to recent warming.

Upon acceptance for publication, the database will be freely available at KNB (*7*; currently meta-data are there); the full database is available to reviewers and editors upon request. This work is a meta-analysis, so data have been previously published; however, the synthesis of these data and the tables, figures, models, and materials presented in this manuscript have not been previously published nor are they under consideration for publication elsewhere.

T. J. Davies, S. Elmendorf and J. Hille Ris Lambers have previously reviewed the manuscript. We recommend the following reviewers: Josep Peñuelas, David Inouye, Ally Phillimore, and Mark Schwartz.

Sincerely,



Ailene Ettinger
Visiting Researcher, Arnold Arboretum of Harvard University

References mentioned in cover letter

1. Körner, C., & Basler, D. 2010. Warming, photoperiods, and tree phenology response. *Science*, 329: 278-278.
2. Chuine, I., Morin, X., & Bugmann, H. 2010. Warming, photoperiods, and tree phenology. *Science*, 329: 277-278.
3. Zohner, C. M., et al. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change*, 6: 1120.
4. Flynn, D. F. B., & Wolkovich, E. M. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*, 219: 1353-1362.
5. Fu, Y. H., et al. 2015. Declining global warming effects on the phenology of spring leaf unfolding." Nature 526: 104.
6. Richardson, A.D., et al. 2018. Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature*, 560: 368.
7. Wolkovich, E., et al. 2019. Observed Spring Phenology Responses in Experimental Environments (OSPREE). Knowledge Network for Biocomplexity. urn:uuid:b2ab2746-b830-436b-a7a9-01b3ef3558e4.