



Dear Dr. Wake:

Please consider our manuscript ‘Temperature and photoperiod drive spring phenology across all species in a temperate forest community’ as a *Letter for Nature Climate Change*. We present new experimental results that show spring phenology is affected by three interactive cues, suggesting responses to continued warming will be complex and non-linear.

Plant phenology plays a crucial role in ecosystem processes and is one of the most reported indicators of climate change (1; 2; 3). Yet as the wealth of observational data highlighting this rapid advance in phenology has increased, research has uncovered variation in these shifts across space, time and species (4; 5; 6). Understanding this variation has led to a number of studies and debates (e.g., 7; 8) about how the major cues known to underlie phenology—spring forcing temperatures, winter chilling temperatures, and photoperiod—vary across species, and whether they may interact. Observational studies have highlighted that a simple model of temperature forcing cannot predict the observed variation (4; 6; 9), but have been hampered from providing further insights because the three major cues generally covary in nature. Advances in our understanding therefore require an experimental approach that manipulates all three cues across a community of species.

Here we present results of a full-factorial experiment varying spring forcing temperatures, photoperiod, and intensity of winter chilling across 28 woody species from two North American forests at two latitudes (requiring 2,136 tree clippings and over 19,000 observations). Using state of the art Bayesian hierarchical models we were able to estimate responses to each cue, and to the interaction of cues, for each species—as well as estimate an overall response. Contrary to hypotheses (7) and recent work (using methods that do not manipulate all cues, 10), we found all species responded to all cues. Responses to photoperiod and forcing temperature were related among species and showed no evidence that some species could be categorized as insensitive to any cue, despite recent efforts to create such binary categories (11; 10; 12). Chilling exerted a strong effect on phenology and interacted importantly with forcing. Our results suggest that predicting the spring phenology of communities will be difficult as all species we studied could have complex, non-linear responses to future warming (13).

We have suggested three possible reviewers (see comments section of online submission system). Both authors substantially contributed to this work and approved of this version for submission. The manuscript is approximately 2,080 words with 184 word preface, and two figures. It is not under consideration elsewhere. We hope that you will find it suitable for publication in *Nature Climate Change*, and look forward to hearing from you.

Thank you for your consideration.

Sincerely,

A handwritten signature in black ink, appearing to read "E. Galimullin".

References:

- [1] Cleland, E. E., Chuine, I., Menzel, A., Mooney, H. A. & Schwartz, M. D. Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* **22**, 357–365 (2007).
- [2] Piao, S. L. *et al.* Weakening temperature control on the interannual variations of spring carbon uptake across northern lands. *Nature Climate Change* **7**, 359–+ (2017).
- [3] Sippel, S., Zscheischler, J. & Reichstein, M. Ecosystem impacts of climate extremes crucially depend on the timing. *Proceedings of the National Academy of Sciences of the United States of America* **113**, 5768–5770 (2016).
- [4] Rutishauser, T., Luterbacher, J., Defila, C., Frank, D. & Wanner, H. Swiss spring plant phenology 2007: Extremes, a multi-century perspective, and changes in temperature sensitivity. *Geophysical Research Letters* **35** (2008).
- [5] Wolkovich, E. M. *et al.* Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**, 494–7 (2012).
- [6] Fu, Y. S. H. *et al.* Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–+ (2015).
- [7] Körner, C. & Basler, D. Phenology under global warming. *Science* **327**, 1461–1462 (2010).
- [8] Chuine, I., Morin, X. & Bugmann, H. Warming, photoperiods, and tree phenology. *Science* **329**, 277–278 (2010).
- [9] Carter, J. M. *et al.* Warmest extreme year in U.S. history alters thermal requirements for tree phenology. *Oecologia* **183**, 1197–1210 (2017).
- [10] Zohner, C. M., Benito, B. M., Svenning, J. C. & Renner, S. S. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123 (2016).
- [11] Laube, J. *et al.* Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182 (2014).
- [12] Donnelly, A. *et al.* Interspecific and interannual variation in the duration of spring phenophases in a northern mixed forest. *Agricultural and Forest Meteorology* **243**, 55–67 (2017).
- [13] Chuine, I. & Cour, P. Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytologist* **143**, 339–349 (1999).