

Dear Dr. Craze:

Please consider our manuscript titled ‘Rethinking False Spring’ as an Opinion piece for *Trends in Ecology and Evolution*. We combine theory from ecology, climatology, physiology, biogeography and crop science to examine the effects of late spring freezing events – or false springs – and the complexity of factors that drive plants’ risk to damage. The aim of the manuscript is to help advance forecasting in climate change and ecological studies.

Temperate tree and shrub species are at risk of damage from late spring freezing events, also known as false springs. However the extent of damage and the frequency and intensity of these events is still largely unknown. Due to shifts in climate, biological spring onset is advancing and many temperate tree and shrub species are initiating leafout 4-6 days earlier per °C of warming [1, 2] but last spring freeze dates are not predicted to advance at the same rate as spring onset in some regions [3]. Climate change could potentially amplify the effects of false springs in these regions, which could result in highly adverse ecological and economic consequences [4, 5].

Many studies have reported false spring events in recent years and have linked these events to climate change [e.g. 6, 7]. Recent false spring events have led to a growing body of research investigating the effects on temperate forests and agricultural crops. However, current definitions for false springs are generally simple – i.e. budburst occurs before the last spring freeze [8]. This simple definition assumes consistency of damage across species, functional group, life stages, and other climatic regimes, ignoring that such factors can greatly impact plants’ false spring risk.

This manuscript is especially timely because new methods are essential to properly evaluate the effects of false spring events across the diverse species and climate regimes, especially under climate change. The ultimate intent of this manuscript is to demonstrate how an integrated view of false spring that incorporates the complexity factors would rapidly advance progress in this field, improve predictions of spring freeze risk under a changing climate, and, potentially, provide novel insights to how plants respond to and are shaped by spring frost.

Our author team provides an international and interdisciplinary approach. Because our manuscript cuts across the fields of ecology, crop science, biogeography and climatology our authorship list is slightly longer than allowed – at four authors – we found this was necessary to bring a robust perspective from each field. We hope that you will find it suitable for publication in *Trends in Ecology and Evolution*.

Please find a list of key references below. This Opinion piece is not under consideration for publication elsewhere. Thank you for your consideration.

Sincerely,

Catherine Chamberlain

References

- [1] Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. L., Travers, S. E., Pau, S., Regetz, J., Davies, T. J., Kraft, N. J. B., Ault, T. R., Bolmgren, K., Mazer, S. J., McCabe, G. J., McGill, B. J., Parmesan, C., Salamin, N., Schwartz, M. D., and Cleland, E. E. Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**(7399), 18–21 (2012).
- [2] Polgar, C., Gallinat, A., and Primack, R. B. Drivers of leaf-out phenology and their implications for species invasions: Insights from Thoreau’s Concord. *New Phytologist* **202**(1), 106–115 (2014).
- [3] Labe, Z., Ault, T., and Zurita-Milla, R. Identifying anomalously early spring onsets in the CESM large ensemble project. *Climate Dynamics* **48**(11-12), 3949–3966, Aug (2016).
- [4] Ault, T. R., Henebry, G. M., de Beurs, K. M., Schwartz, M. D., Betancourt, J. L., and Moore, D. The False Spring of 2012, Earliest in North American Record. *Eos, Transactions American Geophysical Union* **94**(20), 181–182 (2013).
- [5] Vitra, A., Lenz, A., and Vitasse, Y. Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist* **216**(1), 113–123, Jul (2017).
- [6] Augspurger, C. K. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. *Ecology* **94**(1), 41–50 (2013).
- [7] Menzel, A., Helm, R., and Zang, C. Patterns of late spring frost leaf damage and recovery in a european beech (*fagus sylvatica* l.) stand in south-eastern germany based on repeated digital photographs. *Frontiers in Plant Science* **6**, 110 (2015).
- [8] Gu, L., Hanson, P. J., Post, W. M., Kaiser, D. P., Yang, B., Nemani, R., Pallardy, S. G., and Meyers, T. The 2007 Eastern US Spring Freeze: Increased Cold Damage in a Warming World. *BioScience* **58**(3), 253 (2008).
- [9] Vitasse, Y., Lenz, A., Hoch, G., and Körner, C. Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. *Journal of Ecology* **102**(4), 981–988 (2014).
- [10] Vitasse, Y., Lenz, A., and Körner, C. The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science* **5**(October), 541 (2014).
- [11] Zohner, C. M., Benito, B. M., Svenning, J.-C., and Renner, S. S. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**(12), 1120–1123, Oct (2016).
- [12] Lenz, A., Hoch, G., Körner, C., and Vitasse, Y. Convergence of leaf-out towards minimum risk of freezing damage in temperate trees. *Functional Ecology* **30**, 1–11 (2016).
- [13] Allstadt, A. J., Vavrus, S. J., Heglund, P. J., Pidgeon, A. M., Wayne, E., and Radeloff, V. C. Spring plant phenology and false springs in the conterminous U. S. during the 21st century. *Environmental Research Letters (submitted)* **10**(October), 104008 (2015).
- [14] Hofmann, M. and Bruehlheide, H. Frost hardness of tree species is independent of phenology and macroclimatic niche. *Journal of Biosciences* **40**(1), 147–157 (2015).

- [15] Kollas, C., Körner, C., and Randin, C. F. Spring frost and growing season length co-control the cold range limits of broad-leaved trees. *Journal of Biogeography* **41**(4), 773–783 (2014).
- [16] Peterson, A. G. and Abatzoglou, J. T. Observed changes in false springs over the contiguous United States. *Geophysical Research Letters* **41**(6), 2156–2162 (2014).
- [17] Xin, Q. A risk-benefit model to simulate vegetation spring onset in response to multi-decadal climate variability: Theoretical basis and applications from the field to the Northern Hemisphere. *Agriculture and Forest Meteorology* **228-229**, 139–163 (2016).
- [18] Lenz, A., Hoch, G., Vitasse, Y., and Körner, C. European deciduous trees exhibit similar safety margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**(4), 1166–1175 (2013).
- [19] Muffler, L., Beierkuhnlein, C., Aas, G., Jentsch, A., Schweiger, A. H., Zohner, C., and Kreyling, J. Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the northern hemisphere. *Global Ecology and Biogeography* **25**(9), 1061–1071, May (2016).