



1300 Centre Street  
Boston, MA, 20131

Dear Dr. Craze:

Please consider our manuscript entitled 'Rethinking False Spring' as an Opinion piece for *Trends in Ecology and Evolution*. Climate change has brought renewed interest to a major factor that shapes the life history of most temperate and boreal plants: late spring freeze events, commonly called false springs. While increased interest has led to a growing number of studies, much of the research takes a simplified view of these events, which—we argue—can lead to poor and incorrect forecasting. Combining theory from ecology, climatology, physiology, biogeography and crop science we examine the effects of late spring freezing events – or false springs – and the complexity of factors that drive plants' risk to damage.

Many non-tropical tree and shrub species are at risk of damage from late spring freezing events (false springs). However the extent of damage and the frequency and intensity of these events is still largely unknown. Due to shifts in climate, the onset of biological spring is advancing and 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 can amplify the effects of false springs, 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. For example, many species can withstand spring freezes after full leafout through the evolution of plant strategies against frost and are thus most vulnerable only within the narrow temporal window of budburst to leafout.

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 manuscript will 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 to false spring research. 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  
PhD Candidate  
Harvard University

## 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] Hofmann, M. and Bruehlheide, H. Frost hardiness of tree species is independent of phenology and macroclimatic niche. *Journal of Biosciences* **40**(1), 147–157 (2015).
- [14] 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).

- [15] Dolezal, J., Dvorsky, M., Kopecky, M., Liancourt, P., Hiiesalu, I., Macek, M., Altman, J., Chlumska, Z., Rehakova, K., Capkova, K., and et al. Vegetation dynamics at the upper elevational limit of vascular plants in himalaya. *Scientific Reports* **6**(1), May (2016).
- [16] 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).
- [17] 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).
- [18] 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).
- [19] Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J., and et al. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**(7571), 104–107, Sep (2015).
- [20] Xie, Y., Wang, X., and Silander, J. A. Deciduous forest responses to temperature, precipitation, and drought imply complex climate change impacts. *Proceedings of the National Academy of Sciences* **112**(44), 13585–13590, Oct (2015).