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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 many non-tropical plant species: 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 incorrect estimates and forecasting. Combining theory from ecology, climatology, physiology, biogeography and crop science we examine the effects of false springs, and the complexity of factors that drive plants’ risk to frost damage.

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, 3] but last spring freeze dates are not predicted to advance at the same rate as spring onset in some regions [4]. Many studies have reported false spring events in recent years and have linked these events to climate change [e.g. 5, 6]. Continued climate change may amplify the effects of false springs, which could result in highly adverse ecological and economic consequences [7, 8].

While recent false spring events have led to a growing body of research, current definitions for false springs remain generally simple – i.e. budburst occurs before the last spring freeze [9]. This 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 that tolerate frost, and are thus most vulnerable only within the narrow temporal window of budburst to leafout. We show how location within a forest or canopy, interspecific variation in avoidance and tolerance strategies, freeze temperature thresholds, and regional effects unhinge simple metrics of false spring. We argue that a new approach that integrates these and other crucial factors is needed.

This manuscript is especially timely because new methods are essential to properly evaluate and predict the effects of false spring events across diverse species and climate regimes, especially under climate change. The manuscript will demonstrate how an integrated view of false spring that incorporates the complexity of factors underlying plant strategies to frost would rapidly advance progress in this field, including improved predictions of spring freeze risk under a changing climate, and, novel insights into 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 consideration 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,

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## 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] 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).
- [4] 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).
- [5] 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).
- [6] 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).
- [7] 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).
- [8] 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).
- [9] 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).
- [10] 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).
- [11] 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).
- [12] 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).
- [13] 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).
- [14] 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).

- [15] Hofmann, M. and Bruelheide, H. Frost hardiness of tree species is independent of phenology and macroclimatic niche. *Journal of Biosciences* **40**(1), 147–157 (2015).
- [16] 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).
- [17] 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).
- [18] 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).
- [19] 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).
- [20] 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).