1 Regional Risk Outline

2 Authors:

10

- ³ C. J. Chamberlain ^{1,2}, B. I. Cook ³, I. Morales Castilla ^{1,4} & E. M. Wolkovich ^{1,2}
- 4 Author affiliations:
- ⁵ Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;
- ⁶ Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;
- ⁷ NASA Goddard Institute for Space Studies, New York, New York, USA;
- ⁴Edificio Ciencias, Campus Universitario 28805 AlcalÃa de Henares, Madrid, Spain
- *Corresponding author: 248.953.0189; cchamberlain@g.harvard.edu

$_{\scriptscriptstyle 11}$ 1 Introduction

- 1. Temperate tree and shrub species are at risk of damage from late spring freezing events, also known as false springs.
- 2. However, the extent of damage and the frequency and intensity of false spring events is still largely unknown.
- 3. Individuals that initiate budburst before the last spring freeze are at risk of leaf tissue loss, damage to the xylem, and slowed canopy development (Gu et al., 2008; Hufkens et al., 2012).
- 4. Temperate plants are exposed to freezing temperatures numerous times throughout the year, however, individuals are most at risk to damage from stochastic spring frosts, when frost tolerance is lowest (Sakai & Larcher, 1987).
- 5. False spring events can result in photosynthetic tissue loss, which could potentially impact multiple years of growth and, with the growing season extending, individuals could be exposed to more frosts in the future (Liu *et al.*, 2018).
- 6. For these reasons, episodic frosts are one of the largest limiting factors in species range limits (Kollas et al., 2014).
- 1. Plant phenology which is defined as the timing of recurring life-history events such as budburst strongly tracks shifts in climate (Wolkovich *et al.*, 2012).

- 28 2. Trees and shrubs in temperate regions optimize growth by using three cues to initiate budburst: low winter temperatures, warm spring temperatures, and increasing spring daylengths.
- 3. With climate change advancing, this interaction of cues may shift spring phenologies both across and within species.
- 4. Due to the changing climate, spring onset is advancing and many temperate tree and shrub species are initiating leafout 4-6 days earlier per °C of warming (Wolkovich et al., 2012; Polgar et al., 2014).
- 5. The North Atlantic Ossilation (NAO) index is often used to describe winter and spring circulation across Europe.
- 6. More positive NAO phases tend to result in higher than average winter and early spring temperatures, and with climate change, great NAO indices has correlated to earlier budburst dates (Chmielewski & Rötzer, 2001).
- 7. However, last spring freeze dates are not predicted to advance at the same rate as spring onset in some regions of the world (Inouye, 2008; Martin *et al.*, 2010; Labe *et al.*, 2016; Sgubin *et al.*, 2018), potentially amplifying the effects of false spring events in these regions.
- 8. Temperate plants have evolved to minimize false spring damage through a myriad of strategies, with the most effective being avoidance: plants must exhibit flexible spring phenologies in order to maximize growth and minimize frost risk by timing budburst effectively (Polgar & Primack, 2011; Basler & Korner, 2014).
- 9. Thus, there is a trade-off between growing season length and frost risk.
- 10. Individuals that initiate budburst earlier in the season are more frost resistant (Körner *et al.*, 2016), however, as climate change advances, less frost resistant individuals may start initiating budburst before the last freeze date.
- 11. Individuals from more Northern provenances tend to be more susceptible to spring frost damage, whereas more Southern individuals are more sensitive to fall frosts (Montwé *et al.*, 2018).
- 12. The growing season is lengthening across many regions in the northern hemisphere (Chen *et al.*, 2005; Liu *et al.*, 2006; Kukal & Irmak, 2018), but false spring events still pose a threat in many of these regions (Wypych *et al.*, 2016)
- 13. Plants growing in forest systems tend to exhibit staggered days of budburst.
- 14. Lower canopy species typically initiate budburst earlier in the season in order to utilize available resources such as light, whereas larger canopy species usually initiate budburst later in the season.

- 58 15. Frost tolerance greatly diminishes once individuals exit the dormancy phase (i.e. processes leading to 59 budburst) through full leaf expansion (Vitasse *et al.*, 2014).
- 1. False spring incidence has declined in many regions (i.e. across parts of North America and Asia), however the prevalence of spring frosts has increasing across Europe since 1982 (Liu *et al.*, 2018).
- 2. Major false spring events that impacted entire forests have been recorded in recent years (Gu et al., 2008; Augspurger, 2009, 2013; Menzel et al., 2015).
- 3. After such false spring events, it can take 16-38 days for trees to refoliate, which can detrimentally affect processes such as photosynthesis and respiration, carbon updake, and nutrient cycling (Hufkens et al., 2012; Richardson et al., 2013; Klosterman et al., 2018).
- 4. There is large debate over whether or not spring freeze damage will increase (Hänninen, 1991; Augspurger, 2013; Labe *et al.*, 2016), remain the same (Scheifinger *et al.*, 2003) or even decrease (Kramer, 1994) with climate change.
- 5. (PUT QUESTIONS AROUND HERE)
- 6. Many studies have assessed the interplay between cue interactions and budburst dates by investigating potenital latitudinal effects (Partanen, 2004; Vihera-aarnio et al., 2006; Caffarra & Donnelly, 2011; Zohner et al., 2016; Gauzere et al., 2017).
- 7. However, recent studies have demonstrated regional effects may be more closely related to false spring risk through shifts in elevation (Vitra *et al.*, 2017) and from distance to the coast (Wypych *et al.*, 2016).
- 8. By better understanding these regional climatic implications, we may be better able to determine which regions may be at risk currently and which regions may become more at risk over time.
- 9. (METHODS) I assessed the daily gridded climate data across Europe (E-OBS) from 1950-2016.
- 10. (METHODS) By simply using climate data, I compared the frequency of spring freeze events throughout
 Europe before and after anthropogenic climate change began (i.e. around 1980 (Barnett *et al.*, 2001)).
- 11. (METHODS) A spring freeze was considered if the the daily minimum temperature fell below -2°C (Schwartz, 1993) between March 1 and June 30.
- 12. (RESULTS) A few regions experienced increased exposure to spring freeze events, whereas most other regions experienced fewer or similar numbers of years with spring freezes (Figure 1).
- 13. (DISCUSSION) Understanding regional differences in spring freeze intensity and frequency is essential
 for predicting future habitat risk.

87 References

- ⁸⁸ Augspurger, C.K. (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate
- deciduous forest. Functional Ecology 23, 1031–1039.
- ⁹⁰ Augspurger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124
- years: Spring damage risk is increasing. *Ecology* **94**, 41–50.
- 92 Barnett, T., Pierce, D. & Schnur, R. (2001) Detection of anthropogenic climate change in the world's oceans.
- 93 Science **292**, 270–274.
- Basler, D. & Korner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in
- four temperate forest tree species. Tree Physiology 34, 377–388.
- ⁹⁶ Caffarra, A. & Donnelly, A. (2011) The ecological significance of phenology in four different tree species:
- effects of light and temperature on bud burst. International Journal of Biometeorology 55, 711–721.
- ⁹⁸ Chen, X., Hu, B. & Yu, R. (2005) Spatial and temporal variation of phenological growing season and climate
- change impacts in temperate eastern china. Global Change Biology 11, 1118–1130.
- Chmielewski, F.M. & Rötzer, T. (2001) Response of tree phenology to climate change across europe. Agri-
- cultural and Forest Meteorology 108, 101 112.
- Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I. & Chuine, I. (2017) Inte-
- grating interactive effects of chilling and photoperiod in phenological process-based models. A case study
- with two European tree species: Fagus sylvatica and Quercus petraea. Agricultural and Forest Meteorology
- pp. 9–20.
- Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008)
- The 2007 Eastern US Spring Freeze: Increased Cold Damage in a Warming World. *BioScience* 58, 253.
- Hänninen, H. (1991) Does climatic warming increase the risk of frost damage in northern trees? Plant, Cell
- \mathcal{E} Environment 14, 449–454.
- Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J. & Richardson, A.D. (2012)
- Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology 18,
- 112 2365–2377.
- 113 Inouye, D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane
- wildflowers. *Ecology* **89**, 353–362.

- Klosterman, S., Hufkens, K. & Richardson, A.D. (2018) Later springs green-up faster: the relation between onset and completion of green-up in deciduous forests of north america. *International Journal of Biomete-orology*.
- Kollas, C., Körner, C. & Randin, C.F. (2014) Spring frost and growing season length co-control the cold range limits of broad-leaved trees. *Journal of Biogeography* 41, 773–783.
- Körner, C., Basler, D., Hoch, G., Kollas, C., Lenz, A., Randin, C.F., Vitasse, Y. & Zimmermann, N.E. (2016)
- Where, why and how? explaining the low-temperature range limits of temperate tree species. Journal of
- 122 Ecology **104**, 1076–1088.
- Kramer, K. (1994) A modelling analysis of the effects of climatic warming on the probability of spring frost damage to tree species in the netherlands and germany. *Plant, Cell & Environment* 17, 367–377.
- Kukal, M.S. & Irmak, S. (2018) U.s. agro-climate in 20th century: Growing degree days, first and last frost, growing season length, and impacts on crop yields. *Scientific Reports* 8.
- Labe, Z., Ault, T. & Zurita-Milla, R. (2016) Identifying anomalously early spring onsets in the cesm large ensemble project. *Climate Dynamics* **48**, 3949–3966.
- Liu, Q., Piao, S., Janssens, I.A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R.B., Peñuelas, J. & Wang, T. (2018) Extension of the growing season increases vegetation exposure to frost. *Nature Communications* 9.
- Liu, X., Yin, Z., Shao, X. & Qin, N. (2006) Temporal trends and variability of daily maximum and minimum, extreme temperature events, and growing season length over the eastern and central tibetan plateau during 1961–2003. Journal of Geophysical Research: Atmospheres 111.
- Martin, M., Gavazov, K., Körner, C., Hattenschwiler, S. & Rixen, C. (2010) Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO_2 . Global Change Biology 16, 1057–1070.
- Menzel, A., Helm, R. & Zang, C. (2015) 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.
- Montwé, D., Isaac-Renton, M., Hamann, A. & Spiecker, H. (2018) Cold adaptation recorded in tree rings highlights risks associated with climate change and assisted migration. *Nature Communications* 9.
- Partanen, J. (2004) Dependence of photoperiodic response of growth cessation on the stage of development in picea abies and betula pendula seedlings. Forest Ecology and Management 188, 137–148.

- Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications for species invasions: Insights from Thoreau's Concord. New Phytologist 202, 106–115.
- Polgar, C.A. & Primack, R.B. (2011) Leaf-out phenology of temperate woody plants: From trees to ecosystems. New Phytologist 191, 926–941.
- Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural* and Forest Meteorology **169**, 156 173.
- Sakai, A. & Larcher, W. (1987) Frost Survival of Plants. Springer-Verlag.
- Scheifinger, H., Menzel, A., Koch, E. & Peter, C. (2003) Trends of spring time frost events and phenological dates in Central Europe. *Theoretical and Applied Climatology* **74**, 41–51.
- Schwartz, M.D. (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography* **14(6)**, 536–550.
- Sgubin, G., Swingedouw, D., Dayon, G., de Cortázar-Atauri, I.G., Ollat, N., Pagé, C. & van Leeuwen, C. (2018) The risk of tardive frost damage in french vineyards in a changing climate. Agricultural and Forest Meteorology 250-251, 226 242.
- Vihera-aarnio, A., Hakkinen, R. & Junttila, O. (2006) Critical night length for bud set and its variation in two photoperiodic ecotypes of *Betula pendula*. Tree Physiology **26**, 1013–1018.
- Vitasse, Y., Lenz, A. & KÃÂűrner, C. (2014) The interaction between freezing tolerance and phenology in temperate deciduous trees. Frontiers in Plant Science 5.
- Vitra, A., Lenz, A. & Vitasse, Y. (2017) Frost hardening and dehardening potential in temperate trees from
 winter to budburst. New Phytologist 216, 113–123.
- 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., Parme-
- san, C., Salamin, N., Schwartz, M.D. & Cleland, E.E. (2012) Warming experiments underpredict plant
- phenological responses to climate change. Nature 485, 18–21.
- Wypych, A., Ustrnul, Z., Sulikowska, A., Chmielewski, F.M. & Bochenek, B. (2016) Spatial and temporal variability of the frost-free season in central europe and its circulation background. *International Journal* of Climatology 37, 3340–3352.
- Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to constrain climatedriven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123.

Tables and Figures



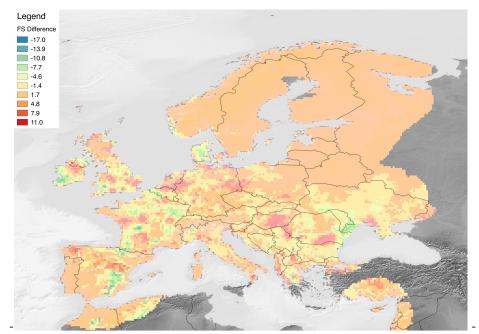


Figure 1: Number of years with freezing events that occured before anthropogenic climate change began (1951-1983) as compared to after anthropogenic climate change began (1984-2016). If temperatures fell below -2°C between March 1 and June 30, a year with a spring freeze was tallied. Some regions experienced more years with spring freezes after climate change began, whereas other years experienced the same number or even fewer years with spring freezes. Regions that had more years with spring freezes after climate change began are blue and regions that had fewer freezes are red.

-