

Rethinking False Spring Risk

Authors:

C. J. Chamberlain^{1,2}, B. I. Cook³, I. Garcia de Cortazar Atauri⁴ & E. M. Wolkovich^{1,2,5}

Author affiliations:

¹Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

²Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

³NASA Goddard Institute for Space Studies, New York, New York, USA;

⁴French National Institute for Agricultural Research, INRA, US1116 AgroClim, F-84914 Avignon, France

⁵Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver,

BC V6T 1Z4

*Corresponding author: 248.953.0189; cchamberlain@g.harvard.edu

Keywords: false spring, phenology, freezing tolerance, climate change, forest communities

Paper type: Opinion

Counts: Total word count for the main body of the text: 2710; Abstract: 119; 4 figures (all in color).

Rethinking False Spring Risk: Submission Questions

What is the scientific question you are addressing? Climate change has brought renewed interest to late spring freeze events, commonly called false springs. 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 to help advance forecasting.

What is/are the key finding(s) that answers this question? Current definitions for false springs remain generally simple – i.e. budburst occurs before the last spring freeze (Gu *et al.*, 2008). This definition fails to incorporate factors such as species, functional group, life stages, and other climatic regimes. We argue that a new approach that integrates these and other crucial factors is needed.

Why is this work important and timely? There has been a growing number of studies that take a simplified view of false springs, which can lead to incorrect forecasting. This manuscript is especially timely because new methods are essential to predict the effects of false spring events across diverse species and climate regimes, especially under climate change.

Does your paper fall within the scope of GCB; what biological AND global change aspects does it address? 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 with global change, and, novel insights into how plants are shaped by spring frost.

What are the three most recently published papers that are relevant to this question? Vitra, A., Lenz, A. & Vitasse, Y. (2017) Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist* **216**, 113–123

Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of freezing damage in temperate trees. *Functional Ecology* **30**, 1–11

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

Abstract

Temperate plants are at risk of being exposed to late spring freezes — often called false springs — which can be damaging ecologically and economically. As climate change may alter the prevalence and severity of false springs, our ability to accurately forecast such events has become more critical. Currently, many false spring studies simplify the ecological and physiological information needed for accurate predictions of the level of plant damage from late spring freezes. Here we review the complexity of factors driving a plant's false spring risk. We highlight how species, life stage, and habitat differences contribute to the damage potential of false springs. Integrating these complexities could help rapidly advance forecasting of false spring events in climate change and ecological studies.

Introduction

Plants growing in temperate environments time their growth each spring to follow rising temperatures alongside increasing light and soil resource availability. While tracking spring resource availability, individuals that burst bud before the last freeze date are at risk of leaf loss, damaged wood tissue, and slowed canopy development (Gu *et al.*, 2008; Hufkens *et al.*, 2012). These damaging late spring freezes are also known as false springs, and are widely documented to result in adverse ecological and economic consequences (Knudson, 2012; Ault *et al.*, 2013).

Climate change is expected to cause an increase in damage from false spring events due to earlier spring onset and potentially greater fluctuations in temperature in some regions (Inouye, 2008; Martin *et al.*, 2010). Already, multiple studies have documented false springs in recent years (Gu *et al.*, 2008; Augspurger, 2009, 2013; Menzel *et al.*, 2015) and some have linked these events to climate change (Ault *et al.*, 2013; Allstadt *et al.*, 2015; Muffler *et al.*, 2016; Xin, 2016; Vitra *et al.*, 2017). This increasing interest in false springs has led to a growing body of research investigating the effects on temperate forests and agricultural crops. But for this research to produce accurate predictions of future trends, researchers need methods that properly evaluate the effects of false spring events across the diverse species and climate regimes they are studying.

Current metrics for estimating false springs events are generally simple, often requiring an estimate for the start of

biological ‘spring’ (i.e. budburst) and whether temperatures occurred below a particular temperature threshold in the following week. Such estimates inherently assume consistency of damage across species, functional group, life stages, and other climatic regimes, ignoring that such factors can greatly impact plants’ false spring risk. As a result, such indices may lead to inaccurate current estimates as well as poor future predictions, slowing our progress in understanding false spring events and how they may shift with climate change.

In this paper we highlight the complexity of factors driving a plant’s false spring risk and provide a road map for improved metrics. 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 would help accurately determine current false spring damage and improve predictions of spring freeze risk under a changing climate — while potentially providing novel insights to how plants respond to and are shaped by spring frost.

Defining False Spring: An example in one temperate plant community

Temperate forest plants experience elevated risk of frost damage during the spring due to the stochastic timing of frosts. Freezing temperatures following a warm spell can result in plant damage or even death (Ludlum, 1968; Mock *et al.*, 2007). Many temperate species exhibit flexible spring phenologies, which help them minimize freezing risk, but freeze damage can still occur, especially in the spring. Dormant buds can withstand low temperatures without freezing. Once buds exit the dormancy phase, they are less freeze tolerant and resistance to bud ice formation is greatly reduced (Taschler *et al.*, 2004; Lenz *et al.*, 2013; Vitasse *et al.*, 2014b). Intracellular ice formation from false spring events often results in severe leaf and stem damage (Burke *et al.*, 1976; Sakai & Larcher, 1987). Ice formation can also occur indirectly (i.e. extracellularly), which results in freezing dehydration and mimics drought conditions (Pearce, 2001; Beck *et al.*, 2004; Hofmann & Bruehlheide, 2015). Both forms of ice formation can cause defoliation and crown dieback (Gu *et al.*, 2008). An effective and consistent definition of false spring would accurately determine the amount and type of ice formation to properly evaluate the level of damage that could occur.

There are several definitions currently used to define a false spring. A common definition describes a false spring as having two phases: rapid vegetative growth prior to a freeze and a post freeze setback (Gu *et al.*, 2008). Other definitions instill more precise temporal parameters, specific to certain regions (e.g., in Augspurger, 2013, false spring for the Midwestern United States is defined as a warmer than average March, a freezing April, and enough growing degree days between budburst and the last freeze date). A widely used definition integrates a mathematical equation to quantify a false spring event. This equation, known as a False Spring Index (FSI), signifies the likelihood of damage to occur from a late spring freeze. Currently, FSI is evaluated annually by the day of budburst and the day of last spring freeze (often calculated at -2.2°C Schwartz, 1993) through the simple equation (Marino *et al.*, 2011):

$$FSI = \text{Day of Year}(\text{LastSpringFreeze}) - \text{Day of Year}(\text{Budburst}) \quad (1)$$

Negative values indicate no risk situations, whereas a damaging FSI is currently defined to be 7 or more days between budburst and the last freeze date (Equation 1) (Peterson & Abatzoglou, 2014). This 7 day threshold captures the reality that leaf tissue is at high risk of damage from frost in the period after budburst, with later vegetative phases (e.g., full leafout) being more resistant to such damage.

To demonstrate how the FSI definition works, we applied it to data from the Harvard Forest Long-term Ecological Research program in Massachusetts. We used three separate methodologies to calculate spring onset: long-term ground observational data (O’Keefe, 2014), PhenoCam data from Harvard Forest (Richardson, 2015), and USA National Phenology Network’s (USA-NPN) Extended Spring Index (SI-x) data (USA-NPN, 2016). These spring onset values were then inputted into the FSI equation (Equation 1) to calculate FSI from 2008 to 2014 (Figure 1).

Each methodology renders different FSI values, suggesting different false spring damage for the same site and same year. For most years, the observational FSI and PhenoCam FSI are about 10-15 days lower than the SI-x data. This is especially important for 2008, when the SI-x data indicates a false spring year, whereas the other two datasets do not. In 2012, the observational data and PhenoCam data diverge slightly and the PhenoCam FSI is over 30 days less than the SI-x value.

The reason for these discrepancies is that each method evaluates spring onset by integrating different attributes such as age, species or functional group. Spring phenology in temperate forests typically progresses by functional group:

understory species and young trees tend to initiate budburst first, whereas larger canopy species may start later in the season (Richardson & O'Keefe, 2009; Xin, 2016). The different FSI values determined in Figure 1 exemplify the differences in functional group spring onset dates and illustrate variations in forest demography and phenology, which is most apparent in 2012. In 2012, a false spring event was reported through many regions of the US due to warm temperatures occurring in March (Ault *et al.*, 2015). These high temperatures would most likely be too early for larger canopy species to initiate budburst but they would have affected smaller understory species, as is seen in Figure 1.

Yet, in contrast to our three metrics of spring onset for one site, most FSI work currently ignores variation across functional groups — instead using one metric of spring onset and assuming it applies to the whole community of plants (Marino *et al.*, 2011; Peterson & Abatzoglou, 2014; Allstadt *et al.*, 2015; Mehdipoor & Zurita-Milla, 2017). The risk of a false spring varies across habitats and with species composition since spring onset is not consistent across functional groups. Therefore, one spring onset date cannot be used as an effective proxy for all species. False spring studies should first assess the forest demographics and functional groups relevant to the study question in order to effectively estimate the date of spring onset. However, as we outline below, considering different functional groups is unlikely to be enough for robust predictions. It is also crucial to integrate species differences within functional groups and consider the various interspecific avoidance and tolerance strategies that species have evolved against false springs.

Plant Physiology and Diversity versus the Current False Spring Definition

Plants have evolved to minimize false spring damage through two strategies: avoidance and tolerance. Many temperate forest plants utilize various morphological strategies to be more frost tolerant: some have toothed leaves to increase 'packability' in winter buds, which permits more rapid leafout (Edwards *et al.*, 2017) and minimizes exposure time of less resistant tissues. Other species have young leaves with more trichomes to act as a buffer against spring frosts (Prozherina *et al.*, 2003; Agrawal *et al.*, 2004). These strategies are probably only a few of the many ways plants work to morphologically avoid frost damage, and more studies are needed to investigate the interplay between morphological traits and false spring tolerance.

Rather than being more tolerant of spring freezing temperatures, some temperate forest species have evolved to avoid frosts via more flexible phenologies. Effective avoidance strategies require well-timed spring phenologies. Most temperate deciduous tree species optimize growth and minimize spring freeze damage by using three cues to initiate budburst: low winter temperatures, warm spring temperatures, and increasing photoperiods (Chuine, 2010). The evolution of these three cues and their interactions has permitted temperate plant species to occupy more northern ecological niches (Kollas *et al.*, 2014) and decrease the risk of false spring damage, which is crucial for avoidance strategies (Charrier *et al.*, 2011). One avoidance strategy, for example, is the interaction between over-winter chilling and spring forcing temperatures. Warm temperatures earlier in the winter will not result in early budburst due to insufficient chilling (Basler & Körner, 2012). Likewise, photoperiod sensitivity is a common false spring avoidance strategy: species that respond strongly to photoperiod cues in addition to warm spring temperatures are unlikely to have large advances in budburst and thus may evade false spring events as warming continues (Basler & Körner, 2014).

Defining Vegetative Risk

Phenology and frost tolerance are intertwined — with important variation occurring across different phenological phases. Flowering and fruiting are generally more sensitive to false spring events than vegetative phases (Augspurger, 2009; Lenz *et al.*, 2013), but false spring events that occur during the vegetative growth phenophases may impose the greatest freezing threat to deciduous plant species. Plants will suffer greater long-term effects from the loss of photosynthetic tissue, which could impact multiple years of growth, reproduction, and canopy development (Vitasse *et al.*, 2014a; Xie *et al.*, 2015). However, there is high variability in defining a damaging temperature threshold across species, including between agricultural and ecological studies (Figure 2).

There is also important variation within certain phenological phases. Most notably, within the vegetative phases of spring leafout, plants that have initiated budburst but have not fully leafed out are more likely to sustain damage from a false spring than individuals past the leafout phase. This is because freezing tolerance is lowest after budburst begins until the leaf is fully unfolded (Lenz *et al.*, 2016). Therefore, the rate of budburst and the length of time between budburst and leafout is essential for predicting the level of damage from a false spring event. We will refer to the

159 timing between these phenophases — budburst to leafout — as the duration of vegetative risk (Figure 3). The duration
160 of vegetative risk can be extended if a freezing event occurs during the phenophases between budburst and full leafout
161 (Augsburger, 2009), which could result in exposure to multiple frost events in one season.

162 **How Species Phenological Cues Shape Vegetative Risk**

163 Predictions of false spring critically depend on understanding what controls the duration of vegetative risk across
164 species. For temperate species, the three major cues (winter chilling temperatures, spring warm temperatures and photo-
165 toperiod) that control budburst (Chuine, 2010) probably play a dominant role. One study, which examined how these
166 cues impact budburst and leafout, shows that the duration of vegetative risk can vary by 21 days or more depending
167 on the suite of cues a plant experiences (Figure 4) (Flynn & Wolkovich, 2018). The experiment examined 9 temperate
168 trees and shrubs using a fully crossed design of three levels of chilling (field chilling, field chilling plus 30 days at either
169 1 or 4 °C), two levels of forcing (20°C/10°C or 15°C/5°C day/night temperatures) and two levels of photoperiod (8
170 versus 12 hour days) resulting in 12 treatment combinations. Increased forcing, photoperiod and chilling all decreased
171 the duration of vegetative risk, with forcing causing the greatest decrease (10 days), followed by daylength (9 days),
172 and chilling (2-3 days depending on the temperature), but the full effect of any one cue depended on the other cues
173 due to important interactions—for example, the combined effect of warmer temperatures and longer days would be 14
174 days, because of -5 days interaction between the forcing and photoperiod cues (Figure 4A).

175 Such cues may provide a starting point for predicting how climate change will alter the duration of vegetative risk.
176 Robust predictions will require much more information, especially the emissions scenario realized over coming decades
177 (IPCC, 2015), but one potential outcome is that higher temperatures will increase forcing and decrease chilling in many
178 locations. Under this scenario experimental results suggest a 2-10 day increase in duration of vegetative risk depending
179 on the species, except for *Betula alleghaniensis* which had a 6 day decrease in duration of vegetative risk (Figure 4B).
180 This cue interaction could thus expose at-risk plants to more intense false spring events or even multiple events in one
181 year.

182 Considering the interaction of cues and climate change further complicates understanding species future vulnerabilities
183 to false spring events. Most species are expected to begin leafout earlier in the season with warming spring temper-
184 atures but some species may have the opposite response due to less winter chilling or decreased photoperiod cues
185 (Cleland *et al.*, 2006; Fu *et al.*, 2015; Xin, 2016). Individuals that initiate budburst earlier in the spring may attempt to
186 limit freezing risk by decreasing the duration of vegetative risk in order to minimize the exposure of less frost tolerant
187 phenophases (Augspurger, 2009). But with a changing climate and thus shifts in phenological cues, this relationship
188 may change (Dolezal *et al.*, 2016). Further studies are essential to understand the interplay between chilling, forc-
189 ing, photoperiod cues and the duration of vegetative risk, especially for species occupying ecological niches more
190 susceptible to false spring events.

191 **Predictable Regional Differences in Climate, Species Responses and False Spring Risk**

192 Robust predictions must consider the full interplay of species cues and a specific location's climate. A single species
193 may have varying cues across space: various studies that investigated latitudinal effects indicate that populations grow-
194 ing further north respond to a different interaction of cues than those growing further south. Thus, based on cues alone,
195 different regions may have different durations of vegetative risk for the same species (Partanen, 2004; Vihera-aarnio
196 *et al.*, 2006; Caffarra & Donnelly, 2011). Studies also show that different species within the same location can exhibit
197 different sensitivities to the three cues (Basler & Körner, 2012; Laube *et al.*, 2013) thus further amplifying the myriad
198 of climatic and phenological shifts that determine false spring risk in a region.

199 Numerous studies have investigated how the relationship between budburst and major phenological cues varies across
200 space, including across populations, by using latitudinal gradients (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra
201 & Donnelly, 2011; Zohner *et al.*, 2016; Gauzere *et al.*, 2017). Fewer, however, have integrated distance from the
202 coast (but see Myking & Skroppa, 2007; Harrington & Gould, 2015; Aitken & Bemmels, 2015) or regional effects.
203 Yet climate and thus false spring risk and phenological cues vary across regions. For example, consider five different
204 regions within a temperate climate (Figure S1). Some regions may experience harsher winters and greater temperature
205 variability throughout the year, and these more variable regions often have a much higher risk of false spring (i.e.

Maine) than others (i.e. Lyon) (Figure S1). Understanding and integrating such spatiotemporal effects and regional differences when investigating false spring risk and duration of vegetative risk would help improve predictions as climate change progresses.

Accurate predictions need to carefully consider how chilling and forcing cues vary across regions. Climatic variation across regions and at different distances from the coast results in varying durations of vegetative risk due to different chilling and forcing temperatures (Myking & Skroppa, 2007). It is therefore important to recognize climate regime extremes (e.g. seasonal trends, annual minima and annual maxima) across regions to better understand the interplay between duration of vegetative risk and climatic variation. The climatic implications of advancing forcing temperatures could potentially lead to earlier dates of budburst and enhance the risk of frost. These shifts in climatic regimes could vary in intensity across regions (i.e. regions currently at risk of false spring damage could become low risk regions over time).

Conclusion

Temperate forest trees are most at risk to frost damage in the spring due to the stochasticity of spring freezes. With warm temperatures advancing in the spring but last spring freeze dates advancing at a slower rate, there could be more damaging false spring events in the future, especially in high risk regions (Gu *et al.*, 2008; Inouye, 2008; Liu *et al.*, 2018). Current equations for evaluating false spring damage (e.g. Equation 1) largely simplify the myriad complexities involved in assessing false spring damage and risks. More studies aimed at understanding relationships between species avoidance and tolerance strategies, climatic regimes, and physiological cue interactions with the duration of vegetative risk would improve predictions. Additionally, research to establish temperature thresholds for damage across functional types and phenophases will help effectively predict false spring risk in the future. An integrated approach to assessing past and future spring freeze damage would provide novel insights into plant strategies, and offer more robust predictions as climate change progresses, which is essential for mitigating the adverse ecological and economic effects of false springs.

Acknowledgments

We thank D. Buonaiuto, W. Daly, A. Ettinger, and I. Morales-Castilla for comments and insights that improved the manuscript.

References

- Agrawal, A.A., Conner, J.K. & Stinchcombe, J.R. (2004) Evolution of plant resistance and tolerance to frost damage. *Ecology Letters* **7**, 1199–1208.
- Aitken, S.N. & Bemmels, J.B. (2015) Time to get moving: assisted gene flow of forest trees. *Evolutionary Applications* **9**, 271–290.
- Allstadt, A.J., Vavrus, S.J., Heglund, P.J., Pidgeon, A.M., Wayne, E. & Radeloff, V.C. (2015) Spring plant phenology and false springs in the conterminous U. S. during the 21st century. *Environmental Research Letters (submitted)* **10**, 104008.
- Augspurger, C.K. (2009) Spring 2007 warmth and frost: Phenology, damage and refoliation in a temperate deciduous forest. *Functional Ecology* **23**, 1031–1039.
- Augspurger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. *Ecology* **94**, 41–50.
- Ault, T.R., Henebry, G.M., de Beurs, K.M., Schwartz, M.D., Betancourt, J.L. & Moore, D. (2013) The False Spring of 2012, Earliest in North American Record. *Eos, Transactions American Geophysical Union* **94**, 181–182.
- Ault, T.R., Schwartz, M.D., Zurita-Milla, R., Weltzin, J.F. & Betancourt, J.L. (2015) Trends and natural variability of spring onset in the coterminous united states as evaluated by a new gridded dataset of spring indices. *Journal of Climate* **28**, 8363–8378.
- Barker, D., Loveys, B., Egerton, J., Gorton, H., Williams, W. & Ball, M. (2005) Co2 enrichment predisposes foliage of a eucalypt to freezing injury and reduces spring growth. *Plant, Cell and Environment* **28**, 1506–1515.

- Barlow, K., Christy, B., O’Leary, G., Riffkin, P. & Nuttall, J. (2015) Simulating the impact of extreme heat and frost events on wheat crop production: A review. *Field Crops Research* **171**, 109–119.
- Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* **165**, 73–81.
- 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.
- Beck, E.H., Heim, R. & Hansen, J. (2004) Plant resistance to cold stress: Mechanisms and environmental signals triggering frost hardening and dehardening. *Journal of Biosciences* **29**, 449–459.
- Burke, M., Gusta, L., Quamme, H., Weiser, C. & Li, P. (1976) Freezing and injury in plants. *Annual Review of Plant Physiology* **27**, 507–528.
- 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.
- Charrier, G., Bonhomme, M., Lacointe, A. & Améglio, T. (2011) Are budburst dates, dormancy and cold acclimation in walnut trees (*Juglans regia* L.) under mainly genotypic or environmental control? *International Journal of Biometeorology* **55**, 763–774.
- Chaine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3149–3160.
- Cleland, E., Chiariello, N., Loarie, S., Mooney, H. & Field, C. (2006) Diverse responses of phenology to global changes in a grassland ecosystem. *PNAS* **103**, 13740–13744.
- Dolezal, J., Dvorsky, M., Kopecky, M., Liancourt, P., Hiiesalu, I., Macek, M., Altman, J., Chlumska, Z., Rehakova, K., Capkova, K. & et al. (2016) Vegetation dynamics at the upper elevational limit of vascular plants in Himalaya. *Scientific Reports* **6**.
- Edwards, E.J., Chatelet, D.S., Spriggs, E.L., Johnson, E.S., Schlutius, C. & Donoghue, M.J. (2017) Correlation, causation, and the evolution of leaf teeth: A reply to Givnish and Kriebel. *Am J Bot* **104**, 509–515.

275 Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across all species in a
276 temperate forest community. *New Phytologist* **0**.

277 Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Peñuelas, J. & et al.
278 (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature* **526**, 104–107.

279 Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I. & Chuine, I. (2017) Integrating inter-
280 active effects of chilling and photoperiod in phenological process-based models. A case study with two European
281 tree species: *Fagus sylvatica* and *Quercus petraea*. *Agricultural and Forest Meteorology* **244-255**, 9–20.

282 Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007
283 Eastern US Spring Freeze: Increased Cold Damage in a Warming World. *BioScience* **58**, 253.

284 Harrington, C.A. & Gould, P.J. (2015) Tradeoffs between chilling and forcing in satisfying dormancy requirements for
285 pacific northwest tree species. *Frontiers in Plant Science* **6**.

286 Hofmann, M. & Bruehlheide, H. (2015) Frost hardiness of tree species is independent of phenology and macroclimatic
287 niche. *Journal of Biosciences* **40**, 147–157.

288 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O’Keefe, J. & Richardson, A.D. (2012) Ecological
289 impacts of a widespread frost event following early spring leaf-out. *Global Change Biology* **18**, 2365–2377.

290 Inouye, D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wild-
291 flowers. *Ecology* **89**, 353–362.

292 IPCC (2015) *Climate change 2014: mitigation of climate change*, vol. 3. Cambridge University Press.

293 Knudson, W. (2012) The Economic Impact of the Spring’s Weather on the Fruit and Vegetable Sectors. *The Strategic*
294 *Marketing Institute Working Paper* **0**.

295 Kollas, C., Körner, C. & Randin, C.F. (2014) Spring frost and growing season length co-control the cold range limits
296 of broad-leaved trees. *Journal of Biogeography* **41**, 773–783.

- Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2013) Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of freezing damage in temperate trees. *Functional Ecology* **30**, 1–11.
- Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety margins against damage by spring freeze events along elevational gradients. *New Phytologist* **200**, 1166–1175.
- 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**.
- Longstroth, M. (2012) Protect blueberries from spring freezes by using sprinklers. url.
- Longstroth, M. (2013) Assessing frost and freeze damage to flowers and buds of fruit trees. url.
- Ludlum, D.M. (1968) *Early American Winters: 1604-1820*. 3, Boston: American Meteorological Society.
- Marino, G.P., Kaiser, D.P., Gu, L. & Ricciuto, D.M. (2011) Reconstruction of false spring occurrences over the south-eastern United States, 1901–2007: an increasing risk of spring freeze damage? *Environmental Research Letters* **6**, 24015.
- 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.
- Mehdipoor, H. & Zurita-Milla, E.I.V.R. (2017) Continental-scale monitoring and mapping of false spring: A cloud computing solution. University of Leeds.
- 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.
- Mock, C.J., Mojzisek, J., McWaters, M., Chenoweth, M. & Stahle, D.W. (2007) The winter of 1827–1828 over eastern

North America: a season of extraordinary climatic anomalies, societal impacts, and false spring. *Climatic Change* **83**, 87–115.

Muffler, L., Beierkuhnlein, C., Aas, G., Jentsch, A., Schweiger, A.H., Zohner, C. & Kreyling, J. (2016) Distribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the northern hemisphere. *Global Ecology and Biogeography* **25**, 1061–1071.

Myking, T. & Skroppa, T. (2007) Variation in phenology and height increment of northern *Ulmus glabra* populations: Implications for conservation. *Scandinavian Journal of Forest Research* **22**, 369–374.

O’Keefe, J. (2014) Phenology of Woody Species at Harvard Forest since 1990. Tech. rep.

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.

Pearce, R. (2001) Plant freezing and damage. *Annals of Botany* **87**, 417–424.

Peterson, A.G. & Abatzoglou, J.T. (2014) Observed changes in false springs over the contiguous United States. *Geophysical Research Letters* **41**, 2156–2162.

Prozherina, N., Freiwald, V., Rousi, M. & Oksanen, E. (2003) Interactive effect of springtime frost and elevated ozone on early growth, foliar injuries and leaf structure of birch (*Betula pendula*). *New Phytologist* **159**, 623–636.

Richardson, A. & O’Keefe, J. (2009) *Phenological differences between understory and overstory: a case study using the long-term harvard forest records*, pp. 87–117. A. Noormets (Ed.), *Phenology of Ecosystem Processes*, Springer, New York.

Richardson, A.D. (2015) PhenoCam images and canopy phenology at Harvard Forest since 2008.

Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants*. Springer-Verlag.

Sánchez, B., Rasmussen, A. & Porter, J.R. (2013) Temperatures and the growth and development of maize and rice: a review. *Global Change Biology* **20**, 408–417.

- Schaber, J. & Badeck, F.W. (2005) Plant phenology in germany over the 20th century. *Regional Environmental Change* **5**, 37–46.
- Schwartz, M.D. (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography* **14**(6), 536–550.
- Soudani, K., Hmimina, G., Delpierre, N., Pontailier, J.Y., Aubinet, M., Bonal, D., Caquet, B., de Grandcourt, A., Burban, B., Flechard, C. & et al. (2012) Ground-based network of ndvi measurements for tracking temporal dynamics of canopy structure and vegetation phenology in different biomes. *Remote Sensing of Environment* **123**, 234–245.
- Taschler, D., Beikircher, B. & Neuner, G. (2004) Frost resistance and ice nucleation in leaves of five woody timberline species measured in situ during shoot expansion. *Tree Physiology* **24**, 331–337.
- USA-NPN (2016) USA National Phenology Network Extended Spring Indices.
- 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., Hoch, G. & Körner, C. (2014a) Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of damage than adult trees. *Journal of Ecology* **102**, 981–988.
- Vitasse, Y., Lenz, A. & Körner, C. (2014b) The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science* **5**, 541.
- Vitra, A., Lenz, A. & Vitasse, Y. (2017) Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist* **216**, 113–123.
- White, M.A., De Beurs, K.M., Didan, K., Inouye, D.W., Richardson, A.D., Jensen, O.P., O’Keefe, J., Zhang, G., Nemani, R.R., Van Leeuwen, W.J.D. & Al., E. (2009) Intercomparison, interpretation, and assessment of spring phenology in north america estimated from remote sensing for 1982–2006. *Global Change Biology* **15**, 2335–2359.
- Xie, Y., Wang, X. & Silander, J.A. (2015) Deciduous forest responses to temperature, precipitation, and drought imply complex climate change impacts. *Proceedings of the National Academy of Sciences* **112**, 13585–13590.

Xin, Q. (2016) 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.

Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123.



Figure 1: FSI values from 2008 to 2014 vary across methodologies. To calculate spring onset, we used the USA-NPN Extended Spring Index tool for the USA-NPN FSI values, which are in red (USA-NPN, 2016), long-term ground observational data for the observed FSI values, which are in green (O'Keefe, 2014), and near-surface remote-sensing canopy data for the PhenoCam FSI values, which are in blue (Richardson, 2015). The dotted line at $y=0$ indicates a false spring and a dotted line at $y=7$ indicates the 7 day threshold frequently used in false spring definitions.

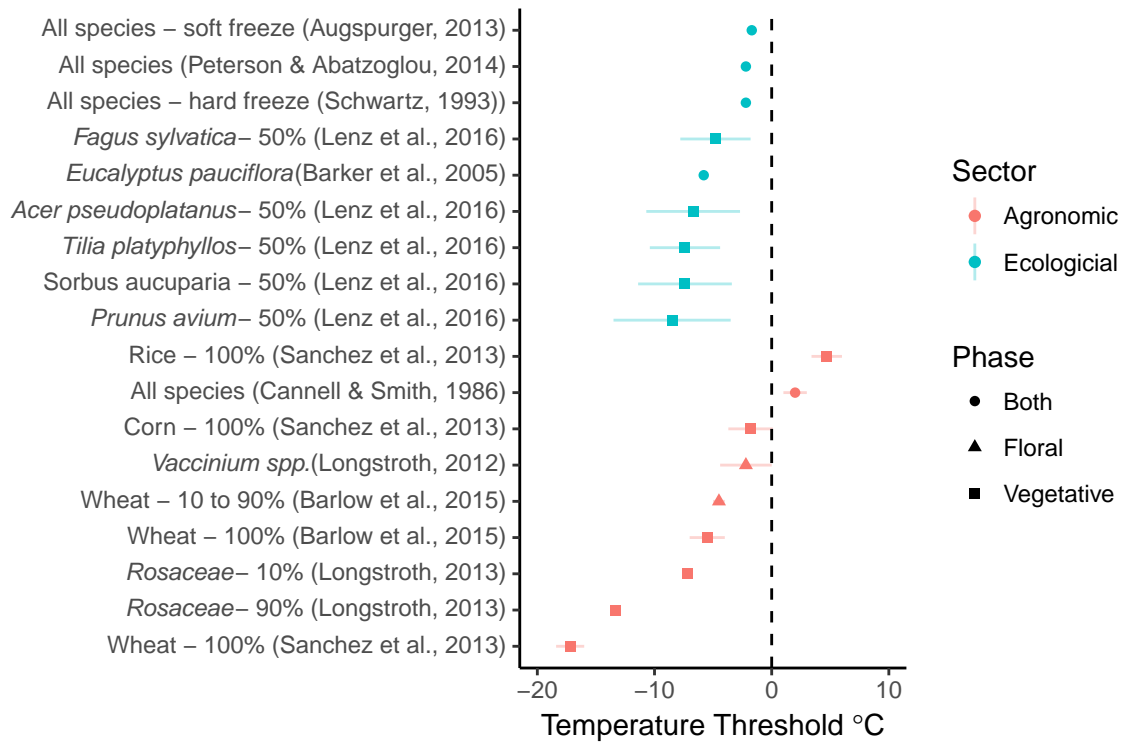


Figure 2: A comparison of damaging spring freezing temperature thresholds across ecological and agronomic studies. Each study is listed on the y axis along with the taxonomic group of focus. Next to the species name is the freezing definition used within that study (e.g. 100% is 100% lethality). Each point is the best estimate recorded for the temperature threshold with standard deviation if indicated in the study. The shape of the point represents the phenophases of interest and the colors indicate the type of study (i.e. agronomic or ecological).

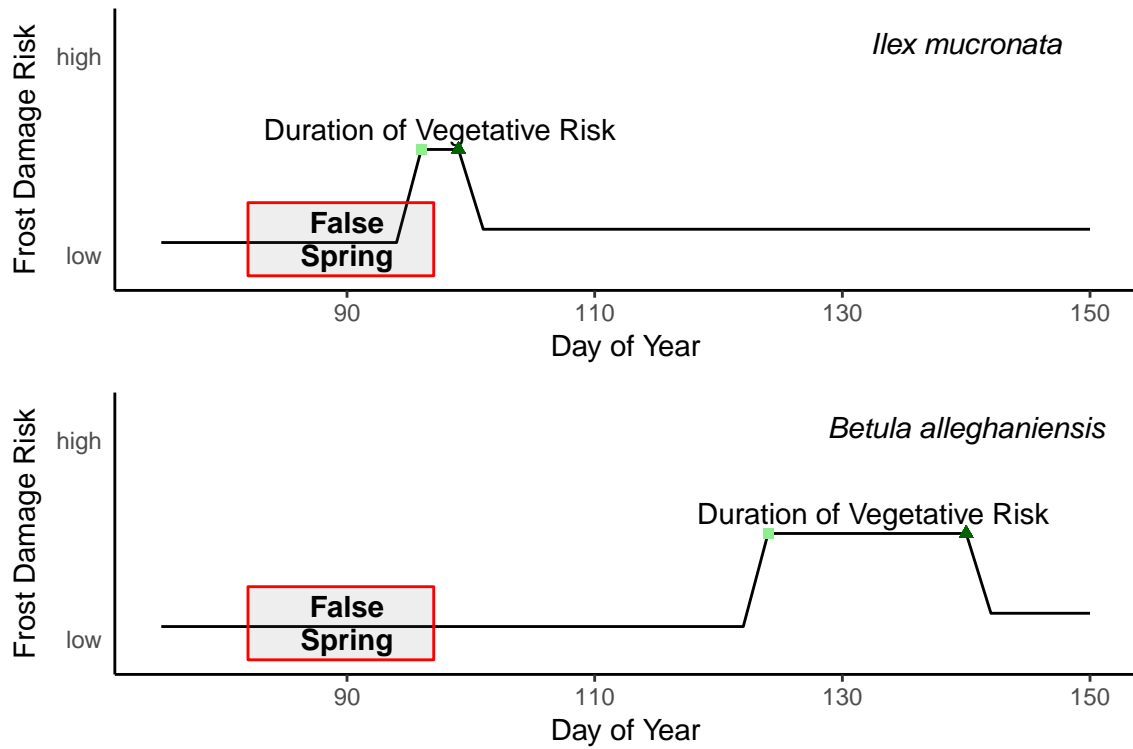


Figure 3: A figure showing the differences in spring phenology and false spring risk across two species: *Ilex mucronata* (L.) and *Betula alleghaniensis* (Marsh.). We mapped a possible false spring event based on historic weather data and compared it to the observational data collected at Harvard Forest (O’Keefe, 2014). In this scenario, the *Ilex mucronata*, which budburst early, would be exposed to a false spring event during its duration of vegetative risk (i.e. from budburst to leafout), whereas the *Betula alleghaniensis* would avoid it entirely, due to later budburst. Budburst is indicated by the light green squares and leafout is indicated by the dark green triangles.

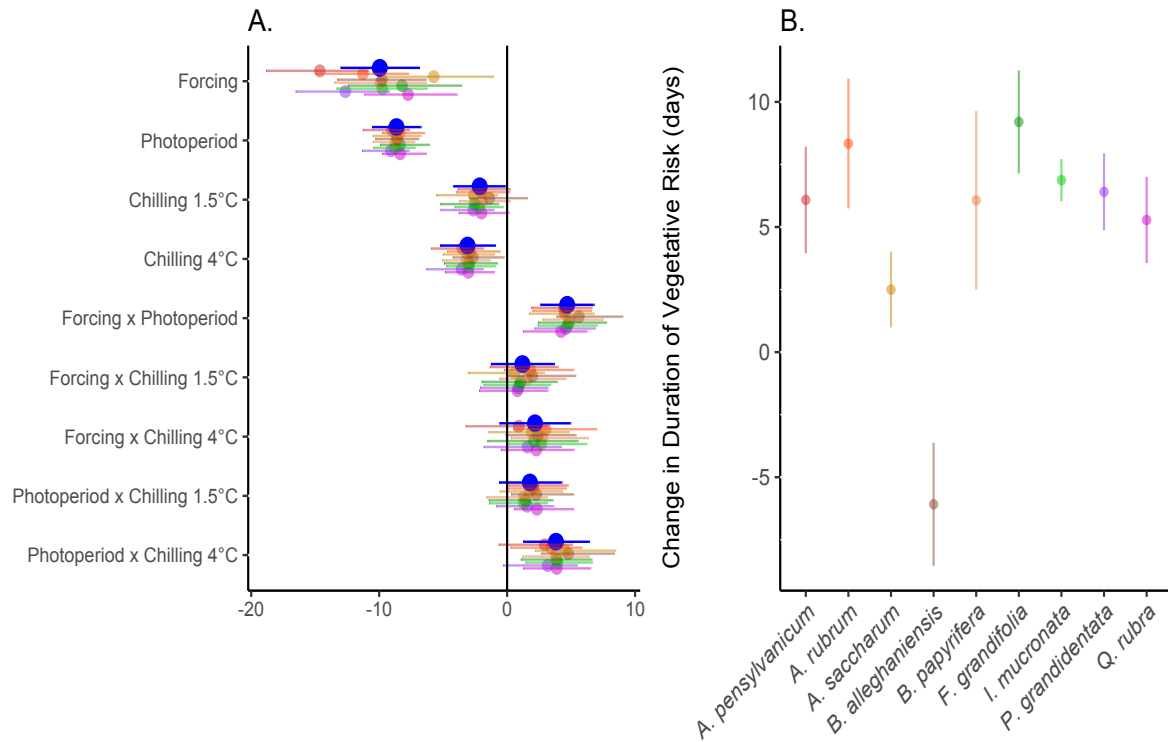


Figure 4: How major cues of spring phenology alter vegetative risk. (A) A plot of the model parameter estimates on the duration of vegetative risk from experimental results (means \pm 95% credible intervals, slightly larger blue circles represent the overall mean estimate, while each species estimate is shown below and colored as shown in B). Higher forcing temperatures decreased the period of vegetative risk the most (by 10 days overall given a 10 degree difference), as did photoperiod (by 9 days overall given a 4 hour increase). However, together these effects offset, thus the combined effect of greater forcing and longer photoperiod would be a reduction in duration of vegetative risk of 14 days due to a 5 day delay through their interaction. (B) A comparison of the durations of vegetative risk (means \pm standard error) across two treatments (high chilling and high forcing temperatures vs. low chilling and low forcing) for each species collected for the experiment. Species along the x-axis are ordered by day of budburst. *Betula alleghaniensis* was the only species that had a shorter duration of vegetative risk under the low chilling and low forcing treatment.