Rethinking False Spring Risk

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1 Abstract

Trees and shrubs growing in temperate environments are at risk of being exposed to late spring freezes, or false spring events, which can be damaging ecologically and economically. As climate change may alter the potential prevalence and severity of false spring events, our ability to accurately forecast such events has become more critical. Yet currently, false spring studies largely simplify the various ecological elements that could predict the level of plant damage from late spring freezing events. Here we review how to improve false spring equations for future projections. In particular we highlight how integrating species, life stage, and habitat differences could help accurately determine the level of damage sustained by a false spring event. (The ultimate intent is to demonstrate how an integrated view of false spring that incorporates these factors would rapidly advance progress in this field.) We believe our suggested approaches could help rapidly advance understanding and forecasting of false spring events in climate change and ecological studies.

2 Introduction

Plants growing in temperate environments time their growth each spring to follow rising temperatures and increasing light and soil resource availability. While tracking spring resource availability, temperate plants are at risk of late spring freezes, which can be detrimental to growth. Individuals that leaf out before the last freeze date are at risk of leaf loss, damaged wood tissue, and slowed or stalled canopy development (Gu *et al.*, 2008; Hufkens *et al.*, 2012). These damaging late spring freezing events are known as false springs, and are widely documented to result in highly 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 greater fluctuations in temperature (Cannell & Smith, 1986; Inouye, 2008; Martin *et al.*, 2010). Temperate forest species around the world are initiating leafout about 4-6 days earlier per degree Celsius (Wolkovich *et al.*, 2012; Polgar *et al.*, 2014) and the magnitude of temperature variation is predicted to increase in certain habitats (Thompson *et al.*, 2013; Vasseur *et al.*, 2014). For these reasons, false spring events are expected to intensify in some regions (Kodra *et al.*, 2011; Allstadt *et al.*, 2015). Already, multiple studies have documented false spring events in recent years (Gu *et al.*, 2008; Augspurger, 2009; Knudson, 2012; Augspurger, 2013) and some have linked these events to climate change (Ault *et al.*, 2013; Allstadt *et al.*, 2015; Muffler *et al.*, 2016; Xin, 2016). This increasing interest in false spring events 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 on future trends, researchers need methods that properly evaluate the effects of false spring events across the diverse species, habitats and climate regimes they are studying.

Current metrics for estimating false springs events are generally simple: often requiring an estimate for the start of 'spring' and whether temperatures occurred below a particular temperature threshold in the following week. Such estimates inherently assume consistency of responses across species, functional group, life stages, habitat type, and other climatic regimes, ignoring that such factors can greatly impact plants' false spring risk. As a result, such indices will most likely 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 aim to highlight the complexity of factors driving a plant's false spring risk and provide a road map for improved metrics. First, we review the currently used definitions of false spring. Then, combining research from plant physiology, climatology and community ecology, we outline major gaps in current definitions. In particular we show how life stage (Caffarra & Donnelly, 2011), location within a forest or canopy (Augspurger, 2013), interspecific variation in avoidance and tolerance strategies (Flynn & Wolkovich 2017?), freeze temperature thresholds, and regional effects (Martin *et al.*, 2010) 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.

3 Defining False Spring: An example in one temperate plant community

Temperate forest plants are most at risk to frost damage from episodic spring frosts (Sakai & Larcher, 1987). Due to the stochastic nature of episodic spring frosts, plants must exhibit flexible spring phenologies in order to minimize freezing risk. Freezing temperatures following a warm spell could result in plant damage or even death (Ludlum, 1968; Mock *et al.*, 2007). Intracellular ice formation from false spring events often results in severe leaf and stem damage. Ice formation can also occur indirectly (i.e. extracellularly), which results in freezing dehydration and mimics extreme drought conditions (Pearce, 2001; Beck *et al.*, 2004; Hofmann & Bruelheide, 2015). Both forms of ice formation can cause defoliation and, ultimately, crown dieback (Gu *et al.*, 2008). 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.*, 2014a). An effective and consistent definition of false spring that more accurately determines the amount and type of ice formation is essential 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). Another definition instills a more precise temporal parameter, specific to the Midwestern United States, and is defined as a warmer than average March, a freezing April, and enough growing degree days between budburst and the last freeze date (Augspurger, 2013). 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 a damage to occur from a late spring freeze. Currently, FSI is evaluated by the day of budburst and the day of last spring freeze through a simple equation as seen below (Marino *et al.*, 2011).

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

A damaging FSI is currently defined to be 7 or more days between budburst and the last freeze date (Equation 1) (Peterson & Abatzoglou, 2014). The 7 day parameter exposes less resistant foliate phenophases to a false spring, thus putting the plant at a higher risk of 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 (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 become unhinged 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 for different species or functional groups within a forest community. 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 affect 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. 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 of the study species 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 against false springs.

4 Plant Physiology and Diversity versus the Current False Spring Definition

Plants have evolved to minimize false spring damage through two strategies: avoidance and tolerance. Effective avoidance strategies require well-timed spring phenologies. 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 (Cleland *et al.*, 2007; Chuine, 2010). The evolution of these three cues and their interactions has permitted temperate plant species to occupy more northern ecological niches and decrease the risk of false spring damage, which is crucial for avoidance strategies (Samish,

1954). One avoidance strategy, for example, is the interaction between over-winter chilling and spring forcing temperatures. Warm temperatures earlier in the year (i.e. in February) 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 will likely delay budburst and evade false spring events as spring continues to advance earlier in the year (Basler & Korner, 2014).

Some temperate forest species have evolved to be more tolerant of spring freezing temperatures, rather than try to avoid frosts via more flexible phenologies. Temperate forest plants utilize various morphological strategies to be more frost tolerant: some have toothed or lobed leaves to increase 'packability' in winter buds, which permits more rapid leafout and minimizes exposure time of less resistant tissues (Edwards *et al.*, 2017). Other species have young leaves with more trichomes to act as a buffer against spring frosts (Agrawal *et al.*, 2004), and many are able to respond to abiotic cues such as consistently dry winters. Species living in habitats with drier winters develop shoots and buds with decreased water content, which makes the buds more tolerant to drought and also to false spring events (Beck *et al.*, 2007; Morin *et al.*, 2007; Norgaard Nielsen & Rasmussen, 2009; Poirier *et al.*, 2010; Kathke & Bruelheide, 2011; Hofmann & Bruelheide, 2015). More studies are needed to investigate the interplay between false spring events, leaf morphology, and precipitation and how these relationships affect false spring tolerance. Given the diverse array of spring freezing defense mechanisms, predicting damage by false spring events requires a greater understanding of avoidance and tolerance strategies across species, especially with a changing climate.

5 Defining Vegetative Risk: Complexities due to Species' Strategies and Climate

Phenology and frost tolerance are intertwined. Different phenological phases respond differently to false spring events. Flowering and fruiting phenophases are generally more sensitive than vegetative phases (Augspurger, 2009; Lenz *et al.*, 2013). (False spring events that occur during the vegetative growth phenophases impose the greatest freezing threat to deciduous tree and shrub species because plants will suffer greater long-term effects from the loss of photosynthetic tissue, which could impact multiple years of growth, reproduction, and canopy development (Sakai & Larcher, 1987; Vitasse *et al.*, 2014b). Within certain phenological phases (i.e. before full leafout of the entire plant) plants are more likely to sustain damage from a false spring than individuals past the leafout phenophase. Spring phenology is thus a crucial measure for how much damage a plant will sustain from a freezing event.

Freezing tolerance steadily decreases 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 level of damage from a false spring event. We will refer to the timing of these collective phenophases (i.e. budburst to leafout) as the duration of vegetative risk. The duration of vegetative risk is usually extended if a freezing event occurs during the phenophases between budburst and full leafout (Augspurger, 2009). One hypothesis suggests that species with short durations of vegetative risk often sustain higher levels of damage but if the duration of vegetative risk is longer, then the buds and leaves will be more tolerant against frosts (Augspurger, 2009), however this has yet to be tested thoroughly.

Different species respond differently to anthropogenic climate change, which causes differences in spring phenologies. Most species are expected to begin leafout earlier in the season with warming spring temperatures but some species may have the opposite response due to less winter chilling or decreased photoperiod cues (Cleland *et al.*, 2006; Yu *et al.*, 2010; Xin, 2016). Studies indicate that species growing at more northern latitudes tend to respond more to photoperiod than species growing further south and, subsequently, these species may have a longer durations of vegetative risk (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011). Furthermore, larger canopy species exhibit greater photoperiod sensitivities than shade tolerant or understory species (Basler & Körner, 2012) and they also, generally, require more chilling in the winter and greater forcing temperatures in the spring to initiate budburst (Laube *et al.*, 2013). Individuals that initiate budburst earlier in the spring may attempt to limit freezing risk by decreasing the duration of vegetative risk. We assessed climate data across Europe, long-term observational data, and experimental data to gain a better understanding of the the interaction between duration of vegetative risk and false spring events.

5.1 Predictable Regional Differences in Climate, Species Response and False Spring Risk

Numerous studies have investigated the the relationship between budburst and photoperiod by using latitudinal gradients (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011; Zohner *et al.*, 2016; Gauzere *et al.*, 2017), however few have integrated longitudinal variation or regional effects. Yet climate and thus false spring risk varies important across regions. For example, consider ... [no walk reader through some of the major results, just like with the Harvard Forest figure of FSI.] We found that some regions had a much higher risk of false spring (i.e. Maine) than others (i.e. Lyon) (Figure **??**). 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.

Predictions will want to consider carefully how chilling and forcing, which are key drivers of budburst and leafout, vary significantly across a longitudinal gradient. Climatic variation across regions results in varying

durations of vegetative risk due to different chilling and forcing temperatures. For this reason, it is important to include climate regime extremes (e.g. annual minima and annual maxima) in future studies. It is essential to recognize the differences in habitats and the amplitude and variation in temperature extremes across regions in order to properly assess spring plant phenology and false spring risk.

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. habitats currently at risk of false spring damage could become low risk regions over time). There are also discrepancies in defining a false spring event, especially with understanding damaging freezing temperatures. Some regions and species may tolerate lower temperature thresholds than others (Figure 5). It is crucial to gain an understanding on which climatic parameters result in false spring events and how these parameters may vary across regions. It is anticipated that most regions will have earlier spring onsets, however, last freeze dates will not advance at the same rate (Inouye, 2008; Martin *et al.*, 2010; Labe *et al.*, 2016), rendering some regions and species to be more susceptible to false spring events in the future.

5.2 Changes in Phenological Cues and the Duration of Vegetative Risk

The risk of false spring may shift regionally as climate change progresses and forcing temperatures advance. When considering false springs, it is important to recognize that forcing temperatures directly affect the duration of vegetative risk: years with lower forcing temperatures and fewer growing degree days will have longer durations of vegetative risk (Donnelly *et al.*, 2017). With spring advancing, it is anticipated that there will be greater fluctuations in spring forcing temperatures (Martin *et al.*, 2010). These fluctuations in spring temperature are expected to oscillate above and below the development threshold within a spring season. With less consistent forcing temperatures, we would expect to see longer durations of vegetative risk in a changing climate. Therefore, it is hypothesized that the species able to track the shifts in spring advancement due to climate change will be more susceptible to false spring damage (Scheifinger *et al.*, 2003). We investigated this interaction using observational data from Harvard Forest (O'Keefe, 2014) and compared two years of data: one year that had an unusually early spring onset (2010) and another year that an unusually late spring onset (2014).

By comparing the durations of vegetative risk to the growing degree days for each year, we found that the number of growing degree days were highly comparable for both years (Figure 2). Observational data failed to demonstrate the expected result. However, phenological data in an experimental context suggests differently.

5.3 Interaction of Phenological Cues and the Duration of Vegetative Risk

Each species responds differently to climate change, therefore, it is important to consider the interaction between cues and species when thinking about the duration of vegetative risk. Spring forcing temperatures and day length requirements for budburst to occur vary among species and across habitats. Since species distributions are largely driven by phenology (Chuine *et al.*, 2001), species less reliant on photoperiod cues are likely to out compete species that are reliant on photoperiod cues as spring forcing temperatures continue to initiate earlier (Vitasse *et al.*, 2011; Gauzere *et al.*, 2017). Similarly, as climate change progresses, higher spring forcing temperatures may be required due to potentially insufficient winter chilling, especially at lower latitudes (McCreary *et al.*, 1990; Morin *et al.*, 2009; Fu *et al.*, 2012; Polgar *et al.*, 2014; Chuine, 2010). Anthropogenic climate change will cause changes in winter and spring temperatures, resulting in greater differences in spring phenology cue requirements across species and regions. This interaction of cues and how climate change will affect that interaction is crucial to understand in order to recognize which species will likely become more at risk of false spring events in the future.

We assessed data from a growth chamber experiment in order to investigate the interaction of cues across species and predict potential shifts in duration of vegetative risk with climate change. We compared 9 temperate forest species between two treatments: high chilling hours, long photoperiod and high forcing temperatures (WL1) against no additional chilling, short photoperiod and low forcing temperatures (CS0) (Flynn and Wolkovich, 2017?). According to the results, individuals that initiate budburst earlier in the season (i.e. *Betula papyrifera* (Marsh.) and *Ilex mucronata* (L.)) tend to initiate budburst early regardless of treatment, but the treatment does affect the duration of vegetative risk significantly (Figure 3). As the season progresses, treatment does not affect the duration of vegetative risk as much but the day of budburst tends to be later in the season with the weaker treatment effects (i.e. CS0). Anova results indicate forcing temperatures and photoperiod length determine the duration of vegetative risk more than chilling requirements. This could suggest that chilling influences budburst and leafout similarly, while photoperiod and forcing temperatures have varying effects on the two phenophases. With a changing climate, forcing temperatures will increase and initiate earlier in the season while photoperiod cues will remain stagnant or decrease. This cue interaction could potentially elongate the duration of vegetative risk and expose at risk plants to more intense false spring events or even multiple events in one year. Further studies are essential to investigate the interplay between chilling, forcing, and photoperiod cues on the duration of vegetative risk, especially for species occupying ecological niches more susceptible to false spring events.

6 Conclusion

The risk of false spring damage varies across years and regions and the timing between last freeze date and date of spring onset may become less consistent. With warm temperatures advancing in the spring but last spring freeze dates staying the same, there could potentially be more damaging events in the future, especially in high risk regions (Gu *et al.*, 2008; Inouye, 2008). This shift in timing could result in more events where understory species leaf out prior to the last freeze and escape frost damage but canopy species may be at higher risk, thus potentially resulting in crown dieback for the larger tree species and subsequently enhanced sun exposure and damage to understory species. For these reasons, a greater understanding of false spring damage as climate change progresses is necessary.

By utilizing only two simple metrics (last freeze date and spring onset date), researchers fail to assess the myriad of factors essential in determining false spring risk and damage. Future studies are necessary to gain an understanding with relationships between species, functional group, phenophase, and region and the differences in false spring damage. It is also essential that a temperature threshold is established for all functional types and phenophases across regions in order to effectively predict false spring risk in the future. An integrated approach to assessing past and future spring freeze damage must be realized as global climate change progresses in order to mitigate the adverse ecological and economic effects of false springs.

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.

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., Zurita-Milla, R. & Schwartz, M.D. (2015) A Matlab{©} toolbox for calculating spring indices from daily meteorological data. *Computers {&} Geosciences* **83**, 46–53.

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., Fettig, S., Knake, C., Hartig, K. & Bhattarai, T. (2007) Specific and unspecific responses of plants to cold and drought stress. *Journal of Biosciences* **32**, 501–510.

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.

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.

Cannell, M. & Smith, R. (1986) Climatic Warming , Spring Budburst and Forest Damage on Trees Author (s): M . G . R . Cannell and R . I . Smith Published by : British Ecological Society Stable URL : http://www.jstor.org/stable/2403090 JSTOR is a not-for-profit service that helps schol. *Journal of Applied Ecology* **23**, 177–191.

Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society B: Biological Sciences* **365**, 3149–3160.

Chuine, I., Aitken, S.N. & Ying, C.C. (2001) Temperature thresholds of shoot elongation in provenances ofpinus contorta. *Canadian Journal of Forest Research* **31**, 1444–1455.

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.

Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.

Donnelly, A., Yu, R., Caffarra, A., Hanes, J.M., Liang, L., Desai, A.R., Liu, L. & Schwartz, M.D. (2017) Interspecific and interannual variation in the duration of spring phenophases in a northern mixed forest. *Agricultural and Forest Meteorology* **243**, 55–67.

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.

Fu, Y.H., Campioli, M., Van Oijen, M., Deckmyn, G. & Janssens, I.A. (2012) *Bayesian comparison of six different temperature-based budburst models for four temperate tree species*, vol. 230.

Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I. & Chuine, I. (2017) Integrating 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.

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

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**, 2365–2377.

Inouye, D.W. (2008) Effects of climate chnage on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**, 353–362.

Kathke, S. & Bruelheide, H. (2011) Differences in frost hardiness of two norway spruce morphotypes growing at mt. brocken, germany. *Flora - Morphology, Distribution, Functional Ecology of Plants* **206**, 120–126.

Knudson, W. (2012) The economic impact of the spring's weather on the fruit and vegetable sectors. *The Strategic Marketing Institute Working Paper* .

Kodra, E., Steinhaeuser, K. & Ganguly, A.R. (2011) Persisting cold extremes under 21st-century warming scenarios. *Geophysical Research Letters* **38**, 1–5.

Labe, Z., Ault, T. & Zurita-Milla, R. (2016) Identifying anomalously early spring onsets in the cesm large ensemble project. *Climate Dynamics* **48**, 3949–3966.

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* pp. 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.

Ludlum, D.M. (1968) *Early American Winters: 1604-1820*. 3, American Meteorological Society.

Marino, G.P., Kaiser, D.P., Gu, L. & Ricciuto, D.M. (2011) Reconstruction of false spring occurrences over the southeastern 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.

McCreary, D.D., Lavender, D.P. & Hermann, R.K. (1990) Predicted global warming and Douglas-fir chilling requirements. *Annales des Sciences Forestieres* **47**, 325–330.

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.

Morin, X., Ameglio, T., Ahas, R., Kurz-Besson, C., Lanta, V., Lebourgeois, F., Miglietta, F. & Chuine, I. (2007) Variation in cold hardiness and carbohydrate concentration from dormancy induction to bud burst among provenances of three european oak species. *Tree Physiology* **27**, 817–825.

Morin, X., Lechowicz, M.J., Augspurger, C., O'keefe, J., Viner, D. & Chuine, I. (2009) Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology* **15**, 961–975.

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.

Norgaard Nielsen, C.C. & Rasmussen, H.N. (2009) Frost hardening and dehardening in abies procera and other conifers under differing temperature regimes and warm-spell treatments. *Forestry* **82**, 43–59.

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.

Poirier, M., Lacointe, A. & Ameglio, T. (2010) A semi-physiological model of cold hardening and dehardening in walnut stem. *Tree Physiology* **30**, 1555–1569.

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.

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. Springer.

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.

Samish, R. (1954) Dormancy in woody plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **5**, 183–204.

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.

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.

Thompson, R.M., Beardall, J., Beringer, J., Grace, M. & Sardina, P. (2013) Means and extremes: building variability into community-level climate change experiments. *Ecology Letters* **16**, 799–806.

USA-NPN (2016) USA National Phenology Network Extended Spring Indices.

Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C., McCann, K.S., Savage, V., Tunney, T.D. & I., O.M. (2014) Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society* **281**, 1–8.

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., Francois, C., Delpierre, N., Dufrene, E., Kremer, A., Chuine, I. & Delzon, S. (2011) Assessing the effects of climate change on the phenology of european temperate trees. *Agricultural and Forest Meteorology* **151**, 969–980.

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.

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. & Cleland, E.E. (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**, 18–21.

Xin, Q. (2016) A risk-benefit model to simulate vegetation spring onset in response to multi-decadal climate variablity: Theoretical basis and applications from the field to the Northern Hemisphere. *Agriculture and Forest Meteorology* pp. 139–163.

Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology on the tibetan plateau. *Proc Natl Acad Sci U S A* **107**, 22151–6.

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.

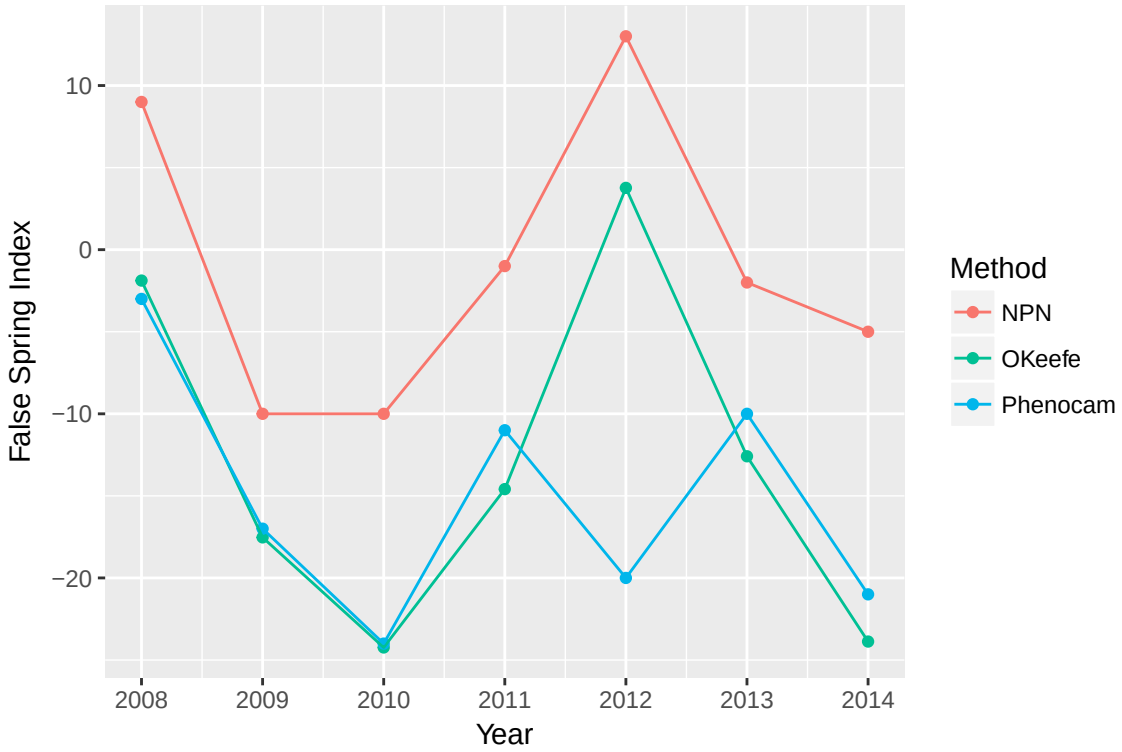

Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methdology used in this study. USA-NPN FSI values are green (USA-NPN, 2016), observed FSI values are blue (O'Keefe, 2014), and PhenoCam FSI values are red (Richardson, 2015).

```
## lmer(formula = risk ~ chilling + warm + photo + (chilling + warm +
##     photo | species), data = dxx)
##             coef.est coef.se
## (Intercept) 53.35     6.15
## chilling    -0.10     0.36
## warm        -1.54     0.19
## photo       -1.19     0.15
##
## Error terms:
##  Groups   Name        Std.Dev. Corr
##  species  (Intercept) 17.27
##           chilling     0.61    -0.73
##           warm         0.50    -1.00  0.78
##           photo        0.29    -0.98  0.84  0.99
##  Residual              7.44
## ---
## number of obs: 996, groups: species, 9
## AIC = 6896.2, DIC = 6861.6
## deviance = 6863.9
```

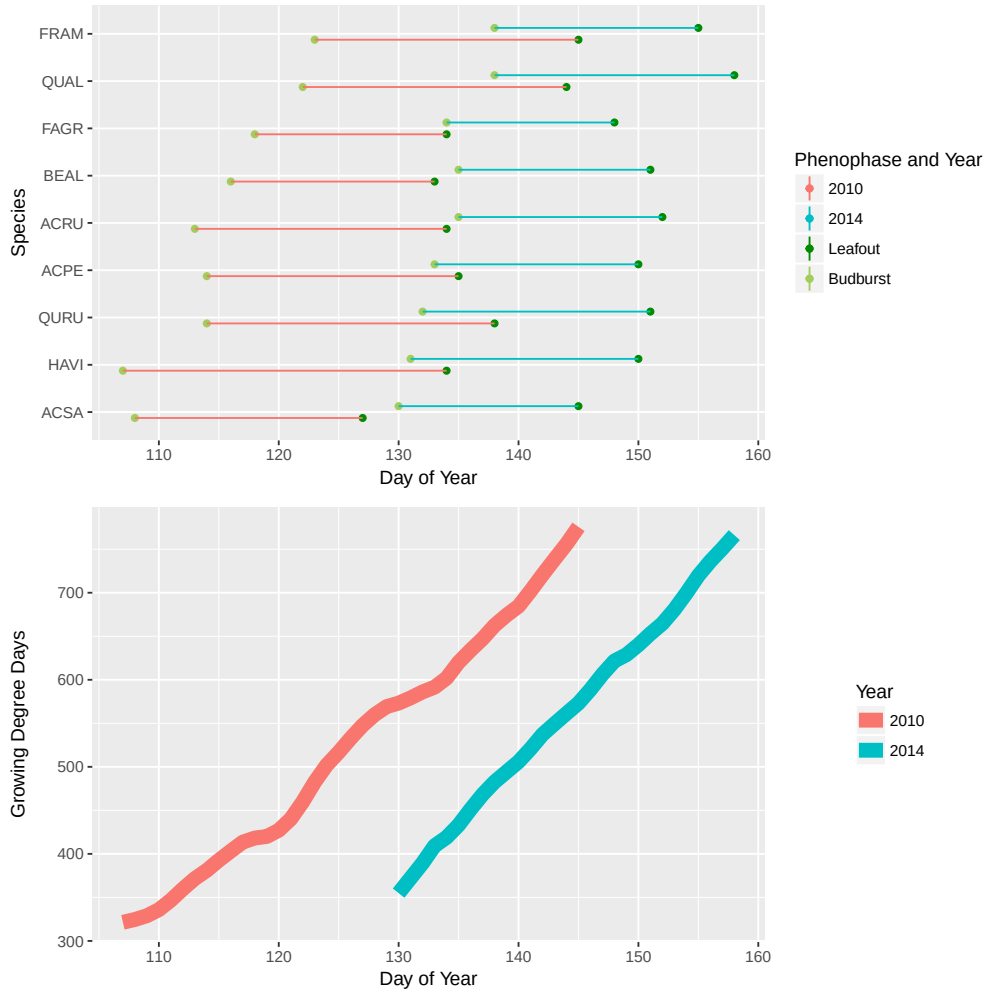

Figure 2: A comparison of two years of observational data investigating the effects of growing degree days on the duration of vegetative risk. The average duration of vegetative risk for 2010 was 21 +/- 3.39 days versus 17.1 +/- 1.96 days in 2014.

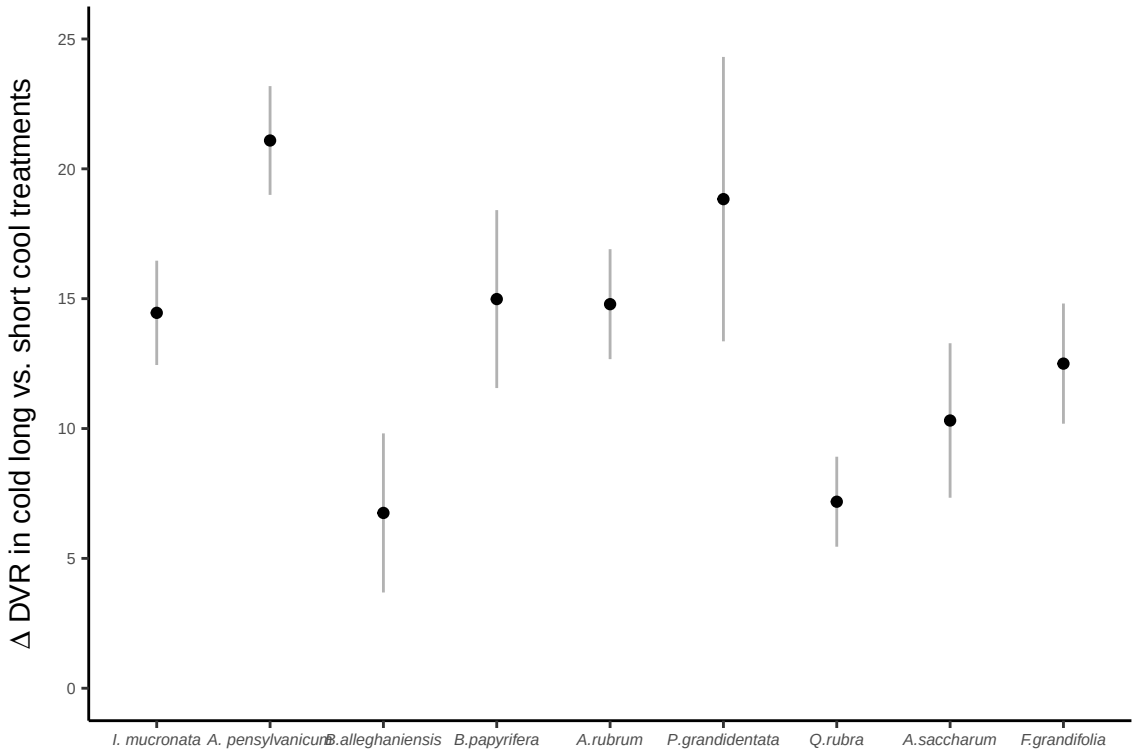

Figure 3: This figure is comparing difference in duration of vegetative risk across two treatments for each species collected for the experiment. Data was collected from a growth chamber experiment where one treatment had no additional overwinter chilling, low spring forcing temperatures, and shorter spring daylengths and the other had additional overwinter chilling, high spring forcing temperatures, and longer spring daylenghts. The standard error is represented by the bars around each point.

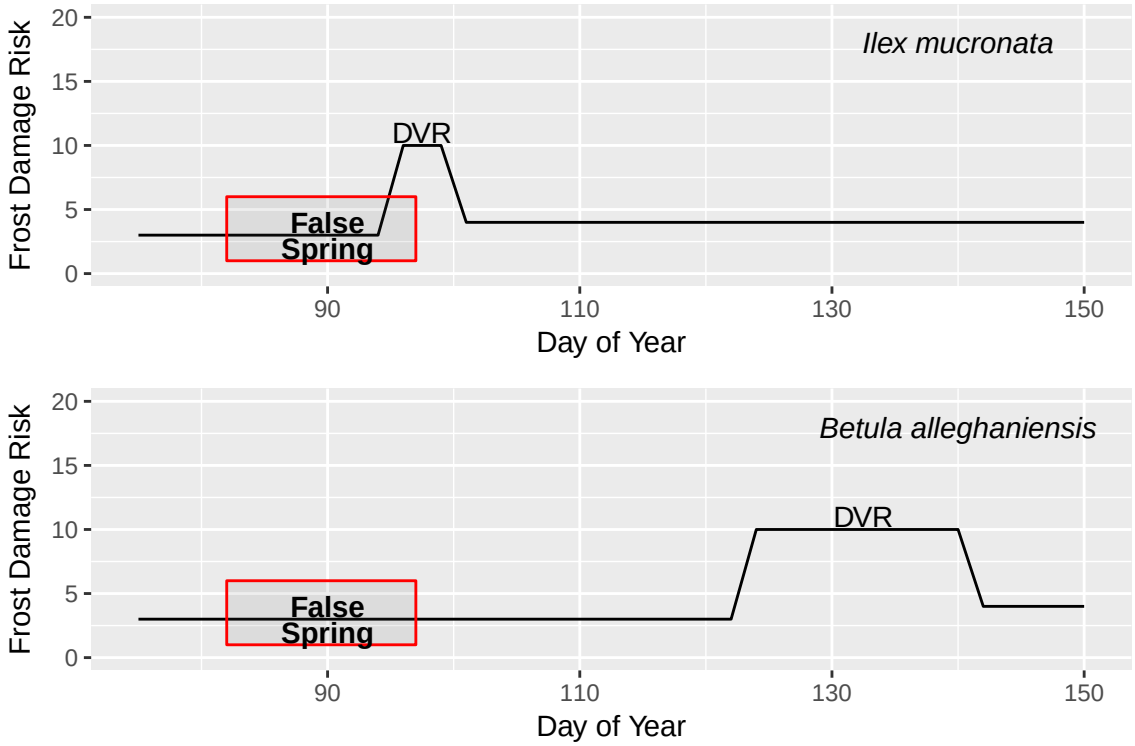

Figure 4: A figure showing the differences in spring phenology and false spring risk across two species: *Ilex mucronata* and *Betula alleghaniensis*. We mapped a possible false spring event based on historic weather data and compared it to the observational data collected at Harvard Forest (O'Keefe, 2014). In this scenario, the *Ilex mucronata* would be exposed to a false spring event, whereas the *Betula alleghaniensis* would avoid it entirely. DVR stands for Duration of Vegetative Risk.

Figure 5: A comparison of damaging spring freezing temperature thresholds across ecological and agrinomic studies. Each study is listed on the y axis along with the taxonimic group of focus. In parenthases 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. agrinomic or ecological).