

Rethinking False Spring Risk

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1 Abstract

Temperate trees and shrubs are at risk of being exposed to late spring freezes—often called 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, many false spring studies simplify the various ecological elements needed for accurate predictions of the level of plant damage from late spring freezing events. Here we review the complexity of factors driving a plant’s false spring risk. ~~In particular we highlight how species, life stage, and habitat differences contribute the level of damage sustained by a false spring event.~~ Integrating some of these complexities 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 potentially greater fluctuations in temperature in some regions (Cannell & Smith, 1986; Inouye, 2008;

Martin *et al.*, 2010). 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 of 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 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) un hinge 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 experience elevated risk of frost damage during the spring due to the stochastic timing of spring frosts. Plants ~~thus 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 & Bruehlheide, 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.*, 2014b). 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 by the day of budburst and the day of last spring freeze through the simple equation (Marino *et al.*, 2011):

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

A damaging FSI is currently defined to be 7 or more days between budburst and the last freeze date (Equation 1) (Peterson & Abatzoglou, 2014). 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 (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 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 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 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 (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 & Körner, 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; Prozherina *et al.*, 2003), 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 drought tolerance 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—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). However, false spring events that occur during the vegetative growth phenophases may impose the greatest freezing threat to deciduous tree and shrub species. Plants will suffer greater long-term effects from the loss of photosynthetic tissue compared to floral and fruit tissue, which could impact multiple years of growth, reproduction, and canopy development (Sakai & Larcher, 1987; Vitasse *et al.*, 2014a).

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 steadily decreases after budburst begins until the leaf is fully unfolded (Lenz *et al.*, 2016) (Figure 2). 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 phenophases—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), which could result in exposure to multiple frost events in one season.

Climate change further complicates understanding species vulnerabilities to false spring events. Most species

are expected to begin leafout earlier in the season with earlier 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). Generally, individuals that initiate budburst earlier in the spring may attempt to limit freezing risk by decreasing the duration of vegetative risk in order to minimize the exposure of less frost tolerant phenophases. But with a changing climate and thus shifts in phenological cues, this relationship may change. Additionally, various studies that investigate latitudinal effects indicate that species growing further north respond to a different interaction of cues than those growing further south and, subsequently, species across different regions may have different durations of vegetative risk (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011). Studies also suggest that species within the same system can exhibit different sensitivities to the three cues (Basler & Körner, 2012; Laube *et al.*, 2013) thus further amplifying the myriad of climatic and phenological shifts as well as the varying species-level effects. We assessed climate data across North America and Europe, long-term observational data, and experimental data to gain a better understanding of the interaction between duration of vegetative risk and false spring events in an attempt to unravel these complexities.

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

Numerous studies have investigated how the relationship between budburst and major phenological cues (warm temperatures, winter chilling and photoperiod) varies across space by using latitudinal gradients (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011; Zohner *et al.*, 2016; Gauzere *et al.*, 2017). Few, however, have integrated longitudinal variation or regional effects. Yet climate and thus false spring risk varies across regions. For example, consider five different regions within a temperate climate (Figure 3). Some regions may experience harsher winters and greater temperature 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 3). 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, which are key drivers of budburst and leafout, vary significantly across a longitudinal gradient. Some studies indicate that populations further inland will initiate budburst first, whereas those closer to the coast will initiate budburst later in the season and that the distance from the coast is a stronger indicator of budburst timing than latitude (Myking & Skroppa, 2007). 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. It is therefore important to

recognize climate regime extremes (e.g. seasonal trends, annual minima and annual maxima) across regions in future studies in order 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. 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 related to understanding the temperature threshold for damage. Some regions and species may tolerate lower temperature thresholds than others (Figure 4). Not only is there debate on what a damaging temperature is, but it is still not well understood how the damage sustained relates to the duration of the frost (Sakai & Larcher, 1987; Augspurger, 2009; Vitasse *et al.*, 2014a; Vitra *et al.*, 2017). 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 as climate change progresses and greater forcing temperatures occur earlier in the year. Temperate trees generally have two phases of dormancy: endodormancy, when trees are inhibited from growing, and ecodormancy, when trees can grow if the external environment is conducive (Basler & Körner, 2012). Chilling cues are considered critical for plants to complete endodormancy and warm temperatures (‘forcing’) are needed for most plants to exit ecodormancy. However, it is unclear when precisely plants enter and complete the ecodormancy phase (Chuine *et al.*, 2016), and what temperatures constitute chilling or forcing. With climate change altering temperatures, some research suggests that trees will experience more oscillations between chilling and forcing cues (Martin *et al.*, 2010), and some phenological models suggest that this could extend the number of required growing degree days necessary for budburst to occur (Vitasse *et al.*, 2011). Studies also suggest that spring 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). 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 was thermally late (1997) and another year that was thermally early (2012). ~~By comparing the two years, we found that the durations of vegetative risk contrasted, with~~ most species in the thermally-early year ~~having~~ longer durations than those in the thermally-late year. In the thermally-early

year, a false spring event was reported across many regions of the US and at Harvard Forest low freezing temperatures were recorded on the 29th of April, after many species had initiated budburst (Figure 5). This contrast across years could be due to the less consistent forcing temperatures after budburst in the thermally-early year, the lower photoperiod experienced during the budburst period in the thermally-early year, the false spring event itself (i.e., plants damaged from the false spring may then have taken longer to reach leafout) or it could be a combination of the three depending on the species. Further, the effects of spring forcing temperatures on the duration of vegetative risk varied across species (Figure 5), which could indicate variation in physiological cues that drive budburst and influence the duration of vegetative risk.

Each species responds differently to climate change, therefore, the duration of vegetative risk depends on the interaction between cues and species. Species dominated by forcing cues may shift earlier and earlier with climate change but most species also have photoperiod and chilling cues, which complicate predictions. For example, as climate change progresses, higher spring forcing temperatures may be required for species experiencing insufficient winter chilling (due to warmer winter temperatures), 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 (MENZEL *et al.*, 2006).

This interaction of cues—and how climate change will affect that interaction—is crucial for recognizing which species will likely become more at risk of false spring events in the future. To begin to examine this we used data from a growth chamber experiment that investigated the interaction of cues across species (and incidentally measured all phases from budburst to leafout). The experiment examined 11 temperate trees and shrubs using a fully crossed design of three levels of chilling (field chilling, field chilling plus 30 days at either 1 or 4 C), two levels of forcing and two levels of photoperiod (8 versus 12 hour days) resulting in 12 treatment combinations. Comparing the most extreme treatments—high chilling hours, long photoperiod and high forcing temperatures (‘high treatment’) against no additional chilling, short photoperiod and low forcing temperatures (‘low treatment’)—shows that plants generally decrease their **DVR** under the high treatment. This appears mainly due to forcing temperatures and photoperiod cues, which showed larger effects on the duration of vegetative risk than chilling. Thus, with greater forcing or longer daylengths, the rate of leafout is expected to accelerate development between budburst and leafout leading to shorter DVR (Figure 6B.). 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 may lead to budburst earlier in the season (Figure 6B.) while photoperiod at the time of budburst will decrease (Basler & Korner, 2014). 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

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 potentially be more damaging false spring events in the future, especially in high risk regions (Gu *et al.*, 2008; Inouye, 2008). The current equation for evaluating false spring damage (Equation 1) largely simplifies the myriad of 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 offer more robust predictions as climate change progresses, which is essential 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.

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

275 Barker, D., Loveys, B., Egerton, J., Gorton, H., Williams, W. & Ball, M. (2005) Co2 enrichment predisposes
276 foliage of a eucalypt to freezing injury and reduces spring growth. *Plant, Cell and Environment* **28**, 1506–
277 1515.

278 Barlow, K., Christy, B., O’Leary, G., Riffkin, P. & Nuttall, J. (2015) Simulating the impact of extreme heat
279 and frost events on wheat crop production: A review. *Field Crops Research* **171**, 109–119.

280 Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species.
281 *Agricultural and Forest Meteorology* **165**, 73–81.

282 Basler, D. & Korner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in
283 four temperate forest tree species. *Tree Physiology* **34**, 377–388.

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

286 Beck, E.H., Heim, R. & Hansen, J. (2004) Plant resistance to cold stress: Mechanisms and environmental
287 signals triggering frost hardening and dehardening. *Journal of Biosciences* **29**, 449–459.

288 Caffarra, A. & Donnelly, A. (2011) The ecological significance of phenology in four different tree species:
289 Effects of light and temperature on bud burst. *International Journal of Biometeorology* **55**, 711–721.

290 Cannell, M. & Smith, R. (1986) Climatic Warming , Spring Budburst and Forest Damage on Trees. *Journal*
291 *of Applied Ecology* **23**, 177–191.

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

294 Chuine, I., Bonhomme, M., Legave, J.M., García de Cortázar-Atauri, I., Charrier, G., Lacoite, A. & Améglio,
295 T. (2016) Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle
296 of endodormancy break. *Global Change Biology* **22**, 3444–3460.

297 Cleland, E., Chiariello, N., Loarie, S., Mooney, H. & Field, C. (2006) Diverse responses of phenology to global
298 changes in a grassland ecosystem. *PNAS* **103**, 13740–13744.

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

302 Edwards, E.J., Chatelet, D.S., Spriggs, E.L., Johnson, E.S., Schlutius, C. & Donoghue, M.J. (2017) Correl-
303 ation, causation, and the evolution of leaf teeth: A reply to Givnish and Kriebel. *Am J Bot* **104**, 509–515.

304 Fu, Y.H., Campioli, M., Van Oijen, M., Deckmyn, G. & Janssens, I.A. (2012) Bayesian comparison of six
305 different temperature-based budburst models for four temperate tree species. *Ecological Modelling* **230**,
306 92–100.

307 Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I. & Chuine, I. (2017) Inte-
308 grating interactive effects of chilling and photoperiod in phenological process-based models. A case study
309 with two European tree species: *Fagus sylvatica* and *Quercus petraea*. *Agricultural and Forest Meteorology*
310 pp. 9–20.

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

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

315 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O’Keefe, J. & Richardson, A.D. (2012)
316 Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change Biology* **18**,
317 2365–2377.

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

320 Kathke, S. & Bruelheide, H. (2011) Differences in frost hardiness of two Norway spruce morphotypes growing
321 at Mt. Brocken, Germany. *Flora - Morphology, Distribution, Functional Ecology of Plants* **206**, 120–126.

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

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

326 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2013) Chilling outweighs
327 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.

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

330 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety margins
331 against damage by spring freeze events along elevational gradients. *New Phytologist* **200**, 1166–1175.

- 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 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.
- MENZEL, A., SPARKS, T.H., ESTRELLA, N., KOCH, E., AASA, A., AHAS, R., ALM-KÜBLER, K., BISSOLLI, P., BRASLAVSKÁ, O., BRIEDE, A. & et al. (2006) European phenological response to climate change matches the warming pattern. *Global Change Biology* **12**, 1969–1976.
- 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.
- 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.
- 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.
- 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.
- Samish, R. (1954) Dormancy in woody plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **5**, 183–204.
- 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.
- 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.

- 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., 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.
- 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.
- 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* pp. 139–163.
- Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America* **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.

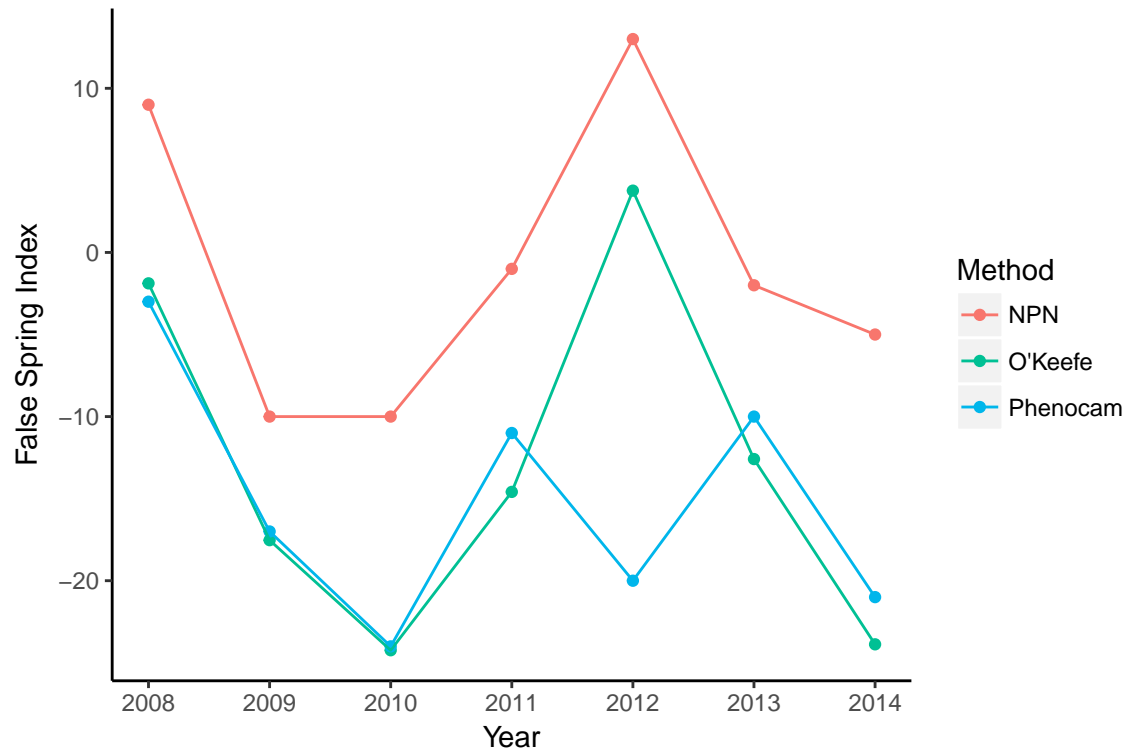


Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methodology used in this study. USA-NPN FSI values are green (USA-NPN, 2016), observed FSI values are blue (O'Keefe, 2014), and **PhenoCam FSI values are red** (Richardson, 2015).

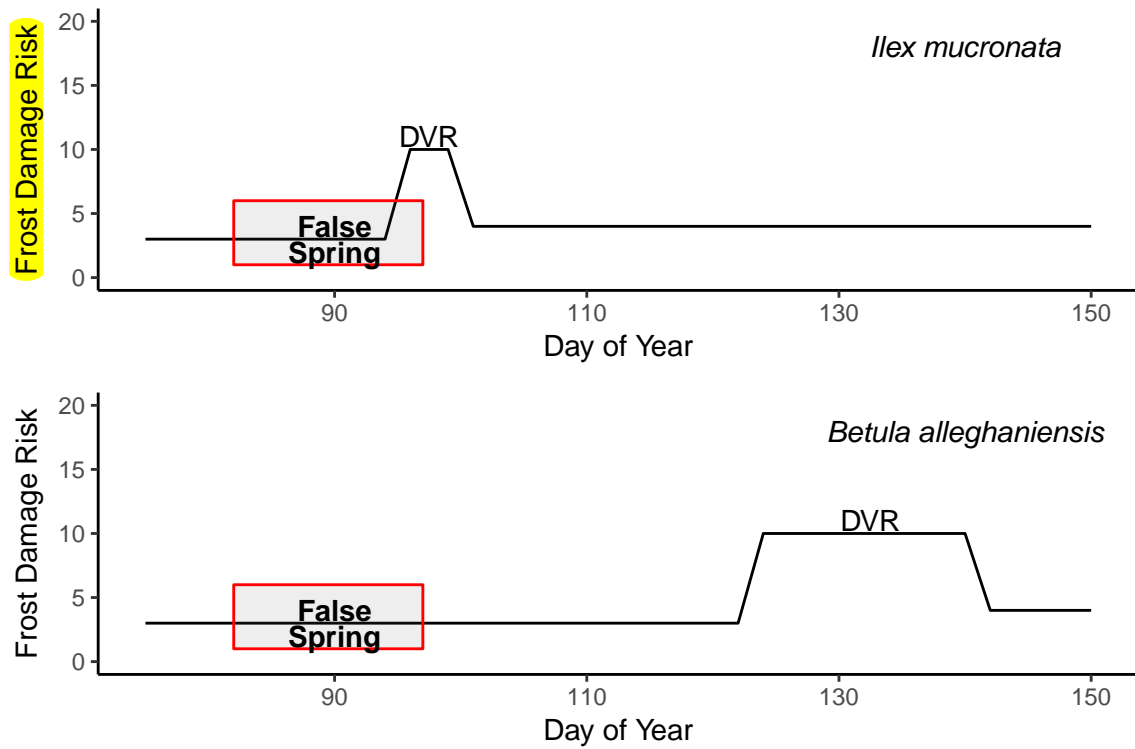


Figure 2: A figure showing the differences in spring phenology and false spring risk across two species: *Ilex mucronata* (L.) and *Betula alleghaniensis* (Marsh.). We mapped a possible false spring event based on historic weather data and compared it to the observational data collected at Harvard Forest (O’Keefe, 2014). In this scenario, the *Ilex mucronata* would be exposed to a false spring event, whereas the *Betula alleghaniensis* would avoid it entirely. DVR stands for Duration of Vegetative Risk.

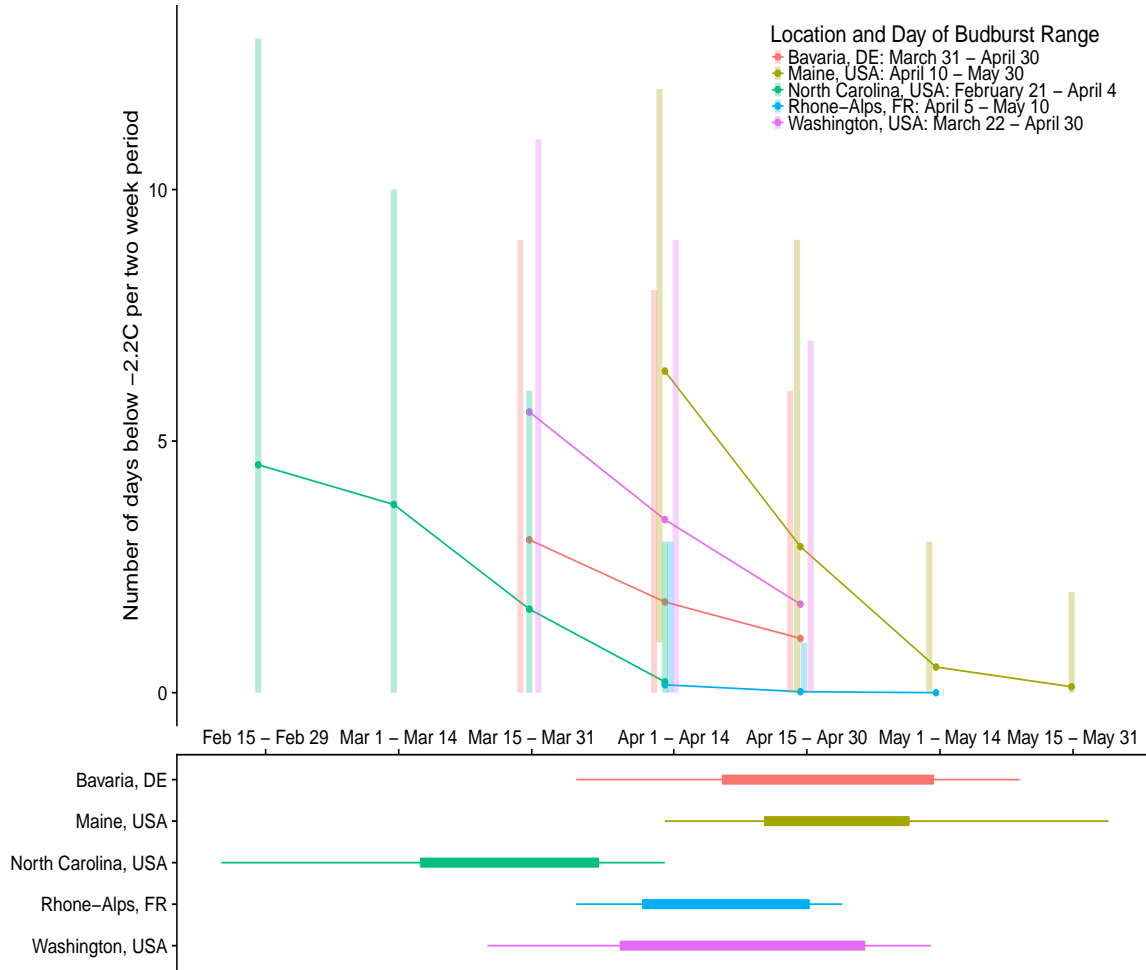


Figure 3: A comparison of false spring risk across five climate regions. By determining the average time of budburst to leafout dates for the dominant species in five archetypal climate regions, we were able to estimate the current spatial variation of false spring risk. We assessed the number of freeze days (-2.2°C) (Schwartz, 1993) that occurred on average over the past 50 years within the average durations of vegetative risk for each region (USA-NPN, 2016; Soudani *et al.*, 2012; White *et al.*, 2009; Schaber & Badeck, 2005).

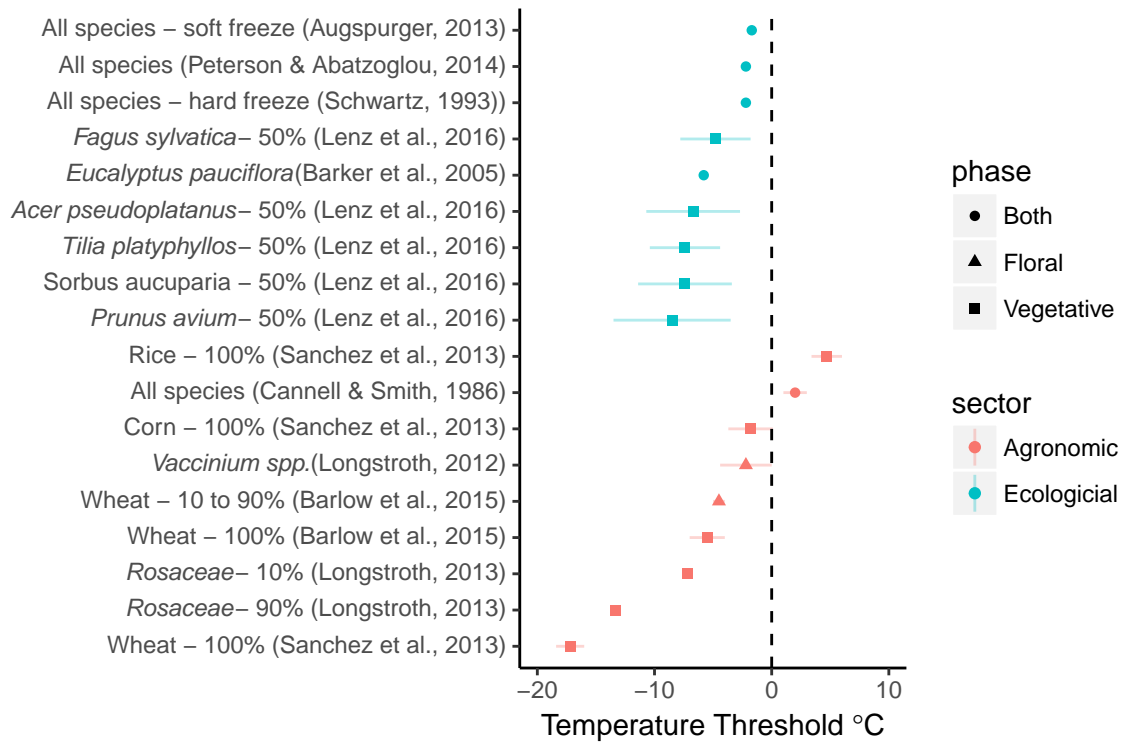


Figure 4: A comparison of damaging spring freezing temperature thresholds across ecological and agronomic studies. Each study is listed on the y axis along with the taxonomic group of focus. Next to the species name is the freezing definition used within that study (e.g. 100% is 100% lethality). Each 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).

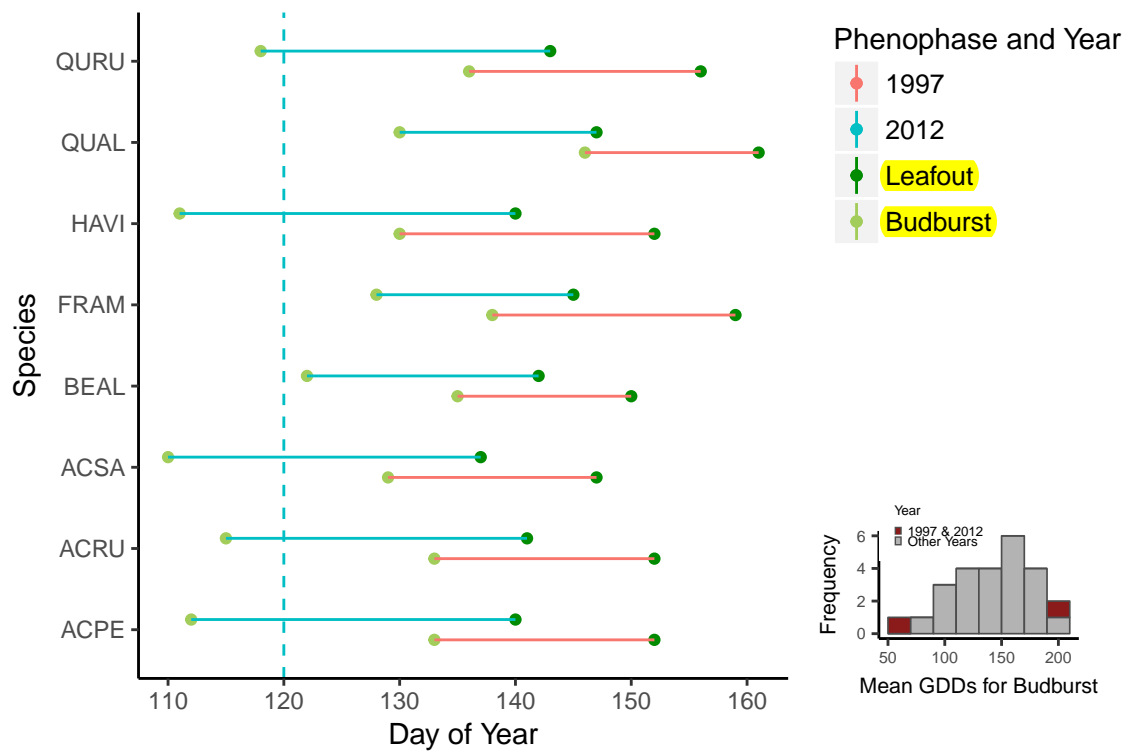


Figure 5: Duration of vegetative risk for 8 species at Harvard Forest, comparing 1997 and 2012. In 1997, the aggregated GDDs to budburst were the lowest and the durations of vegetative risk overall were shorter, whereas in 2012, the aggregated GDDs to budburst were the highest and the durations of vegetative risk were longer. The dotted line indicates a false spring event in 2012, which is defined as freezing temperatures (-2°C) occurring after budburst. The histogram at the bottom right corner indicates the frequency of accumulated GDDs to budburst for each year between 1990 and 2016. It indicates that 1997 was a thermally late year and 2012 was a thermally early year.

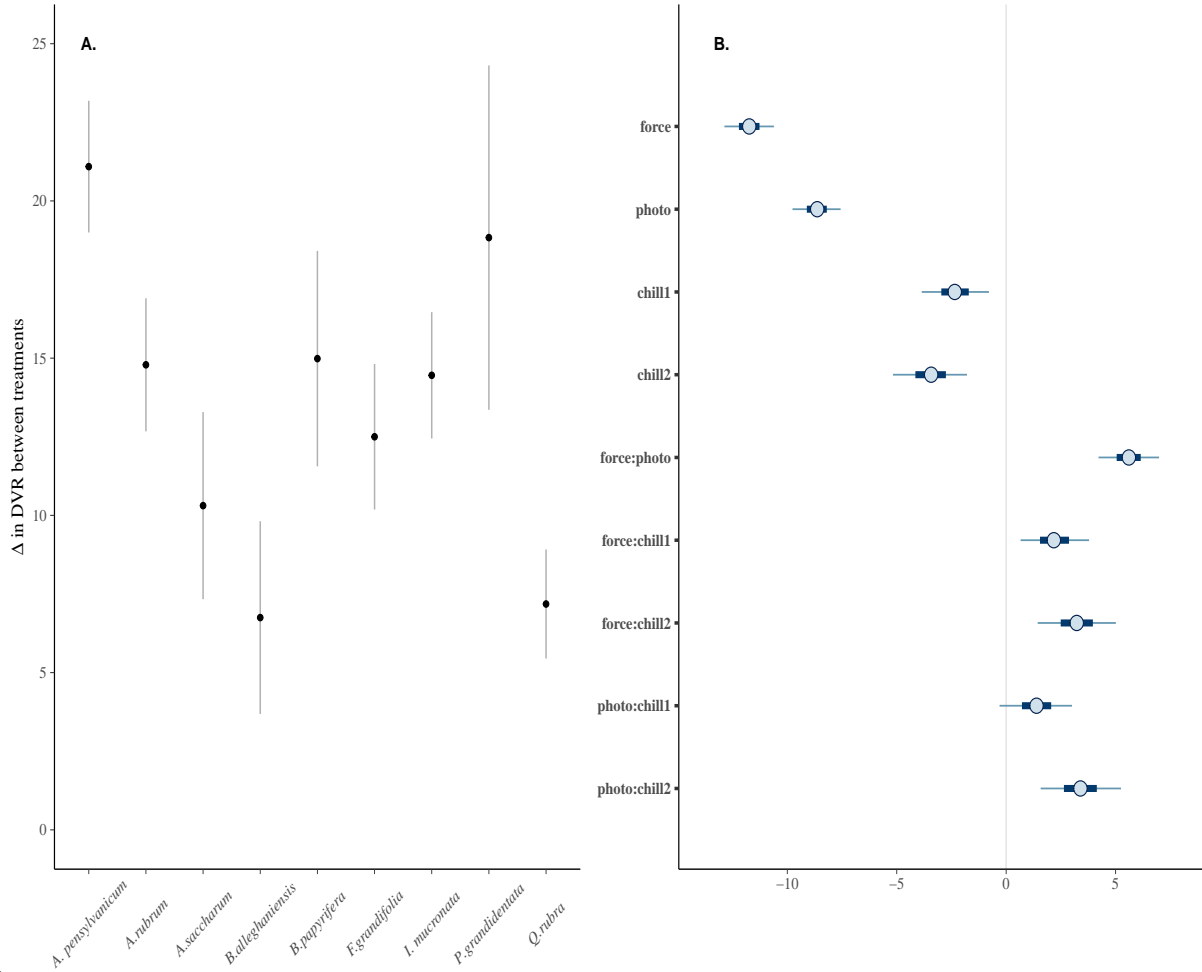


Figure 6: Results from the growth chamber experiment. (A) Is a comparison of the durations of vegetative risk across two treatments for each species collected for the experiment. Species along the x-axis are ordered by day of budburst. Data was collected from a growth chamber experiment where one treatment 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 daylengths. The standard error is represented by the bars around each point. (B) A plot of the parameter effects on the duration of vegetative risk. Spring forcing temperatures had the largest effect on the rate of leafout, with photoperiod also being a critical factor. Thus, while greater forcing or longer photoperiods alone will shorten the duration of vegetative risk by 11 and 7 days respectively, their combined effect would be 14 days due to a 4 day delay through their interaction ($11 + 7 - 4 = 14$).