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. In particular we highlight how integrating species, life stage, and habitat differences in temperature thresholds could help accurately determine the level of damage sustained by a false spring event. If researchers could integrate our suggested approach to investigate false spring events, they could rapidly advance understanding and forecasting 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. At the same time they are tracking these resources, they are also aiming to avoid late spring freezes, which can be detrimental to growth. Individuals that leaf out before the last freeze date are at risk of leaf loss, damaging wood tissue, and slowed or stalled canopy development (Gu *et al.*, 2008; Hufkens *et al.*, 2012). These 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 around the world due to earlier spring onset and greater fluctuations in temperature (Cannell & Smith, 1986; Inouye, 2008; Martin

et al., 2010). It is anticipated that there will be a decrease in false spring frequency overall, however, 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 also likely to increase. For these reasons, false spring events are expected to amplify in intensity (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 this to climate change (Ault *et al.*, 2013; Allstadt *et al.*, 2015; Muffler *et al.*, 2016; Xin, 2016). The growing interest in false spring events has led to a lot of research investigating the effects on temperate forests and agricultural crops. Due to these reasons, it is crucial for researchers to properly evaluate the effects of false spring events in order to make more accurate predictions on future trends.

Currently, estimates of false springs assume consistency across species, functional group, life stage, habitat type, and other climatic regimes. Yet, in contrast to these simplifications, we argue these factors can greatly impact plants' false spring risk such that simple indices will most likely lead to inaccurate predictions and ultimately do little to advance the field. A new approach that integrates these other crucial factors is necessary to accurately determine current false spring damage and, importantly, future spring freeze risk under a changing climate.

In this paper we aim to highlight the complexity of factors driving a plant's false spring risk and provide a roadmap for improved metrics. First, we review the currently used definitions of false spring. We outline in particular how life stage of the individual (Caffarra & Donnelly, 2011), location within a forest or canopy (Augspurger, 2013), winter chilling hours (Flynn & Wolkovich 2017?), freeze duration/intensity, and range limits of the species (Martin *et al.*, 2010) unhinge simple metrics of false spring. The ultimate intent is to demonstrate how an integrated view of false spring that incorporates these factors would rapidly advance progress in this field.

3   Defining False Spring

Temperate forest plants are most at risk to frost damage from episodic spring frosts (Sakai & Larcher, 1987). [Define episodic spring frosts and create a connection between previous and next sentence.] Due to the stochasticity of episodic spring frosts, plants must exhibit flexible spring phenologies in order to minimize freezing risk, especially in a region that typically experiences fluctuating spring temperatures. Freezing temperatures following a warm spell could result in plant damage or even death (Ludlum, 1968; Mock *et al.*, 2007). False spring events are injurious due to ice forming intracellularly, resulting in leaf and stem damage. Ice formation can also occur indirectly, 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). It is important for researchers to properly evaluate the level of damage that could occur in order to make more accurate future predictions. Therefore, an effective and consistent definition of false spring is essential.

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). Frost damage usually occurs when there is 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. 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).

$$FSI = JulianDate(LastSpringFreeze) - JulianDate(Budburst) \qquad (1)$$

A damaging false spring is currently defined as having 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. Once budburst has initiated, buds cannot respond to cold temperatures and freeze resistance is greatly reduced (Taschler *et al.*, 2004; Lenz *et al.*, 2013; Vitasse *et al.*, 2014).

To demonstrate how the definition works, we applied it to data from the Harvard Forest field site in Massachusetts. We compared three methodologies to calculate spring onset: long-term ground observational data (O'Keefe, 2014), PhenoCam data from Harvard Forest (Richardson, 2015), and USA-NPN SI-x (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).

[Can you adjust below paragraph to be more about functional groups? Or at least mention them? It would then link better to next section.] Each methodology renders different FSI values, suggesting different false spring damage for the same site and same year. The reason for this apparent discrepancy is the different spring onset data we used: because each metric evaluates spring onset for different species or functional groups within a forest community the false spring events clearly vary by functional group contained in our differing spring onsets. Currently, most FSI work ignores such variation–instead using one metric of spring onset and assuming it applies to the whole community of plants. Yet since the equation is built half on spring onset date, it is critical to choose the most appropriate methodology, or to use a more integrative equation. [Transition? I think you could replace your final sentence here with more of a signpost to what will come next.]

4 Determining Spring Onset in Temperate Plant Communities

[Be careful to make the previous paragraph and this one not overlap too much.] 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. [Transition ...] 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 by the discrepancy in results for 2012 (Figure 1). The risk of a false spring varies across habitat type and 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. [Insert quick sentence(s) here to transition to avoidance and tolerance ...]

5 Plant Physiology and Diversity Versus the Current False Spring Definition

Plants have evolved multiple strategies to avoid false springs, which must be considered in any false spring definition. 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; Polgar & Primack, 2011) (Figure 2). [Transition.] Deciduousness and the evolution of dormancy in temperate forest trees has permitted species to occupy more northern ecological niches and decrease the risk of false spring damage (Samish, 1954). Therefore, 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 to photoperiod cues more than 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. Temperate forest plants utilize various morphological strategies to be more frost tolerant: some have toothed or lobed leaves to increase 'packability' in winter buds (Edwards *et al.*, 2017), others 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 environmental cues such as dry winters. Dry winters typically result in new, frost-tolerant shoots due to the decreased water content and osmotic potential from the reduced number of accumulated solutes (Morin *et al.*, 2007; Hofmann & Bruelheide, 2015). It is hypothesized that increased bud dehydration results in increased frost hardiness (Beck *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 much more nuance. [Need transition to next section.]

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

Different species respond differently to anthropogenic climate change. Most species are expected to begin leafout earlier in the season with warming spring temperatures but some species may have the opposite response (Cleland *et al.*, 2006; Yu *et al.*, 2010; Xin, 2016). Studies indicate that species growing at more northern latitudes tend to respond greater to photoperiod than species growing further south (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011). Similarly, larger canopy species exhibit greater photoperiod sensitivities than shade tolerant or understory species (Basler & Körner, 2012) and they also require more chilling in the winter and greater forcing temperatures in the spring to initiate budburst (Laube *et al.*, 2013). It is anticipated that these more opportunistic individuals that initiate budburst earlier in the spring would attempt to limit freezing risk by increasing the rate of budburst and progress to full leaf expansion faster.

[Need better topic sentence.] Reproductive phases 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 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 than trees that lose one year of reproductive growth (Sakai & Larcher, 1987). Plants at certain vegetative phenophases (i.e. before full leafout of the entire plant) are more likely to sustain damage from a false spring than individuals past the leafout phenophase. Spring phenology is a crucial indicator 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. Species with short durations of vegetative risk often sustain higher levels of damage (Augspurger, 2009). It is hypothesized that if the duration of vegetative risk is longer, then the buds and leaves will be heartier against frosts, however this has yet to be tested thoroughly. We assess the interaction between duration of vegetative risk and false spring events using two datasets: from long-term observational data and a growth chamber chilling experiment.

6.1 Spring Forcing Temperatures and the Duration of Vegetative Risk

[You're talking about forcing temperatures here; can you link back for the reader to what you mentioned above? This will create better flow and connection among the text.] Forcing temperatures in the spring 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). This high variation in temperature (i.e. oscillating above and below the development threshold) may result in longer durations of vegetative risk across more species. [Transition.] Using observational data from Harvard Forest (O'Keefe, 2014), we 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, however, in 2010, the duration of vegetative risk was slightly longer overall (Figure 3). With climate change progressing, it is likely there will be more years like 2010 in the future and that the durations of vegetative risk will continue to extend. Therefore, species that are better able to phenologically track the shifts in spring advancement due to climate change are more likely to sustain damage from false springs (Scheifinger *et al.*, 2003).

6.2 Interaction of Phenological Cues and the Duration of Vegetative Risk

[Need to make clear for the reader the difference between the previous section and this one but altering BOTH sections a little .... the previous one is mostly about climate; the below is about species differences in cues ... work on clarifying this.] Spring forcing temperatures and daylength requirements for budburst to occur vary among species and habitats. Since species distributions are largely driven by phenology (Chuine *et al.*, 2001), species less reliant on photoperiod cues are likely to outcompete species that are reliant on photoperiod cues as spring forcing temperatures continue to initiate earlier (Vitasse *et al.*, 2011; Gauzere

et al., 2017). 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 habitats. 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.

[Transition!]

Data from a growth chamber experiment were used to compare 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 4). 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 while photoperiod cues will remain stagnant or decrease as spring forcing begins earlier in the season. Thus, potentially elongating the duration of vegetative risk and exposing 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.

[Transition? I wondered if maybe the below section belonged above with the one on forcing temperatures.... If you did that you would have a sort of intro on vegetative risk (a re-write of your last two paragraphs in section 6: Defining Vegetative Risk but focused really on just defining it) and then two major vegetative risk sections that dive in deeper: (1) How climate alters vegetative risk and (2) How species vary in their vegetative risk and then a shorter section on (3) How climate change will alter vegetative risk which would be the first paragraph of section 6 which puts it all together – climate and species ....]

7 Predictable Regional Differences in False Spring Risk and Temperature Thresholds

There have been numerous studies investigating 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 most studies fail to integrate longitudinal variation or regional effects. Chilling and forcing are key drivers of budburst and leafout and can 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 continental vs. coastal 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 for frost or drought risk. 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 discrepancies in defining a false spring event, especially with understanding damaging freezing temperatures. Some regions and species may be more able to tolerate lower temperature thresholds than others (Table 1). 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 occur at the same rate, rendering some regions and species to be more susceptible to false spring events in the future (Labe *et al.*, 2016).

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 (Figure 5). We assessed the number of freeze days (-2.2°C) (Schwartz, 1993) that occurred on average over the past 50 years within the date ranges for each region. We found that Maine has the highest risk for frost damage and Lyon, France as the lowest (Figure 5). Future research should aim to integrate spatiotemporal effects and regional differences when investigating false spring risk in order to make better predictions as climate change progresses.

8 Conclusion

The risk of false spring damage can vary from year to year 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.

Barker, D., Loveys, B., Egerton, J., Gorton, H., Williams, W. & Ball, M. (2005) Co2 enrichment predisposes

266 foliage of a eucalypt to freezing injury and reduces spring growth. *Plant, Cell and Environment* **28**, 1506–
267 1515.

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

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

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

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

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

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

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

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

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

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

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

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

295 Edwards, E.J., Chatelet, D.S., Spriggs, E.L., Johnson, E.S., Schlutius, C. & Donoghue, M.J. (2017) Correla-
296 tion, causation, and the evolution of leaf teeth: A reply to givnish and kriebel. *Am J Bot* **104**, 509–515.

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

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

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

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

307 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J. & Richardson, A.D. (2012)
308 Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change Biology* **18**,
309 2365–2377.

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

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

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

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

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

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

322 Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of freezing
323 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.

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, 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.

Meier, U. (2001) Growth stages of mono-and dicotyledonous plants BBCH Monograph Edited by Uwe Meier Federal Biological Research Centre for Agriculture and Forestry. *Agriculture* **12**, 141—-147 ST —- Geo-chemical study of the organic mat.

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.

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

354 Partanen, J. (2004) Dependence of photoperiodic response of growth cessation on the stage of development
355 in picea abies and betula pendula seedlings. *Forest Ecology and Management* **188**, 137–148.

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

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

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

361 Polgar, C., Gallinat, A. & Primack, R.B. (2014) Drivers of leaf-out phenology and their implications for
362 species invasions: Insights from Thoreau's Concord. *New Phytologist* **202**, 106–115.

363 Polgar, C.A. & Primack, R.B. (2011) Leaf-out phenology of temperate woody plants: From trees to ecosys-
364 tems. *New Phytologist* **191**, 926–941.

365 Richardson, A. & O'Keefe, J. (2009) *Phenological differences between understory and overstory: a case study*
366 *using the long-term harvard forest records*, pp. 87–117. Springer.

367 Richardson, A.D. (2015) Phenocam images and canopy phenology at harvard forest since 2008.

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

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

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

373 Schaber, J. & Badeck, F.W. (2005) Plant phenology in germany over the 20th century. *Regional Environmental*
374 *Change* **5**, 37–46.

375 Scheifinger, H., Menzel, A., Koch, E. & Peter, C. (2003) Trends of spring time frost events and phenological
376 dates in central europe. *Theoretical and Applied Climatology* **74**, 41–51.

377 Schwartz, M.D. (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography* **14(6)**,
378 536–550.

379 Soudani, K., Hmimina, G., Delpierre, N., Pontailler, J.Y., Aubinet, M., Bonal, D., Caquet, B., de Grandcourt,
380 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.

Vavrus, S., Walsh, J.E., Chapman, W.L. & Portis, D. (2006) The behavior of extreme cold air outbreaks under greenhouse warming. *International Journal of Climatology* **26**, 1133–1147.

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. (2014) 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.

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.

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.
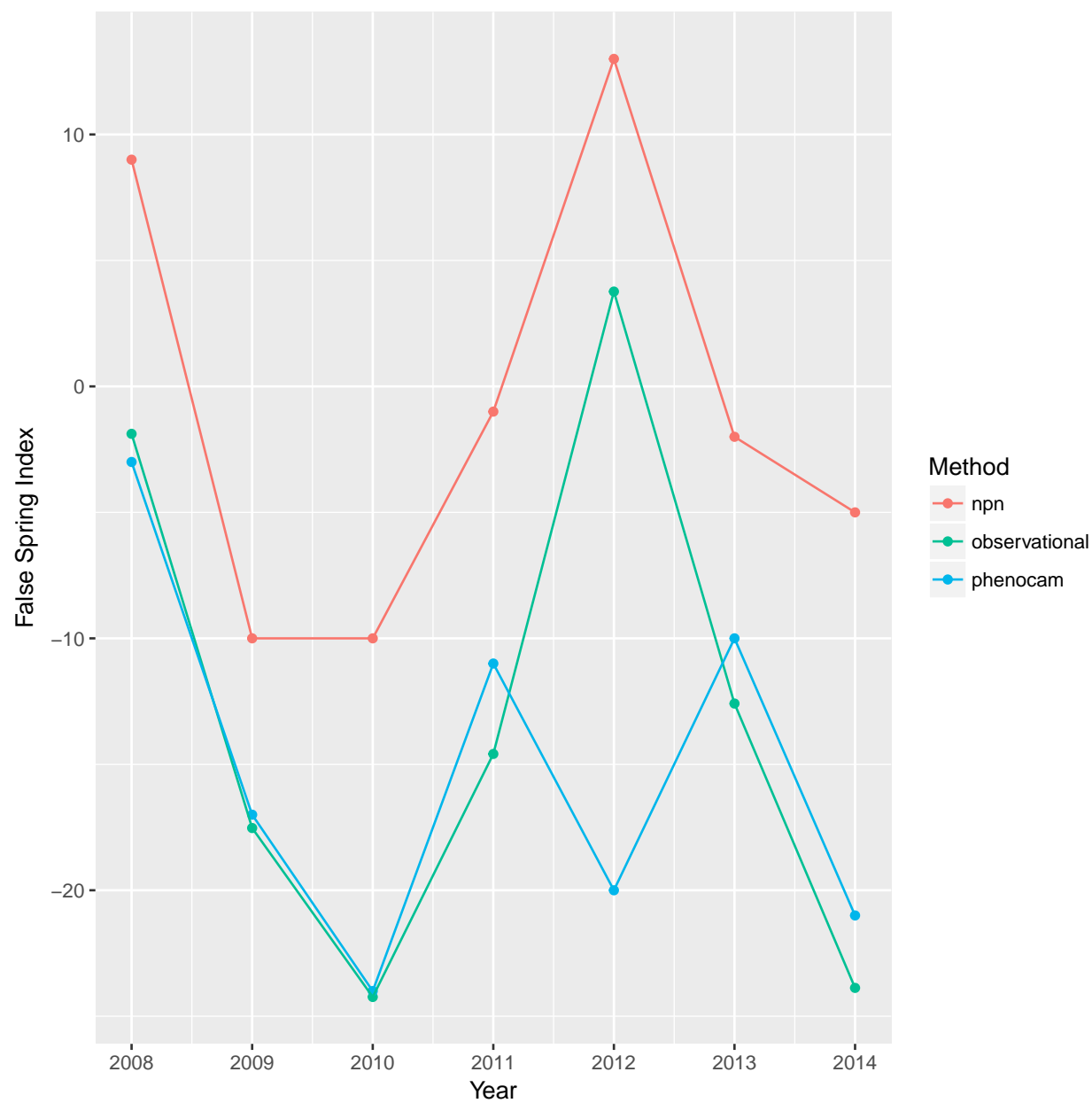
Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methdology used in this study. PhenoCam FSI values are red, Observed FSI values are blue, and USA-NPN FSI values are green.

Supplement

```
## 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
```
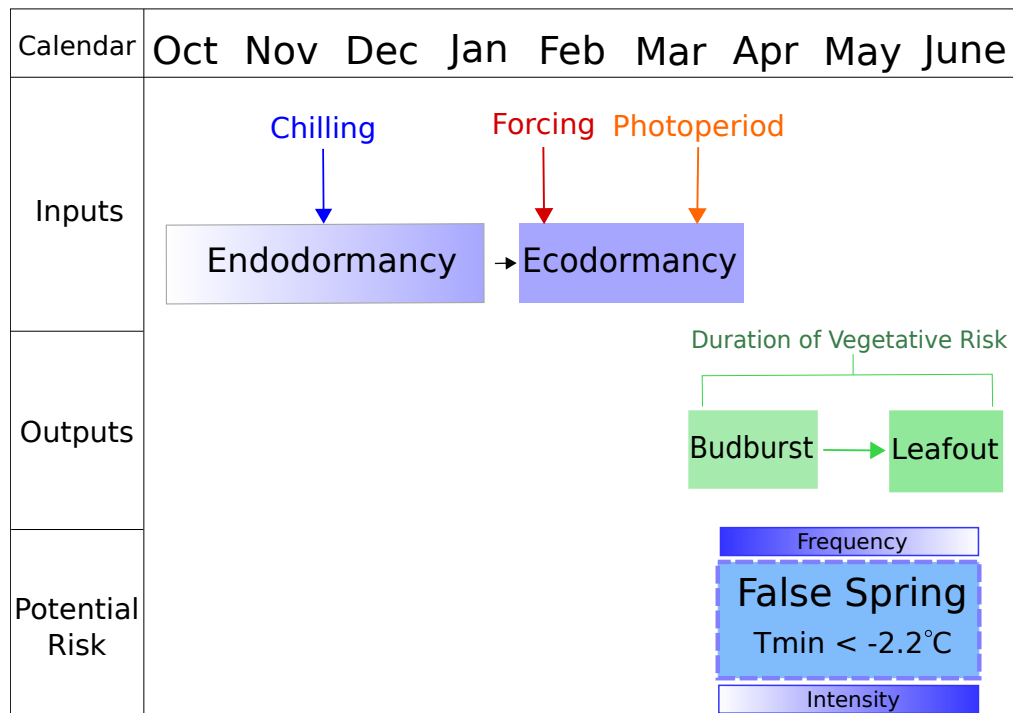
16

Figure 2: Temperate forest trees utilize three main drivers to induce budburst in the spring: chilling over the winter, forcing temperatures in the spring, and longer photoperiod cues. During the endodormancy phase, individuals accumulate chilling hours and cannot break dormancy and false springs cannot occur during the this time. During the ecodormancy phase, however, false spring damage can occur. Damage from a false spring increases as the season progresses, however the likelihood of an event decreases.
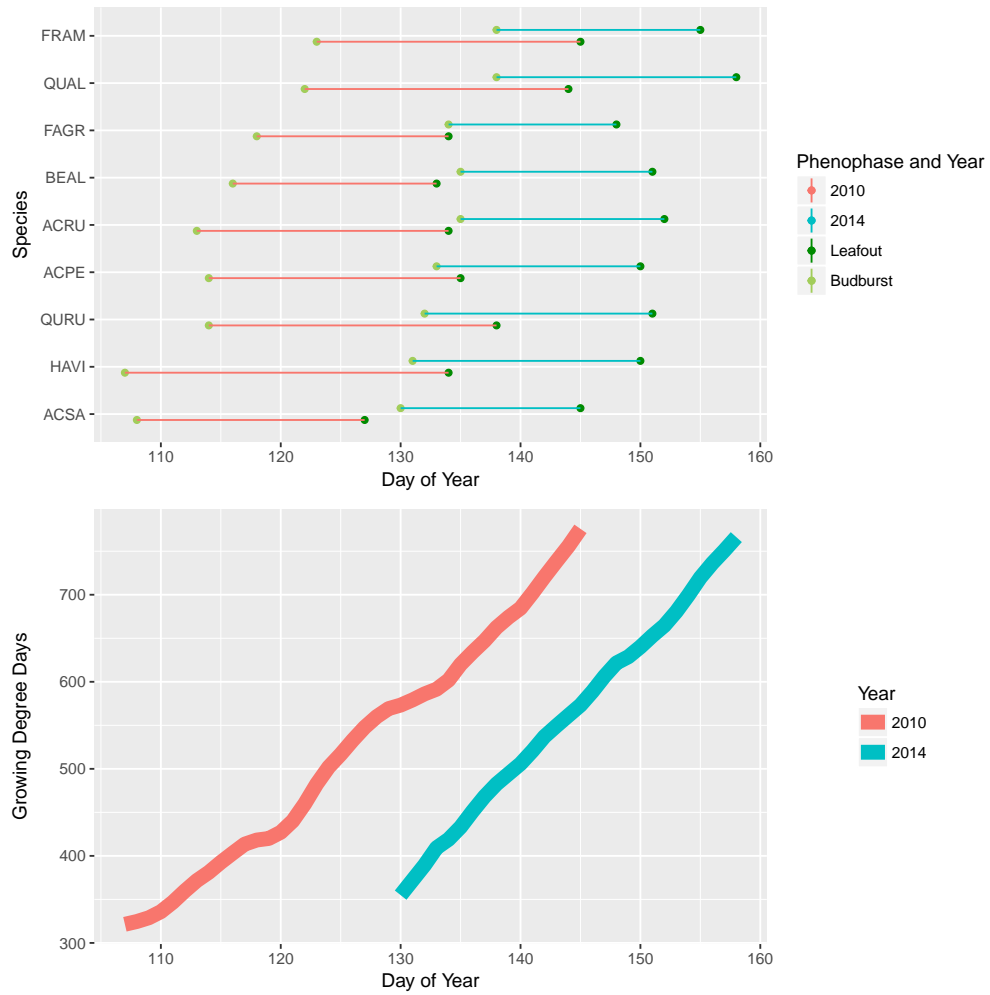
Figure 3: A comparison of two years of observational data investigating the effects of growing degree days on the duration of vegetative risk. The average duration of vegetative risk for 2010 was 21 +/- 3.39 days versus 17.1 +/- 1.96 days in 2014.
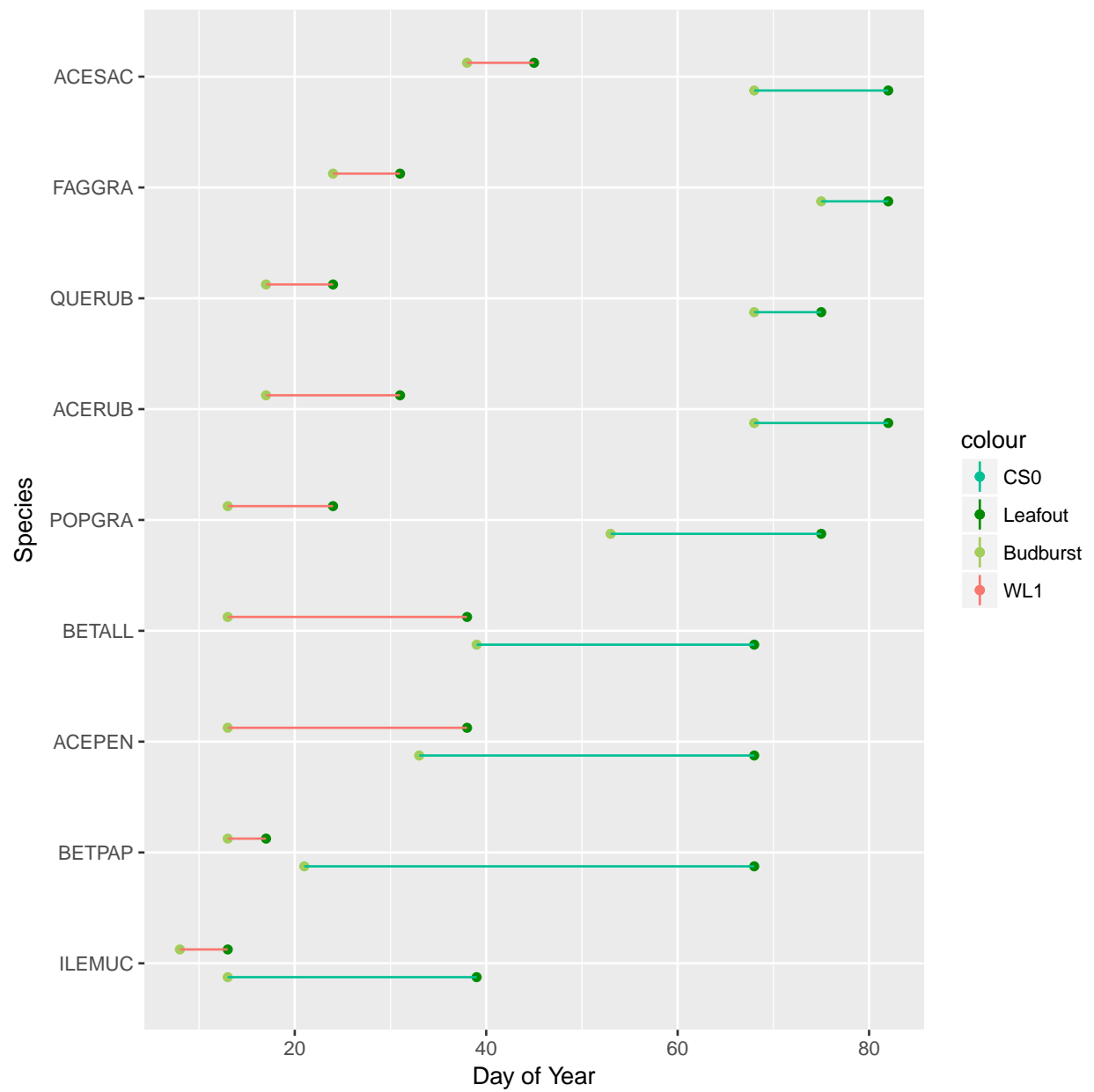
Figure 4: Day of budburst and the day of leaf out for native tree species in New England. Data was collected from a growth chamber experiment using any combination of two photoperiod treatments, two forcing treatments, and three chilling treatments. The standard deviation is represented in blue for budburst and green for leaf out.

411 Table 1: Comparing damaging spring temperature thresholds in ecological and agronomical studies across various species and phenophases.

412

| Sector	BBCH (Meier, 2001)	Species	Temperature (°C)	Type	Source
Ecological	9-15	Sorbus aucuparia	-7.4	50% lethality	Lenz *et al.* (2016)
Ecological	9-15	Prunus avium	-8.5	50% lethality	Lenz *et al.* (2016)
Ecological	9-15	Tilia platyphyllos	-7.4	50% lethality	Lenz *et al.* (2016)
Ecological	9-15	Acer pseudoplatanus	-6.7	50% lethality	Lenz *et al.* (2016)
Ecological	9-15	Fagus sylvatica	-4.8	50% lethality	Lenz *et al.* (2016)
Ecological	9+	All	-2.2	hard	Schwartz (1993)
Ecological	9+	All	-1.7	soft	Augspurger (2013)
Ecological	All	All	2 SD below winter TAVG	cold-air outbreaks	Vavrus *et al.* (2006)
Ecological	9+	Eucalyptus pauciflora	-5.8	elevated CO2 and temperature threshold	Barker *et al.* (2005)
Ecological	9+	All	-2.2	7 day threshold	Peterson & Abatzoglou (2014)
Agrinomical	9+	All	2	Risk threshold for clear nights	Cannell & Smith (1986)
Agrinomical	Floral	Vaccinium spp.	-4.4 to 0	sprinkler protection threshold	Longstroth (2012)
Agrinomical	9	Rosaceae	-7.2	10% lethality	Longstroth (2013)
Agrinomical	9	Rosaceae	-13.3	90% lethality	Longstroth (2013)
Agrinomical	All	All	Varies	Radiation Frost	Barlow *et al.* (2015)
Agrinomical	Floral	Wheat	-4 to -5	10-90% lethality	Barlow *et al.* (2015)
Agrinomical	Vegetative	Wheat	-7 for 2hrs	100% lethality	Barlow *et al.* (2015)
Agrinomical	Vegetative	Rice	4.7	lethal limit	Sánchez *et al.* (2013)
Agrinomical	Vegetative	Corn	-1.8	lethal limit	Sánchez *et al.* (2013)
Agrinomical	Vegetative	Wheat	-17.2	lethal limit	Sánchez *et al.* (2013)

413
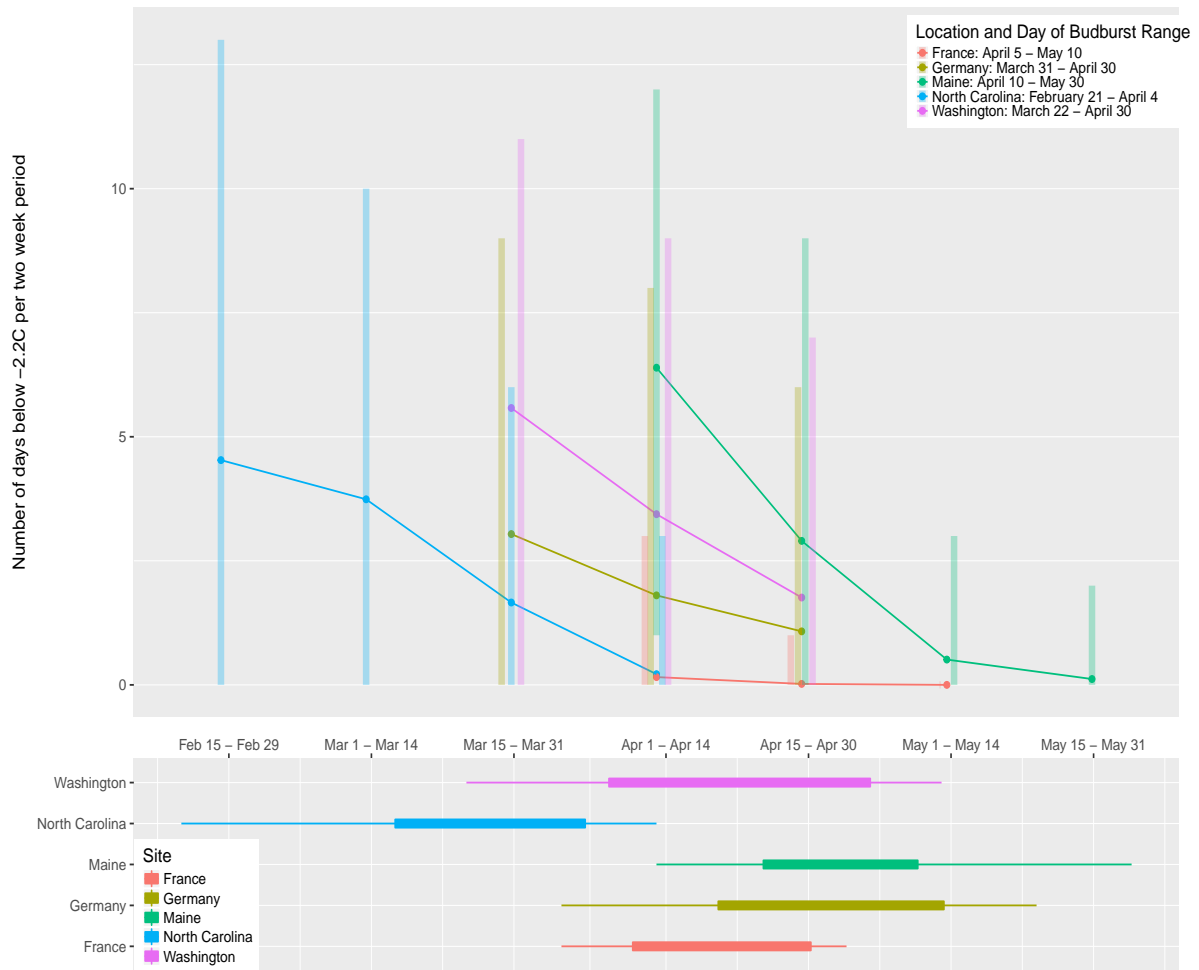
Figure 5: A comparison of false spring risk across five climate regions. The data was subsetted for each region based on earliest historical spring onset date to the latest historical leafout date and was divided into biweekly time periods (Schaber & Badeck, 2005; White *et al.*, 2009; Soudani *et al.*, 2012; USA-NPN, 2016).