

Rethinking False Spring Risk

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1 Introduction

Plants growing in temperate environments are at risk of being exposed to 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. False spring events can 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). 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). It is anticipated that there will be a decrease in false spring frequency overall but the magnitude of temperature variation is likely to increase, therefore amplifying the expected intensity of false spring events (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). So, there's growing interest in false spring 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 on temperate forests and agricultural crops in order to make more accurate predictions on future trends.

In this paper we aim to highlight the complexity of factors driving a plant's false spring risk. 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) unthine 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.

2 Defining False Spring

Temperate forest plants are most at risk to frost damage from episodic spring frosts (Sakai & Larcher, 1987). Freezing temperatures following a warm spell could result in plant damage or even death (Ludlum, 1968; Mock *et al.*, 2007). Freeze damage can occur directly via intracellular ice formation or indirectly via freezing dehydration (Pearce, 2001; Beck *et al.*, 2004; Hofmann & Bruelheide, 2015). Intracellular ice formation can cause defoliation, which can result in crown dieback (Gu *et al.*, 2008).

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).

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

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).

We applied this definition to the Harvard Forest field site in Massachusetts. Three methodologies to calculate spring onset were compared: 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). The FSI values vary across methodology because each metric represents a different group of species and currently, most FSI work ignores such variation. 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.

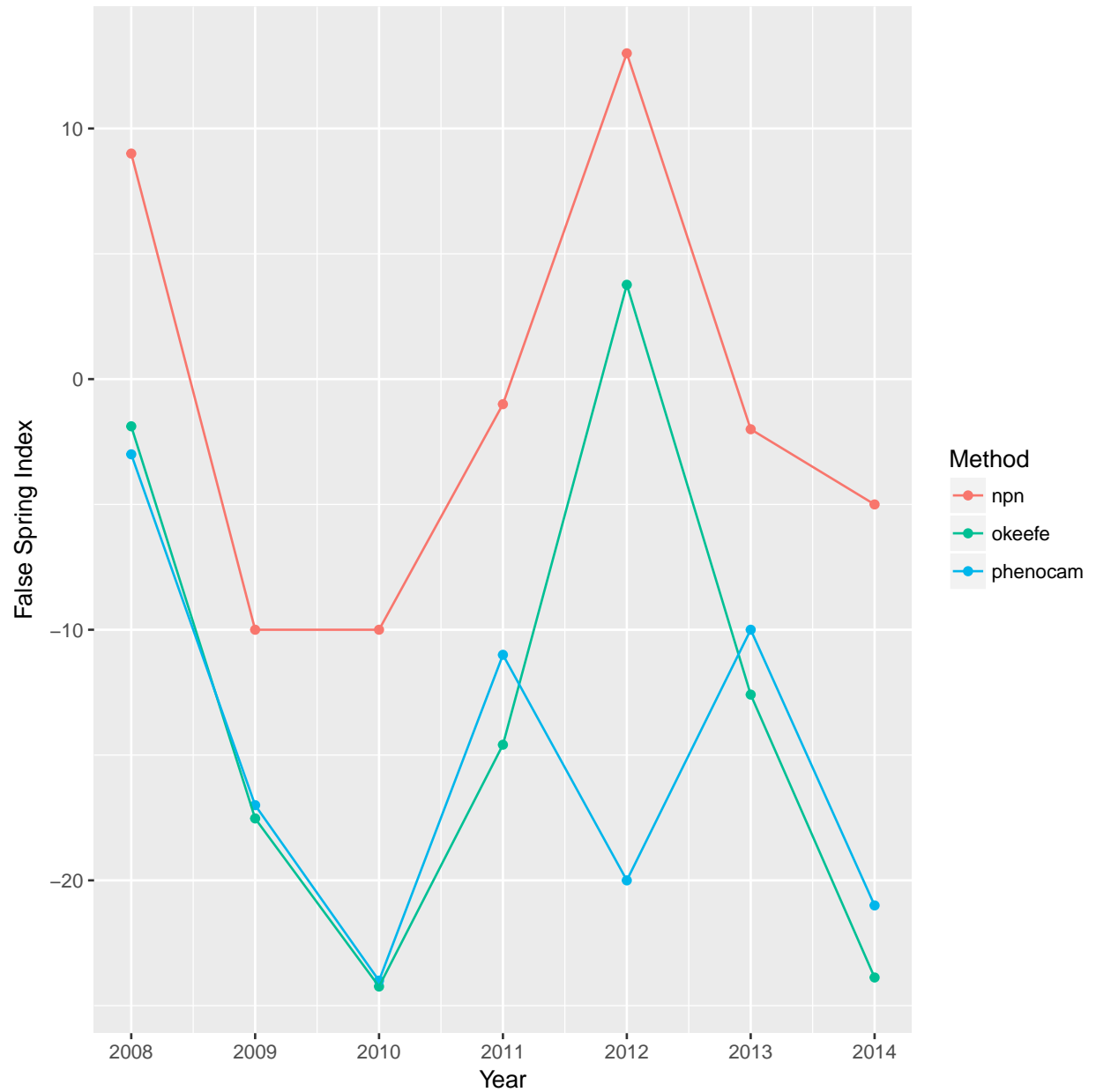


Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methodology used in this study. PhenoCam FSI values are red, Observed FSI values are blue, and USA-NPN FSI values are green.

3 Determining Spring Onset in Temperate Plant Communities

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. 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, considering different functional groups is unlikely to be enough for robust predictions.

The FSI equation and 7 day parameter assumes consistency across species, functional group, life stage, habitat type, and other climatic regimes, which is largely inadequate. In contrast to these simplifications, we argue that a wealth of factors greatly impacts plants’ false spring risk such that simple indices will most likely lead to inaccurate predictions and ultimately do little to advance the field. Considering the different avoidance and tolerance strategies commonly seen in temperate forest species is critical. A new approach that integrates these other crucial factors is necessary to accurately determine current false spring damage and future spring freeze risk.

4 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 longer photoperiods (Cleland *et al.*, 2007; Polgar & Primack, 2011) (Figure 2). 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).

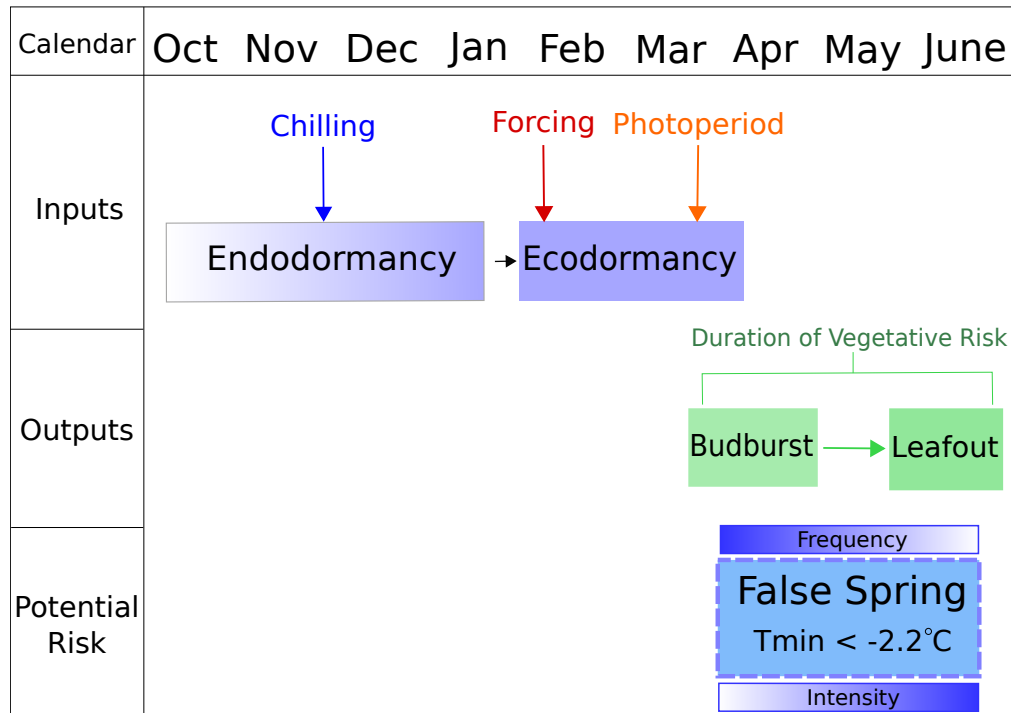


Figure 2: Temperate forest trees utilize three main drivers to induce budburst in the spring: chilling over the winter, forcing temperatures in the spring, and longer photoperiod cues. During the endodormancy phase, individuals accumulate chilling hours and cannot break dormancy and false springs cannot 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.

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.

5 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, late successional 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.

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.

5.1 Spring Forcing Temperatures and the Duration of Vegetative Risk

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. 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).

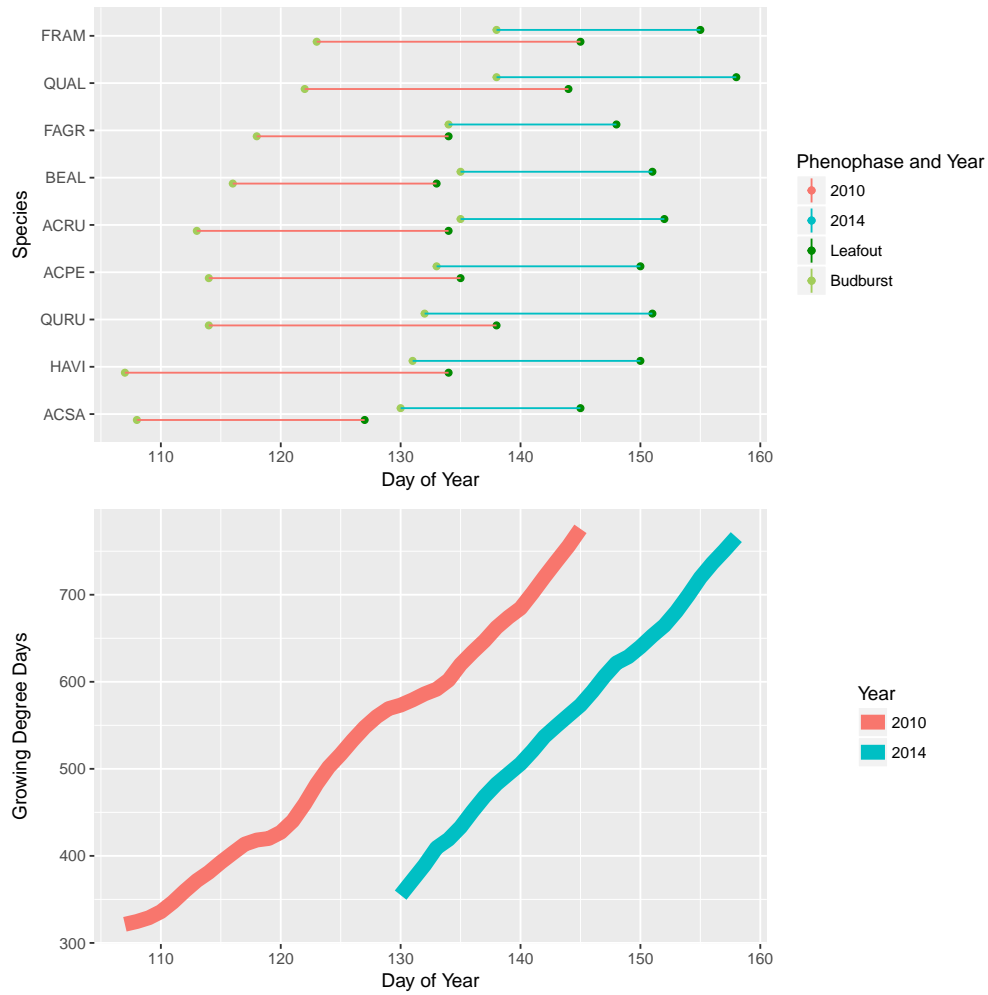


Figure 3: A comparison of two years of observational data investigating the effects of growing degree days on the duration of vegetative risk. The average duration of vegetative risk for 2010 was 21 ± 3.39 days versus 17.1 ± 1.96 days in 2014.

5.2 Interaction of Phenological Cues and the Duration of Vegetative Risk

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 the species that will be affected and to understand which species will likely become more at risk of false spring events in the future.

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 even decrease as forcing begin earlier in the season, 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.

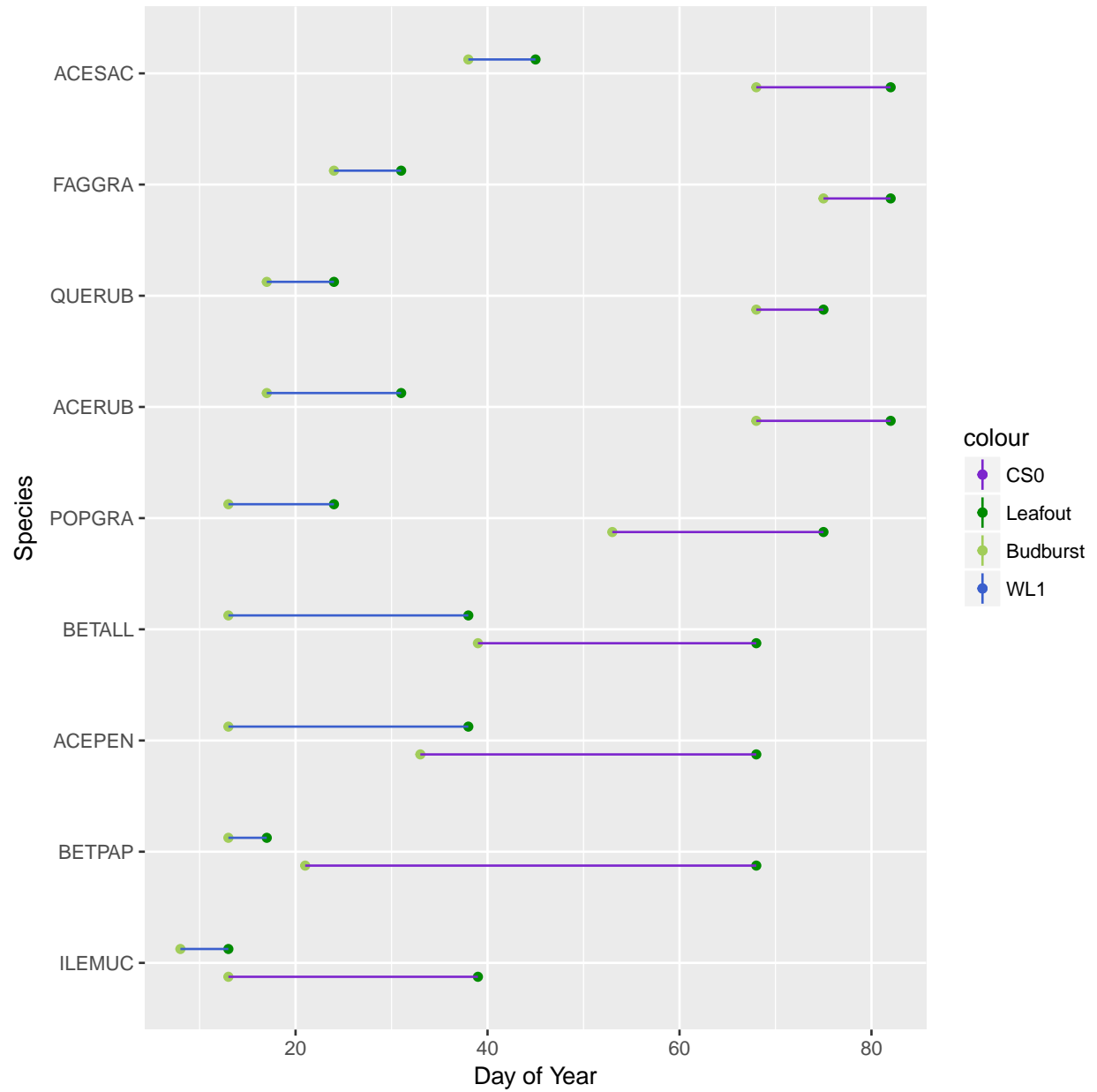


Figure 4: Day of budburst and the day of leaf out for native tree species in New England. Data was collected from a growth chamber experiment using any combination of two photoperiod treatments, two forcing treatments, and three chilling treatments. The standard deviation is represented in blue for budburst and green for leaf out.

6 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.

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

Sector	BBCH	Species	Temperature (°C)	Type	Source
Ecological	9-15	Sorbus aucuparia	-7.4	50% lethality	Lenz <i>et al.</i> (2016)
Ecological	9-15	Prunus avium	-8.5	50% lethality	Lenz <i>et al.</i> (2016)
Ecological	9-15	Tilia platyphyllos	-7.4	50% lethality	Lenz <i>et al.</i> (2016)
Ecological	9-15	Acer pseudoplatanus	-6.7	50% lethality	Lenz <i>et al.</i> (2016)
Ecological	9-15	Fagus sylvatica	-4.8	50% lethality	Lenz <i>et al.</i> (2016)
Ecological	9+	All	-2.2	hard	Schwartz (1993)
Ecological	9+	All	-1.7	soft	Augsburger (2013)
Ecological	All	All	2 SD below winter TAVG	cold-air outbreaks	Vavrus <i>et al.</i> (2006)
Ecological	9+	Eucalyptus pauciflora	-5.8	elevated CO2 and temperature threshold	Barker <i>et al.</i> (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 <i>et al.</i> (2015)
Agrinomical	Floral	Wheat	-4 to -5	10-90% lethality	Barlow <i>et al.</i> (2015)
Agrinomical	Vegetative	Wheat	-7 for 2hrs	100% lethality	Barlow <i>et al.</i> (2015)
Agrinomical	Vegetative	Rice	4.7	lethal limit	Sánchez <i>et al.</i> (2013)
Agrinomical	Vegetative	Corn	-1.8	lethal limit	Sánchez <i>et al.</i> (2013)
Agrinomical	Vegetative	Wheat	-17.2	lethal limit	Sánchez <i>et al.</i> (2013)

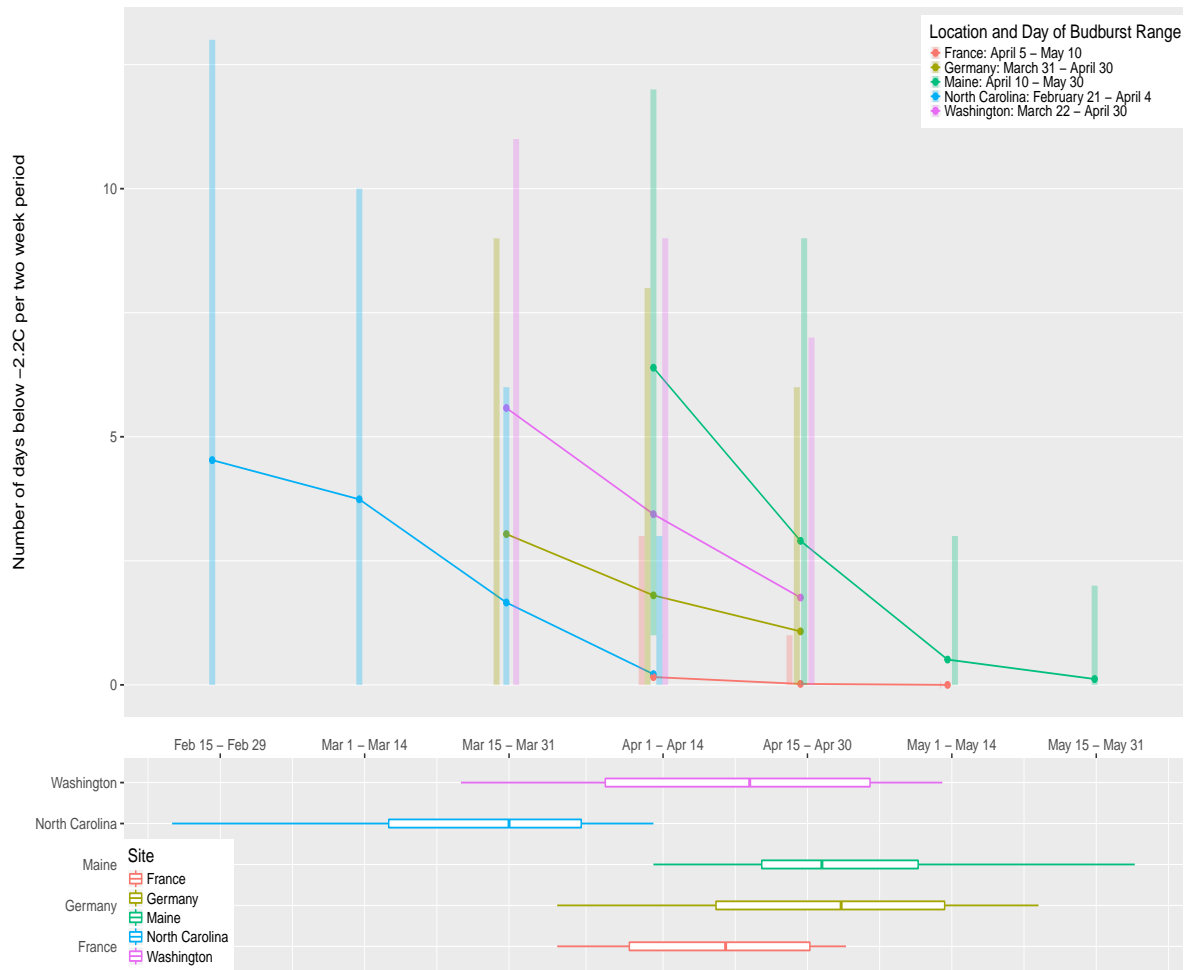


Figure 5: A comparison of false spring risk across five climate regions. The data was subsetted for each region based on earliest historical spring onset date to the latest historical leafout date and was divided into biweekly time periods (Schaber & Badeck, 2005; White *et al.*, 2009; Soudani *et al.*,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

7 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.

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