

¹ **Rethinking False Spring Risk**

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¹⁵ **1 Abstract**

¹⁶ Temperate plants are at risk of being exposed to late spring freezes — often called false springs — which
¹⁷ can be damaging ecologically and economically. As climate change may alter the prevalence and severity
¹⁸ of false springs, our ability to accurately forecast such events has become more critical. Currently, many
¹⁹ false spring studies simplify the various ecological elements needed for accurate predictions of the level of
²⁰ plant damage from late spring freezing events. Here we review the complexity of factors driving a plant's
²¹ false spring risk. We highlight how species, life stage, and habitat differences contribute to the likelihood of
²² occurrence and damage potential of false springs. Integrating some of these complexities could help rapidly
²³ advance forecasting of false springs in climate change and ecological studies.

²⁴ **2 Introduction**

²⁵ Plants growing in temperate environments time their growth each spring to follow rising temperatures along-
²⁶ side increasing light and soil resource availability. While tracking spring resource availability, temperate
²⁷ plants are at risk of late spring freezes, which can be detrimental to growth. Individuals that leaf out before
²⁸ the last freeze date are at risk of leaf loss, damaged wood tissue, and slowed canopy development (Gu *et al.*,

²⁹ 2008; Hufkens *et al.*, 2012). These damaging late spring freezes are also known as false springs, and are widely
³⁰ documented to result in adverse ecological and economic consequences (Knudson, 2012; Ault *et al.*, 2013).

³¹ Climate change is expected to cause an increase in damage from false spring events due to earlier spring onset
³² and potentially greater fluctuations in temperature in some regions (Cannell & Smith, 1986; Inouye, 2008;
³³ Martin *et al.*, 2010). Already, multiple studies have documented false springs in recent years (Gu *et al.*, 2008;
³⁴ Augspurger, 2009; Knudson, 2012; Augspurger, 2013) and some have linked these events to climate change
³⁵ (Ault *et al.*, 2013; Allstadt *et al.*, 2015; Muffler *et al.*, 2016; Xin, 2016). This increasing interest in false
³⁶ springs has led to a growing body of research investigating the effects on temperate forests and agricultural
³⁷ crops. But for this research to produce accurate predictions of future trends, researchers need methods that
³⁸ properly evaluate the effects of false spring events across the diverse species and climate regimes they are
³⁹ studying.

⁴⁰ Current metrics for estimating false springs events are generally simple, often requiring an estimate for the
⁴¹ start of biological ‘spring’ (i.e. budburst) and whether temperatures occurred below a particular temperature
⁴² threshold in the following week. Such estimates inherently assume consistency of damage across species,
⁴³ functional group, life stages, and other climatic regimes, ignoring that such factors can greatly impact plants’
⁴⁴ false spring risk. As a result, such indices may lead to inaccurate current estimates as well as poor future
⁴⁵ predictions, slowing our progress in understanding false spring events and how they may shift with climate
⁴⁶ change.

⁴⁷ In this paper we highlight the complexity of factors driving a plant’s false spring risk and provide a road map
⁴⁸ for improved metrics. We show how location within a forest or canopy, interspecific variation in avoidance
⁴⁹ and tolerance strategies, freeze temperature thresholds, and regional effects unhinge simple metrics of false
⁵⁰ spring. We argue that a new approach that integrates these and other crucial factors would help accurately
⁵¹ determine current false spring damage and improve predictions of spring freeze risk under a changing climate
⁵² — while potentially providing novel insights to how plants respond to and are shaped by spring frost.

⁵³ **3 Defining False Spring: An example in one temperate plant com- 54 munity**

⁵⁵ Temperate forest plants experience elevated risk of frost damage during the spring due to the stochastic
⁵⁶ timing of spring frosts. Plants must therefore exhibit flexible spring phenologies to minimize freezing risk.
⁵⁷ Freezing temperatures following a warm spell could result in plant damage or even death (Ludlum, 1968; Mock
⁵⁸ *et al.*, 2007). Intracellular ice formation from false spring events often results in severe leaf and stem damage

59 (Burke *et al.*, 1976; Sakai & Larcher, 1987). Ice formation can also occur indirectly (i.e. extracellularly), which
60 results in freezing dehydration and mimics drought conditions (Pearce, 2001; Beck *et al.*, 2004; Hofmann &
61 Bruelheide, 2015). Both forms of ice formation can cause defoliation and crown dieback (Gu *et al.*, 2008).
62 Once buds exit the dormancy phase, they are less freeze tolerant and resistance to bud ice formation is greatly
63 reduced (Taschler *et al.*, 2004; Lenz *et al.*, 2013; Vitasse *et al.*, 2014b). An effective and consistent definition
64 of false spring would accurately determine the amount and type of ice formation to properly evaluate the
65 level of damage that could occur.

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

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

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

79 To demonstrate how the FSI definition works, we applied it to data from the Harvard Forest Long-term Eco-
80 logical Research program in Massachusetts. We used three separate methodologies to calculate spring onset:
81 long-term ground observational data (O'Keefe, 2014), PhenoCam data from Harvard Forest (Richardson,
82 2015), and USA National Phenology Network (USA-NPN) Extended Spring Index (SI-x) data (USA-NPN,
83 2016). These spring onset values were then inputted into the FSI equation (Equation 1) to calculate FSI
84 from 2008 to 2014 (Figure 1).

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

90 The reason for these discrepancies is that each method evaluates spring onset by integrating different at-
91 tributes such as age, species or functional group. Spring phenology in temperate forests typically progresses
92 by functional group (e.g. deciduous broadleaf trees). Understory species and young trees tend to initiate
93 budburst first, whereas larger canopy species may start later in the season (Richardson & O'Keefe, 2009;
94 Xin, 2016). The different FSI values determined in Figure 1 exemplify the differences in functional group
95 spring onset dates and illustrate variations in forest demography and phenology, which is most apparent in
96 2012. In 2012, a false spring event was reported through many regions of the US due to warm temperatures
97 occurring in March (Ault *et al.*, 2015). These high temperatures would most likely be too early for larger
98 canopy species to initiate budburst but they would affect smaller understory species as is seen in Figure 1.

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

109 4 Plant Physiology and Diversity versus the Current False Spring 110 Definition

111 Plants have evolved to minimize false spring damage through two strategies: avoidance and tolerance. Many
112 temperate forest plants utilize various morphological strategies to be more frost tolerant: some have toothed
113 leaves to increase ‘packability’ in winter buds, which permits more rapid leafout (Edwards *et al.*, 2017) and
114 minimizes exposure time of less resistant tissues. Other species have young leaves with more trichomes to
115 act as a buffer against spring frosts (Agrawal *et al.*, 2004; Prozherina *et al.*, 2003). More studies are needed
116 to investigate the interplay between leaf morphology and false spring tolerance.

117 Rather than being more tolerant of spring freezing temperatures, some temperate forest species have evolved
118 to avoid frosts via more flexible phenologies. Effective avoidance strategies require well-timed spring phe-
119 nologies. Temperate deciduous tree species optimize growth and minimize spring freeze damage by using
120 three cues to initiate budburst: low winter temperatures, warm spring temperatures, and increasing pho-

121 to periods (Chuine, 2010). The evolution of these three cues and their interactions has permitted temperate
122 plant species to occupy more northern ecological niches (Kollas *et al.*, 2014) and decrease the risk of false
123 spring damage, which is crucial for avoidance strategies (Charrier *et al.*, 2011). One avoidance strategy, for
124 example, is the interaction between over-winter chilling and spring forcing temperatures. Warm tempera-
125 tures earlier in the year will not result in early budburst due to insufficient chilling (Basler & Körner, 2012).
126 Likewise, photoperiod sensitivity is a common false spring avoidance strategy: species that respond strongly
127 to photoperiod cues in addition to warm spring temperatures will likely delay budburst and evade false spring
128 events as spring continues to advance earlier in the year (Basler & Korner, 2014).

129 5 Defining Vegetative Risk

130 Phenology and frost tolerance are intertwined — with important variation occurring across different phe-
131 nological phases. Flowering and fruiting are generally more sensitive to false spring events than vegetative
132 phases (Augspurger, 2009; Lenz *et al.*, 2013). However, false spring events that occur during the vegeta-
133 tive growth phenophases may impose the greatest freezing threat to deciduous plant species. Plants will
134 suffer greater long-term effects from the loss of photosynthetic tissue compared to floral and fruit tissue,
135 which could impact multiple years of growth, reproduction, and canopy development (Sakai & Larcher, 1987;
136 Vitasse *et al.*, 2014a).

137 There is also important variation within certain phenological phases. Most notably, within the vegetative
138 phases of spring leafout, plants that have initiated budburst but have not fully leafed out are more likely to
139 sustain damage from a false spring than individuals past the leafout phase. This is because freezing tolerance
140 is lowest after budburst begins until the leaf is fully unfolded (Lenz *et al.*, 2016). Therefore, the rate of
141 budburst and the length of time between budburst and leafout is essential for predicting level of damage
142 from a false spring event. We will refer to the timing of these phenophases — budburst to leafout — as the
143 duration of vegetative risk (Figure 2). The duration of vegetative risk is usually extended if a freezing event
144 occurs during the phenophases between budburst and full leafout (Augspurger, 2009), which could result in
145 exposure to multiple frost events in one season.

146 6 How Species' Phenological Cues Shape Vegetative Risk

147 Predictions of false spring critically depend on understanding what controls the duration of vegetative risk
148 across species. For temperate species, the three major cues that control budburst (Chuine, 2010) probably
149 play a dominant role. One study, which examined how these cues impact budburst and leafout, shows that

150 the duration of vegetative risk can vary by 21 days or more depending on the suite of cues a plant experiences
151 (Figure 5). The experiment examined 9 temperate trees and shrubs using a fully crossed design of three levels
152 of chilling (field chilling, field chilling plus 30 days at either 1 or 4 °C), two levels of forcing (20°C/10°C
153 or 15°C/5°C day/night temperatures) and two levels of photoperiod (8 versus 12 hour days) resulting in 12
154 treatment combinations. Increased forcing, daylength and chilling all decreased the duration of vegetative
155 risk with forcing causing the greatest decrease (10 days), followed by daylength (9 days), and chilling (2-3
156 days depending on the temperature), but the full effect of any one cue depended on the other cues due to
157 important interactions—for example, the combined effect of warmer temperatures and longer days would be
158 14 days, because of -5 days interaction between the forcing and photoperiod cues.

159 Such cues may provide a starting point for predicting how climate change will alter the duration of vegetative
160 risk. Robust predictions will require much more information, especially the emissions scenario realized over
161 coming decades (IPCC, 2015), but one potential outcome is that higher temperatures will increase forcing
162 and decrease chilling in many locations. Under this scenario experimental results suggest a 5-21 day increase
163 in duration of vegetative risk depending on the species (Figure 5B). This cue interaction could thus expose
164 at risk plants to more intense false spring events or even multiple events in one year.

165 Considering the interaction of cues and climate change further complicates understanding species future
166 vulnerabilities to false spring events. Most species are expected to begin leafout earlier in the season with
167 earlier warming spring temperatures but some species may have the opposite response due to less winter
168 chilling or decreased photoperiod cues (Cleland *et al.*, 2006; Yu *et al.*, 2010; Xin, 2016). Generally, individuals
169 that initiate budburst earlier in the spring may attempt to limit freezing risk by decreasing the duration of
170 vegetative risk in order to minimize the exposure of less frost tolerant phenophases. But with a changing
171 climate and thus shifts in phenological cues , this relationship may change. Further studies are essential to
172 understand the interplay between chilling, forcing, and photoperiod cues on the duration of vegetative risk,
173 especially for species occupying ecological niches more susceptible to false spring events.

174 **6.1 Predictable Regional Differences in Climate, Species Responses and False 175 Spring Risk**

176 Robust predictions must consider the full interplay of species cues and a specific location's climate. A single
177 species may have varying cues across space: various studies that investigate latitudinal effects indicate that
178 species and individuals growing further north respond to a different interaction of cues than those growing
179 further south and, subsequently, species across different regions may have different durations of vegetative
180 risk (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011). Studies also suggest that
181 species within the same system can exhibit different sensitivities to the three cues (Basler & Körner, 2012;

¹⁸² Laube *et al.*, 2013) thus further amplifying the myriad of climatic and phenological shifts as well as the
¹⁸³ varying species-level effects. We assessed climate data across North America and Europe to gain a better
¹⁸⁴ understanding of the interaction between duration of vegetative risk and false spring events in an attempt to
¹⁸⁵ unravel these complexities.

¹⁸⁶ Numerous studies have investigated how the relationship between budburst and major phenological cues
¹⁸⁷ varies across space and the genetic variations that occur between populations by using latitudinal gradients
¹⁸⁸ (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011; Zohner *et al.*, 2016; Gauzere *et al.*,
¹⁸⁹ 2017). Few, however, have integrated distance from the coast or regional effects. Yet climate and thus false
¹⁹⁰ spring risk and phenological cues vary across regions. For example, consider five different regions within
¹⁹¹ a temperate climate (Figure 3). Some regions may experience harsher winters and greater temperature
¹⁹² variability throughout the year, and these more variable regions often have a much higher risk of false spring
¹⁹³ (i.e. Maine) than others (i.e. Lyon) (Figure 3). Understanding and integrating such spatiotemporal effects
¹⁹⁴ and regional differences when investigating false spring risk and duration of vegetative risk would help improve
¹⁹⁵ predictions as climate change progresses.

¹⁹⁶ Accurate predictions need to carefully consider how chilling and forcing cues vary across regions. Climatic
¹⁹⁷ variation across regions and at different distances from the coast results in varying durations of vegetative
¹⁹⁸ risk due to different chilling and forcing temperatures (Myking & Skroppa, 2007). It is therefore important to
¹⁹⁹ recognize climate regime extremes (e.g. seasonal trends, annual minima and annual maxima) across regions
²⁰⁰ in future studies in order to better understand the interplay between duration of vegetative risk and climatic
²⁰¹ variation. The climatic implications of advancing forcing temperatures could potentially lead to earlier dates
²⁰² of budburst and enhance the risk of frost. These shifts in climatic regimes could vary in intensity across
²⁰³ regions (i.e. habitats currently at risk of false spring damage could become low risk regions over time).

²⁰⁴ There are also discrepancies in defining a false spring event related to understanding the temperature threshold
²⁰⁵ for damage. Some regions and species may tolerate lower temperature thresholds than others (Figure S1).
²⁰⁶ It is crucial to gain an understanding on which climatic parameters result in false spring events and how
²⁰⁷ these parameters may vary across regions. It is anticipated that most regions will have earlier spring onsets,
²⁰⁸ however, last freeze dates will not advance at the same rate (Inouye, 2008; Martin *et al.*, 2010; Labe *et al.*,
²⁰⁹ 2016; Sgubin *et al.*, 2018), rendering some regions and species to be more susceptible to false spring events
²¹⁰ in the future.

₂₁₁ **7 Conclusion**

₂₁₂ Temperate forest trees are most at risk to frost damage in the spring due to the stochasticity of spring freezes.
₂₁₃ With warm temperatures advancing in the spring but last spring freeze dates advancing at a slower rate,
₂₁₄ there could potentially be more damaging false spring events in the future, especially in high risk regions
₂₁₅ (Gu *et al.*, 2008; Inouye, 2008). The current equation for evaluating false spring damage (Equation 1) largely
₂₁₆ simplifies the myriad of complexities involved in assessing false spring damage and risks. More studies aimed
₂₁₇ at understanding relationships between species avoidance and tolerance strategies, climatic regimes, and
₂₁₈ physiological cue interactions with the duration of vegetative risk would improve predictions. Additionally,
₂₁₉ research to establish temperature thresholds for damage across functional types and phenophases will help
₂₂₀ effectively predict false spring risk in the future. An integrated approach to assessing past and future spring
₂₂₁ freeze damage would offer more robust predictions as climate change progresses, which is essential in order
₂₂₂ to mitigate the adverse ecological and economic effects of false springs.

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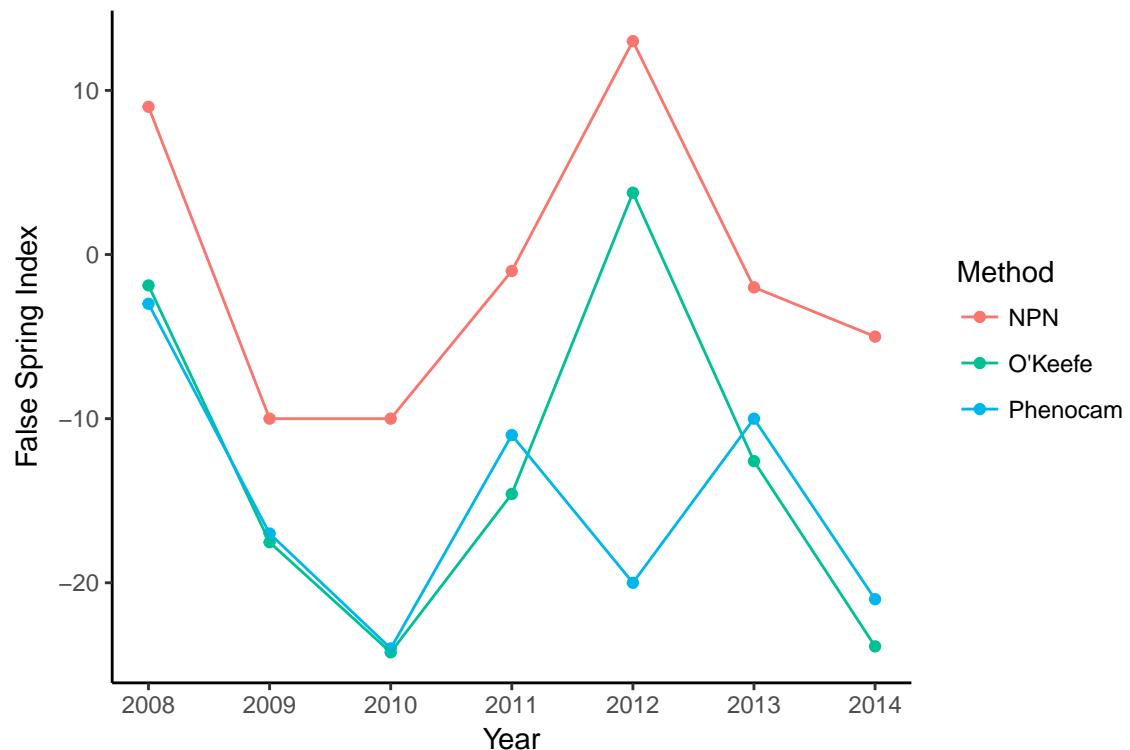


Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methodology used in this study. To calculate spring onset, we used the USA-NPN Extended Spring Index tool for the USA-NPN FSI values, which are in red (USA-NPN, 2016), long-term ground observational data for the observed FSI values, which are in green (O'Keefe, 2014), and near-surface remote-sensing canopy data for the PhenoCam FSI values, which are in blue (Richardson, 2015).

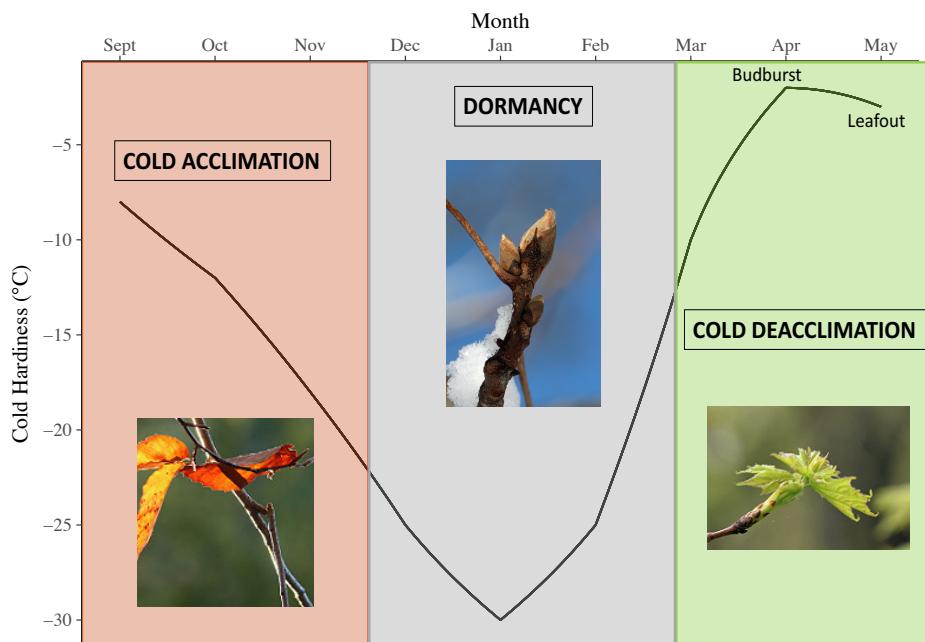
Box 1:

Cold hardiness (i.e. freezing tolerance) is essential for all temperate plants in order to survive cold winters and stochastic freezes (Vitasse *et al.*, 2014a).

Cold Hardiness: Ability to resist injury to low temperatures

Cold Acclimation: Adjustment period of freezing tolerance by decreasing risk of intracellular freezing through various mechanisms (Charrier *et al.*, 2011)

Cold Deacclimation: Dehardening of buds and increase in metabolism and development (Vitasse *et al.*, 2014a)



Sept-Nov (Orange): During the cold acclimation phase, cold hardiness in the bud increases rapidly as temperate plants begin to enter dormancy.

Nov-Feb (Blue): Once buds reach the dormancy phase, buds are able to tolerate temperatures as low as -25°C to -40°C or lower (Charrier *et al.*, 2011; Vitasse *et al.*, 2014a).

Feb-May (Green): Freezing tolerance diminishes again during the cold deacclimation phase once buds begin to swell (-8°C) and is lowest between budburst (-2°C) to leafout (-3°C).

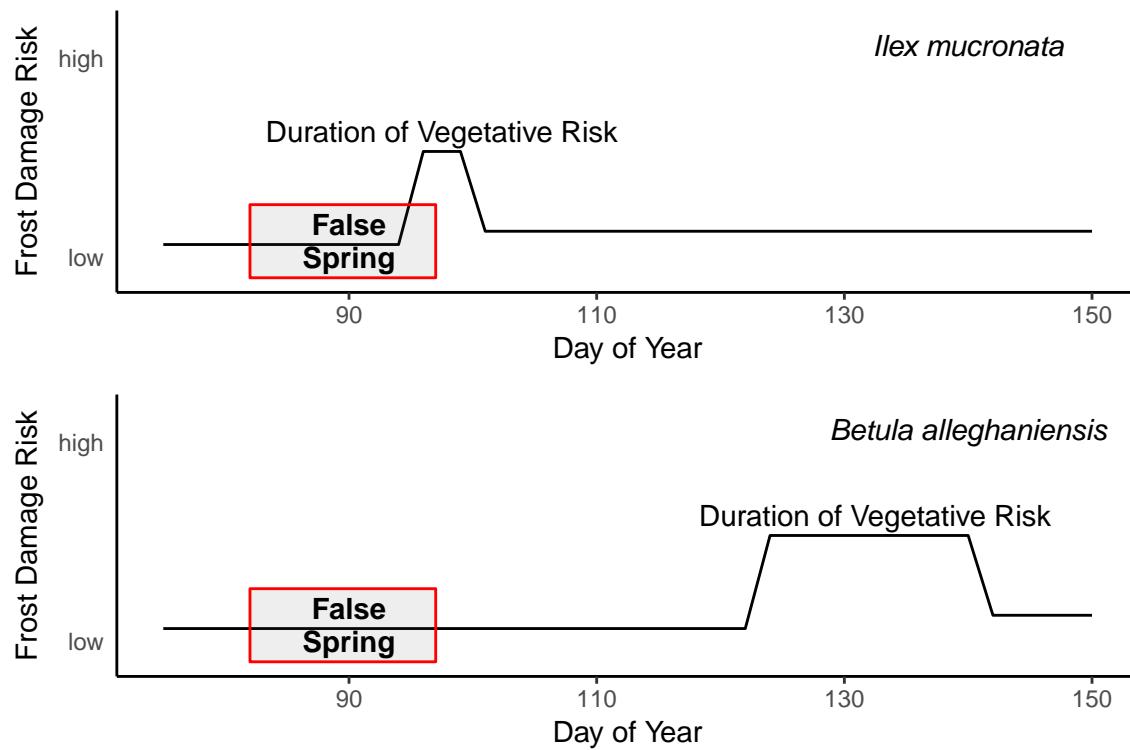


Figure 2: A figure showing the differences in spring phenology and false spring risk across two species: *Ilex mucronata* (L.) and *Betula alleghaniensis* (Marsh.). We mapped a possible false spring event based on historic weather data and compared it to the observational data collected at Harvard Forest (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.

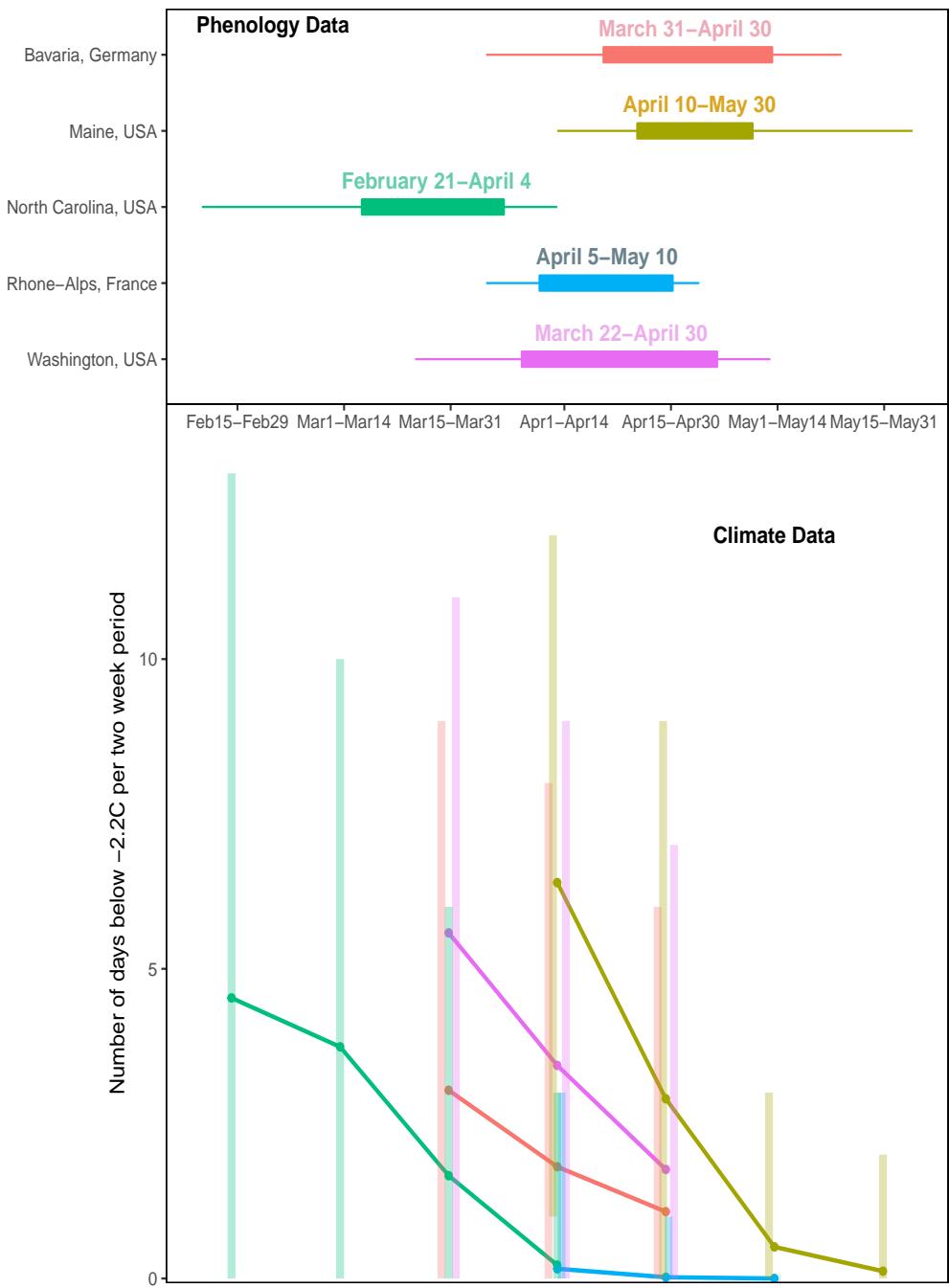


Figure 3: False spring risk can vary dramatically across regions. Here we show the period when plants are most at risk to tissue loss – between budburst and leafout (upper, lines represent the range with the thicker line representing the interquartile range) and the variation in the number of freeze days (-2.2°C) (Schwartz, 1993) that occurred on average over the past 50 years for five different sites (lower, bars represent the range, points represent the mean). Data come from USA-NPN SI-x tool (1981-2016) and observational studies (1950-2016) for phenology (USA-NPN, 2016; Soudani et al., 2012; White et al., 2009; Schaber & Badeck, 2005) and NOAA Climate Data Online tool for climate (from 1950-2016).

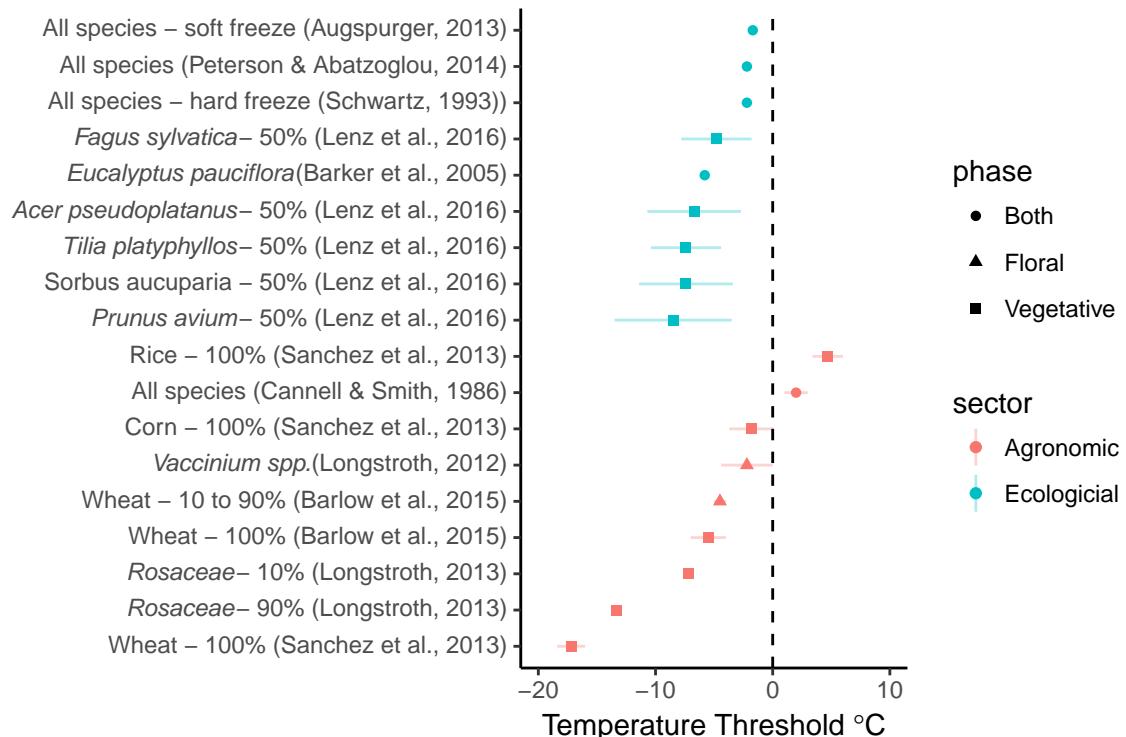


Figure 4: A comparison of damaging spring freezing temperature thresholds across ecological and agronomic studies. Each study is listed on the y axis along with the taxonomic group of focus. Next to the species name is the freezing definition used within that study (e.g. 100% is 100% lethality). Each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

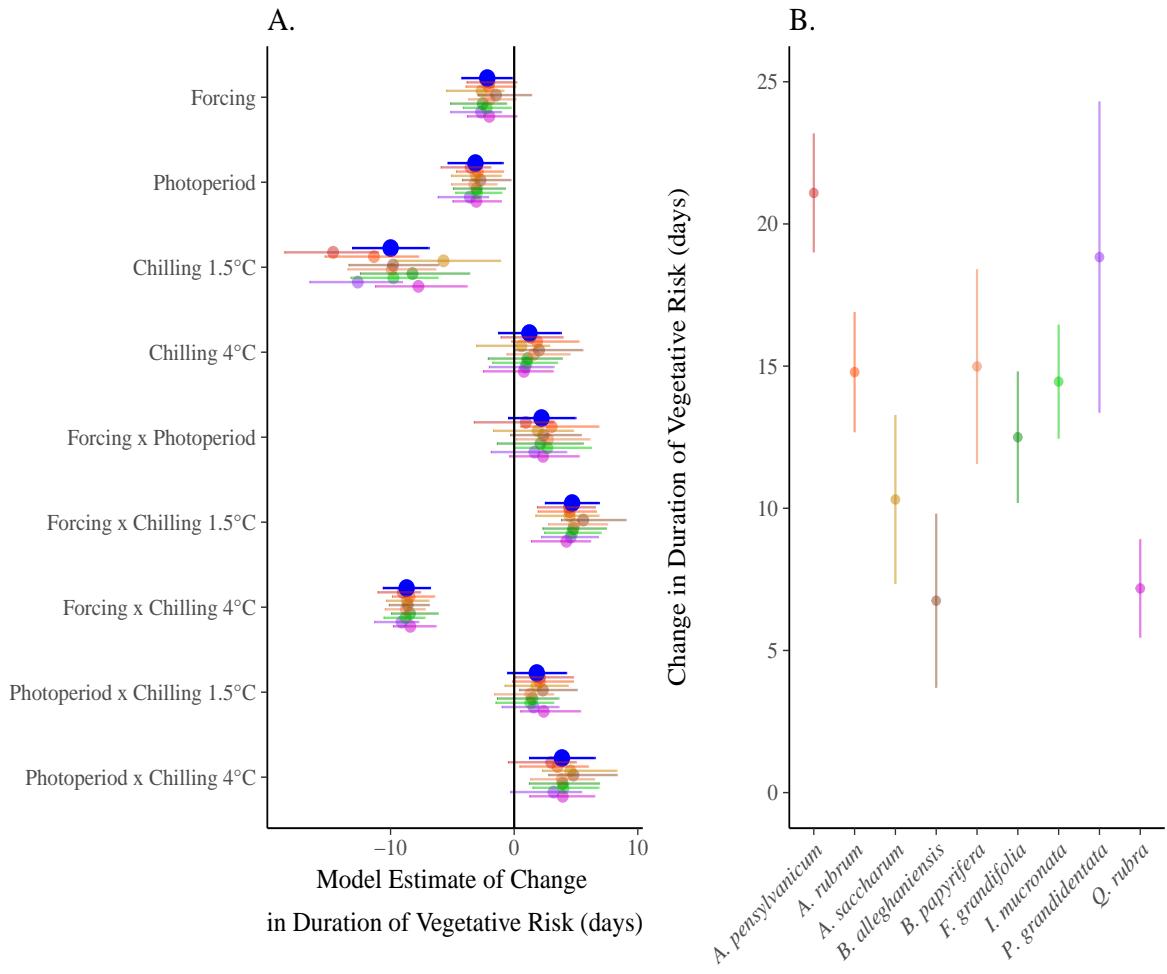


Figure 5: Results from the growth chamber experiment. (A) A plot of the model parameter estimates on the duration of vegetative risk. Spring forcing temperatures had the largest effect on the rate of leafout, with photoperiod also being a critical factor. Thus, while greater forcing or longer photoperiods alone will shorten the duration of vegetative risk by 10 and 9 days respectively, their combined effect would be 14 days due to a 5 day delay through their interaction ($10 + 9 - 5 = 14$). 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. (B) 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. The standard error is represented by the bars around each point.