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Rethinking False Spring Risk

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¹ Rethinking False Spring Risk

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15 Abstract

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

24 Introduction

25 Plants from temperate environments time their growth each spring to follow rising temperatures alongside
26 increasing light and soil resource availability. While tracking spring resource availability, individuals that
27 budburst before the last freeze date are at risk of leaf loss, damaged wood tissue, and slowed canopy devel-
28 opment (Gu *et al.*, 2008; Hufkens *et al.*, 2012). These damaging late spring freezes are also known as false
29 springs, and are widely documented to result in adverse ecological and economic consequences (Ault *et al.*,
30 2013; Knudson, 2012).

31 Climate change is expected to cause an increase in damage from false spring events due to earlier spring
32 onset and potentially greater fluctuations in temperature in some regions (Inouye, 2008; Martin *et al.*, 2010).
33 Already, multiple studies have documented false springs in recent years (Augspurger, 2009, 2013; Gu *et al.*,
34 2008; Menzel *et al.*, 2015) and some have linked these events to climate change (Allstadt *et al.*, 2015; Ault
35 *et al.*, 2013; Muffler *et al.*, 2016; Vitra *et al.*, 2017; Xin, 2016). This interest in false springs has led to a
36 growing body of research investigating the effects on temperate forests. For this research to produce accurate
37 predictions, however, researchers need methods that properly evaluate the effects of false springs across diverse
38 species and climate regimes.

³⁹ Measuring False Spring

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 below a particular threshold occurred in
⁴² the following week. Such estimates inherently assume consistency of damage across species, functional group,
⁴³ life stages, and other climatic regimes, ignoring that such factors can greatly impact plants’ false spring risk.
⁴⁴ As a result, such indices may lead to inaccurate estimates and predictions.

⁴⁵ In this paper we highlight the complexity of factors driving a plant’s false spring risk and provide a road
⁴⁶ map for improved metrics. We show how location within a forest or canopy (Augspurger, 2013), interspecific 
⁴⁷ variation in avoidance and tolerance strategies (Martin *et al.*, 2010; Muffler *et al.*, 2016), freeze temperature
⁴⁸ thresholds (Lenz *et al.*, 2013), and regional effects (Muffler *et al.*, 2016) unhinge simple metrics of false spring.
⁴⁹ We argue that a new approach that integrates these and other crucial factors would help accurately determine
⁵⁰ current false spring damage and improve predictions of spring freeze risk under a changing climate — while
⁵¹ potentially providing novel insights to how plants respond to and are shaped by spring frost.

⁵² Defining False Spring: An example in one temperate plant commu- ⁵³ nity

⁵⁴ Temperate forest plants experience elevated risk of frost damage during the spring due to the stochastic
⁵⁵ timing of frosts. Freezing temperatures following a warm spell can result in plant damage or even death
⁵⁶ (Ludlum, 1968; Mock *et al.*, 2007). Many temperate species exhibit flexible spring phenologies, which help
⁵⁷ them minimize spring freezing risk, but freeze damage can still occur. Once buds exit the dormancy phase,
⁵⁸ they are less  freeze tolerant and less resistant to ice formation (Lenz *et al.*, 2013; Taschler *et al.*, 2004; Vittasse
⁵⁹ *et al.*, 2014b). Intracellular ice formation from false spring events often results in severe leaf and stem damage
⁶⁰ (Burke *et al.*, 1976; Sakai & Larcher, 1987). Ice formation can also occur indirectly (i.e. extracellularly), which
⁶¹ results in freezing dehydration and mimics drought conditions (Beck *et al.*, 2004; Hofmann & Bruelheide,
⁶² 2015; Pearce, 2001). Both forms of ice formation can cause defoliation and crown dieback (Gu *et al.*, 2008).
⁶³ An effective and  consistent definition of false spring would accurately determine the amount and type of ice
⁶⁴ formation to properly evaluate the level of damage that could occur.

⁶⁵ Currently there are several ways to define a false spring. A common definition describes a false spring as

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

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

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

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

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

The reason for these discrepancies is that each method evaluates spring onset by integrating different attributes such as age, species or functional group. Spring phenology in temperate forests typically progresses by functional group: understory species and young trees tend to initiate budburst first, whereas larger canopy species start later in the season (Richardson & O'Keefe, 2009; Xin, 2016). The different FSI values deter-

93 mined in Figure 1 exemplify the differences in functional group spring onset dates and illustrate variations in
 94 forest  phenology and phenology. While the SI-x data (based on observations of early-active shrub species,
 95 including lilac, *Syringa vulgaris*) may best capture understory dynamics, the PhenoCam and observational
 96 FSI data integrate over larger canopy species. Such differences are visible each year, as the canopy-related
 97 metrics show lower risk, but are especially apparent in 2012. In 2012, a false spring event was reported
 98 through many regions of the US due to warm temperatures occurring in March (Ault *et al.*, 2015). These
 99 high temperatures would most likely have been too early for larger canopy species to initiate budburst but
 100 they would have affected smaller understory species, as is seen by the high risk of the SI-x FSI in Figure 1.

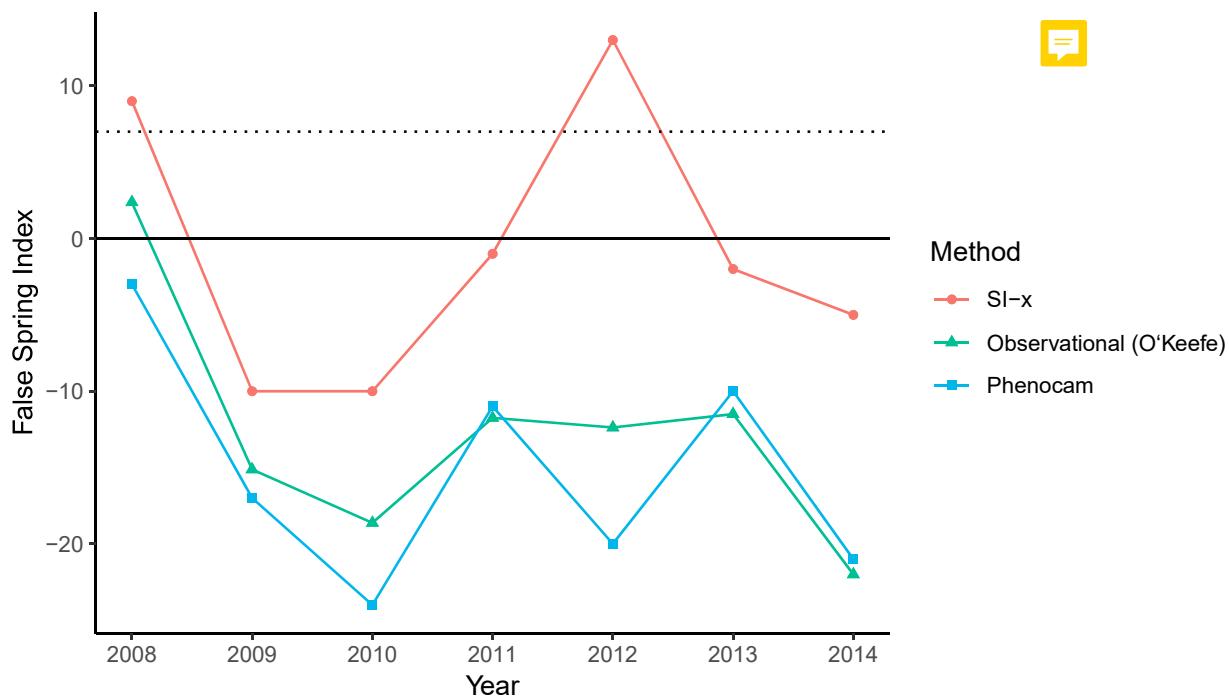


Figure 1: False Spring Index (FSI) values from 2008 to 2014 vary across methodologies. To calculate spring onset, we used the USA-NPN Extended Spring Index tool for the USA-NPN FSI values, which are in red (USA-NPN, 2016), long-term ground observational data for the observed FSI values, which are in green (O'Keefe, 2014), and near-surface remote-sensing canopy data for the PhenoCam FSI values, which are in blue (Richardson, 2015). The solid line at FSI=0 indicates a boundary between a likely false spring event or not, with positive numbers indicating a false spring likely occurred and negative numbers indicating a false spring most likely did not occur. The dotted line at FSI=7 indicates the seven day threshold frequently used in false spring definitions, which suggests years with FSI values greater than seven very likely had false spring events.

101 Yet, in contrast to our three metrics of spring onset for one site, most FSI work currently ignores variation
 102 across functional groups — instead using one metric of spring onset and assuming it applies to the whole
 103 community of plants (Allstadt *et al.*, 2015; Marino *et al.*, 2011; Mehdipoor & Zurita-Milla, 2017; Peterson

¹⁰⁴ & Abatzoglou, 2014). The risk of a false spring varies across habitats and with species composition since
¹⁰⁵ spring onset is not consistent across functional groups (Martin *et al.*, 2010). Therefore, one spring onset
¹⁰⁶ date cannot be used as an effective proxy for all species. False spring studies should first assess the forest
¹⁰⁷ demographics and functional groups relevant to the study question in order to effectively estimate the date of
¹⁰⁸ spring onset. However, as we outline below, considering different functional groups is unlikely to be enough
¹⁰⁹ for robust predictions. It will also be important to integrate species differences within functional groups and
¹¹⁰ to consider the various interspecific avoidance and tolerance strategies that species have evolved against false
¹¹¹ springs.



¹¹² Plant Physiology and Diversity versus the Current False Spring ¹¹³ Definition

¹¹⁴ Plants have evolved to minimize false spring damage through two strategies: avoidance and tolerance. Many
¹¹⁵ temperate forest plants utilize various morphological strategies to be more frost tolerant: some have increased
¹¹⁶ ‘packability’ of leaf primordia in winter buds, which may permit more rapid leafout (Edwards *et al.*, 2017) and
¹¹⁷ minimize the exposure time of less resistant tissues. Other species have young leaves with more trichomes to
¹¹⁸ act as a buffer against spring frosts (Agrawal *et al.*, 2004; Prozherina *et al.*, 2003). And many other individuals
¹¹⁹ are able to respond to abiotic cues such as consistently dry winters. Species living in habitats with drier
¹²⁰ winters develop shoots and buds with decreased water content, which makes the buds more tolerant to drought
¹²¹ and also to false spring events (Beck *et al.*, 2007; Kathke & Bruelheide, 2011; Hofmann & Bruelheide, 2015;
¹²² Morin *et al.*, 2007; Muffler *et al.*, 2016; Norgaard Nielsen & Rasmussen, 2009; Poirier *et al.*, 2010). These
¹²³ strategies are probably only a few of the many ways plants work to morphologically avoid frost damage, and
¹²⁴ more studies are needed to investigate the interplay between morphological traits and false spring tolerance.

¹²⁵ Rather than being more tolerant of spring freezing temperatures, some temperate forest species have evolved
¹²⁶ to avoid frosts via their phenologies. Effective avoidance strategies require well-timed spring phenologies.
¹²⁷ Most temperate deciduous tree species optimize growth and minimize spring freeze damage by using three cues
¹²⁸ to initiate budburst: low winter temperatures (chilling), warm spring temperatures (forcing), and increasing
¹²⁹ photoperiods (Chuine, 2010). The evolution of these three cues and their interactions has permitted temperate
¹³⁰ plant species to occupy more northern ecological niches (Kollas *et al.*, 2014) and decrease the risk of false
¹³¹ spring damage (Charrier *et al.*, 2011). One avoidance strategy, for example, is the interaction between over-

132 winter chilling and spring forcing temperatures. Warm temperatures earlier in the winter will not result in
133 early budburst due to insufficient chilling (Basler & Körner, 2012). Likewise, photoperiod sensitivity is a
134 common false spring avoidance strategy: species that respond strongly to photoperiod cues in addition to
135 warm spring temperatures are unlikely to have large advances in budburst with warming, and thus may evade
136 false spring events as warming continues (Basler & Korner, 2014).

137 Defining Vegetative Risk

138 Phenology and frost tolerance are clearly intertwined — with important variation occurring across different
139 phenological phases. Flowering and fruiting are generally more sensitive to false spring events than vegetative
140 phases (Augspurger, 2009; Caradonna & Bain, 2016; Lenz *et al.*, 2013), but false spring events that occur
141 during the vegetative growth phenophases may impose the greatest freezing threat to deciduous plant species.
142 Plants will suffer greater long-term effects from the loss of photosynthetic tissue, which could impact multiple
143 years of growth, reproduction, and canopy development (Vitasse *et al.*, 2014a; Xie *et al.*, 2015). However,
144 there is high variability in defining a damaging temperature threshold across species, including between
145 agricultural and ecological studies (Figure 2).

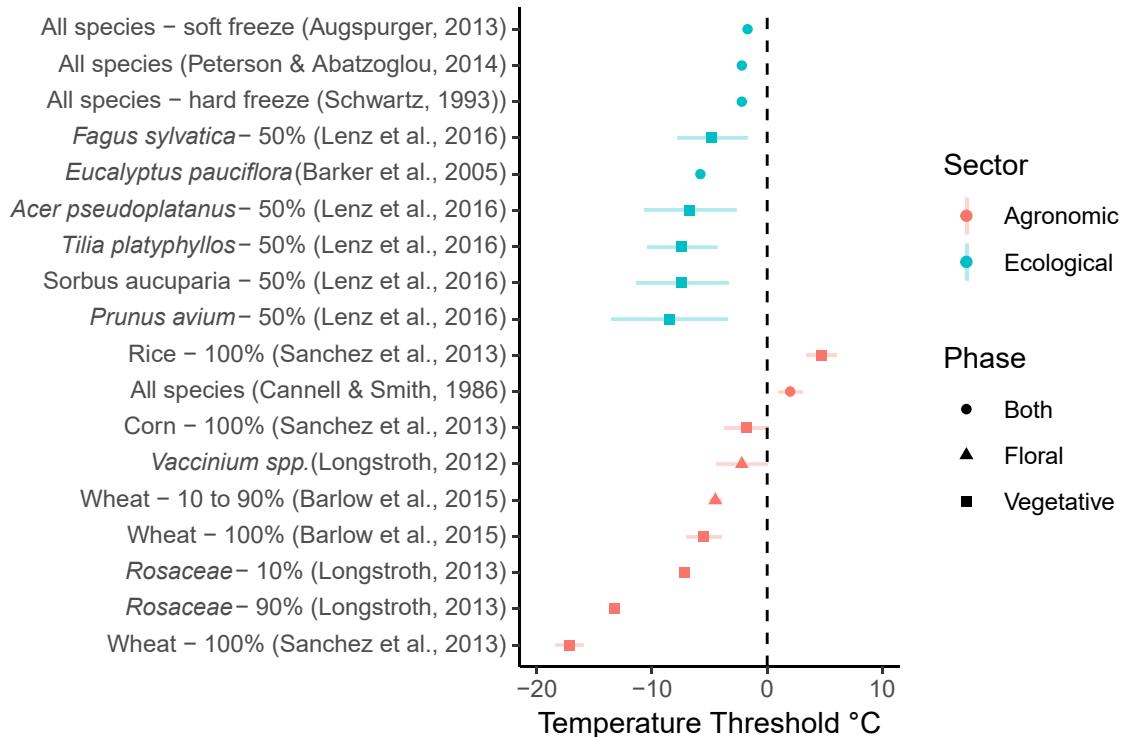


Figure 2: A comparison of damaging spring freezing temperature thresholds across ecological and agronomic studies. Each study is listed on the vertical axis along with the taxonomic group of plants. Next to the species name is the freezing definition used within that study (e.g. 100% is 100% lethality). Each point is the best estimate recorded for the temperature threshold with standard deviation if indicated in the study.

146 There is also important variation within certain phenological phases. Most notably, within the vegetative
 147 phases of spring leafout, plants that have initiated budburst but have not fully leafed out are more likely to
 148 sustain damage from a false spring than individuals past the leafout phase. This is because freezing tolerance
 149 is lowest after budburst begins until the leaf is fully unfolded (Lenz *et al.*, 2016). Therefore, the rate of
 150 budburst and the length of time between budburst and leafout is essential for predicting the level of damage
 151 from a false spring event. We will refer to the timing between these phenophases — budburst to leafout —
 152 as the duration of vegetative risk (Figure 3).

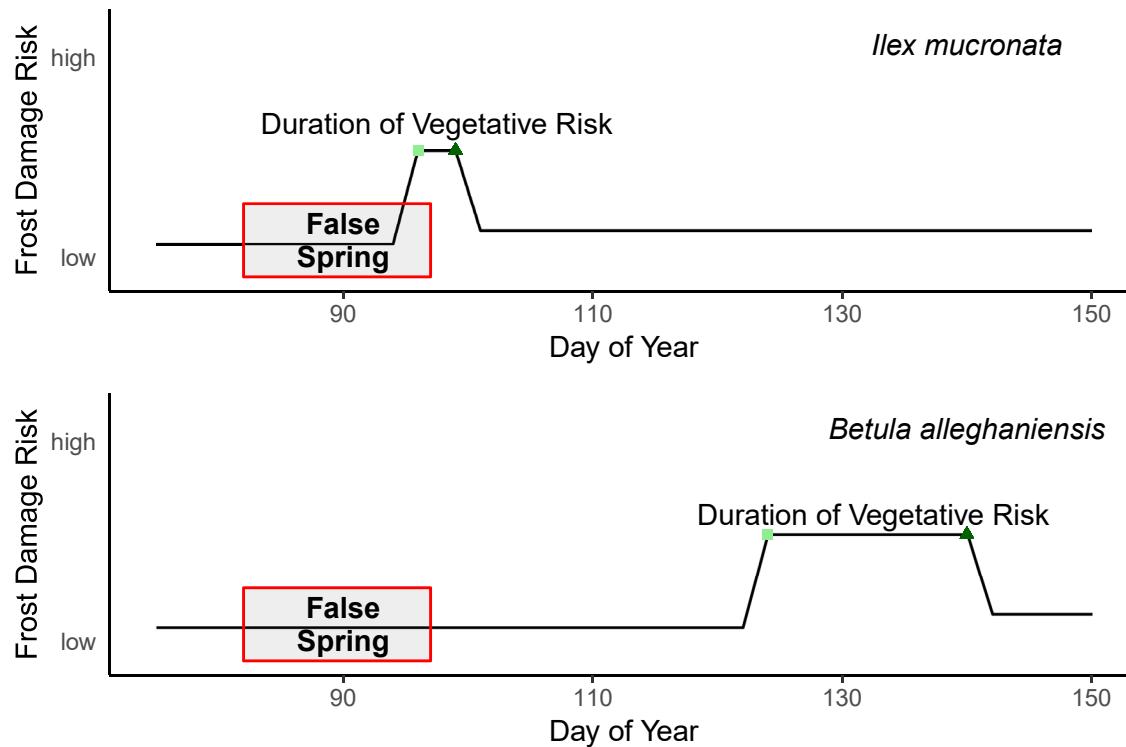


Figure 3: Differences in spring phenology and false spring risk across two species: *Ilex mucronata* (L.) and *Betula alleghaniensis* (Marsh.). We mapped a hypothetical false spring event based on historical weather data and long-term observational phenological data collected at Harvard Forest (O'Keefe, 2014). In this scenario, *Ilex mucronata*, which budbursts early and generally has a short period between budburst (light green squares) and leafout (dark green triangles), would be exposed to a false spring event during its duration of vegetative risk (i.e. from budburst to leafout), whereas *Betula alleghaniensis* would avoid it entirely (even though it has a longer duration of vegetative risk), due to later budburst.

¹⁵³ How Species Phenological Cues Shape Vegetative Risk

- ¹⁵⁴ Predictions of false spring critically depend on understanding what controls the duration of vegetative risk
¹⁵⁵ across species. For temperate species, the three major cues (winter chilling temperatures, spring warming
¹⁵⁶ temperatures and photoperiod) that control budburst (Chuine, 2010) play a dominant role. Most phenological
¹⁵⁷ studies currently focus on one phenophase (i.e. budburst or leafout) but, to examine false spring risk, it is
¹⁵⁸ important to examine the effects of the three phenological cues and their interactions on the duration of
¹⁵⁹ vegetative risk—that is, researchers must collect data on both budburst and leafout timing.
- ¹⁶⁰ Such cues may provide a starting point for predicting how climate change will alter the duration of vegetative
¹⁶¹ risk. Robust predictions will require more information, especially the emissions scenario realized over coming

162 decades (IPCC, 2015), but some outcomes with warming are more expected than others. For example, higher
163 temperatures are generally expected to increase forcing and decrease chilling in many locations, as well as
164 to trigger budburst at times of the year when daylength is shorter. Using data from a recent study that
165 manipulated all three cues and measured budburst and leafout (Flynn & Wolkovich, 2018) shows that any
166 one of these effects alone can have a large impact on the duration of vegetative risk (Figure 4): more forcing
167 shortens it substantially (-15 to -8 days), while shorter photoperiods and less chilling increase it to a lesser
168 extent (+3 to 9 days). Together, however, the expected shifts generally shorten the duration of vegetative
169 risk by 4-13 days, both due to the large effect of forcing and the combined effects of multiple cues. How
170 shortened the risk period is, however, varies strongly by species and highlights how climate change may speed
171 some species through this high risk period, but not others. Additionally, as our results are for a small set
172 of species we expect other species may have more diverse responses, as has already been seen in shifts in
173 phenology with warming (Cleland *et al.*, 2006; Fu *et al.*, 2015; Xin, 2016).

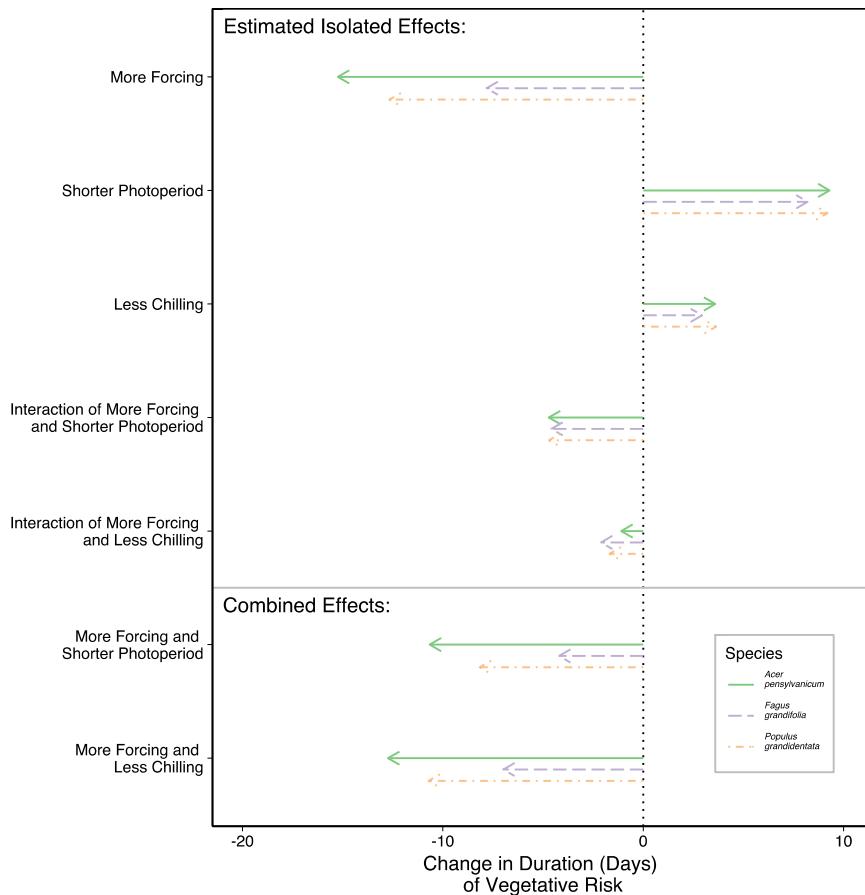


Figure 4: We examine the effects of phenological cues on the duration of vegetative risk across three species: *Acer pensylvanicum*, *Fagus grandifolia*, and *Populus grandidentata*. ‘More Forcing’ is a 5°C increase in spring warming temperatures, ‘Shorter Photoperiod’ is a 4 hour decrease in photoperiod and ‘Less Chilling’ is a 30 day decrease in over-winter chilling. Along with the estimated isolated effects, we show the combined predicted shifts in phenological cues with potential climate change (i.e. more forcing with shorter photoperiod and more forcing with less chilling) and the subsequent shifts in duration of vegetative risk across species. To calculate the combined effects, we added the estimated isolated effects of each cue alone with the interaction effects for the relevant cues for each species.

These findings highlight the need for further studies on the interplay between chilling, forcing, and photoperiod cues and the duration of vegetative risk across species. This is especially true for species occupying ecological niches more susceptible to false spring events; even if warming causes a shortened duration of vegetative risk for such species, the related earlier budburst dates could still lead to greater risk of false spring exposure.



¹⁷⁸ Predictable Regional Differences in Climate, Species Responses and False Spring
¹⁷⁹ Risk

¹⁸⁰ Robust predictions must consider the interplay of species cues with a specific location's climate. Climate and
¹⁸¹ thus false spring risk vary across regions. So  regions experience harsher winters and greater temperature
¹⁸² variability throughout the year (Figure 5 e.g. Maine, USA), and these more variable regions often have a
¹⁸³ much higher risk of false spring than others (Figure 5 e.g. Lyon, France). Understanding and integrating
¹⁸⁴ spatiotemporal effects and regional differences when investigating false spring risk and duration of vegetative
¹⁸⁵ risk would help improve predictions as climate change progresses. Such differences depend both on the local
¹⁸⁶ climate, the local species and the cues for each species at that location, as a single species may have varying
¹⁸⁷ cues across space. Therefore, based on cues alone, different regions may have different durations of vegetative
¹⁸⁸ risk for the same species (Caffarra & Donnelly, 2011; Partanen, 2004; Viheraaarnio *et al.*, 2006). Studies
¹⁸⁹ also show that different species within the same location can exhibit different sensitivities to the three cues
¹⁹⁰ (Basler & Körner, 2012; Laube *et al.*, 2013), further amplifying the myriad of climatic and phenological shifts
¹⁹¹ that determine false spring risk in a region.

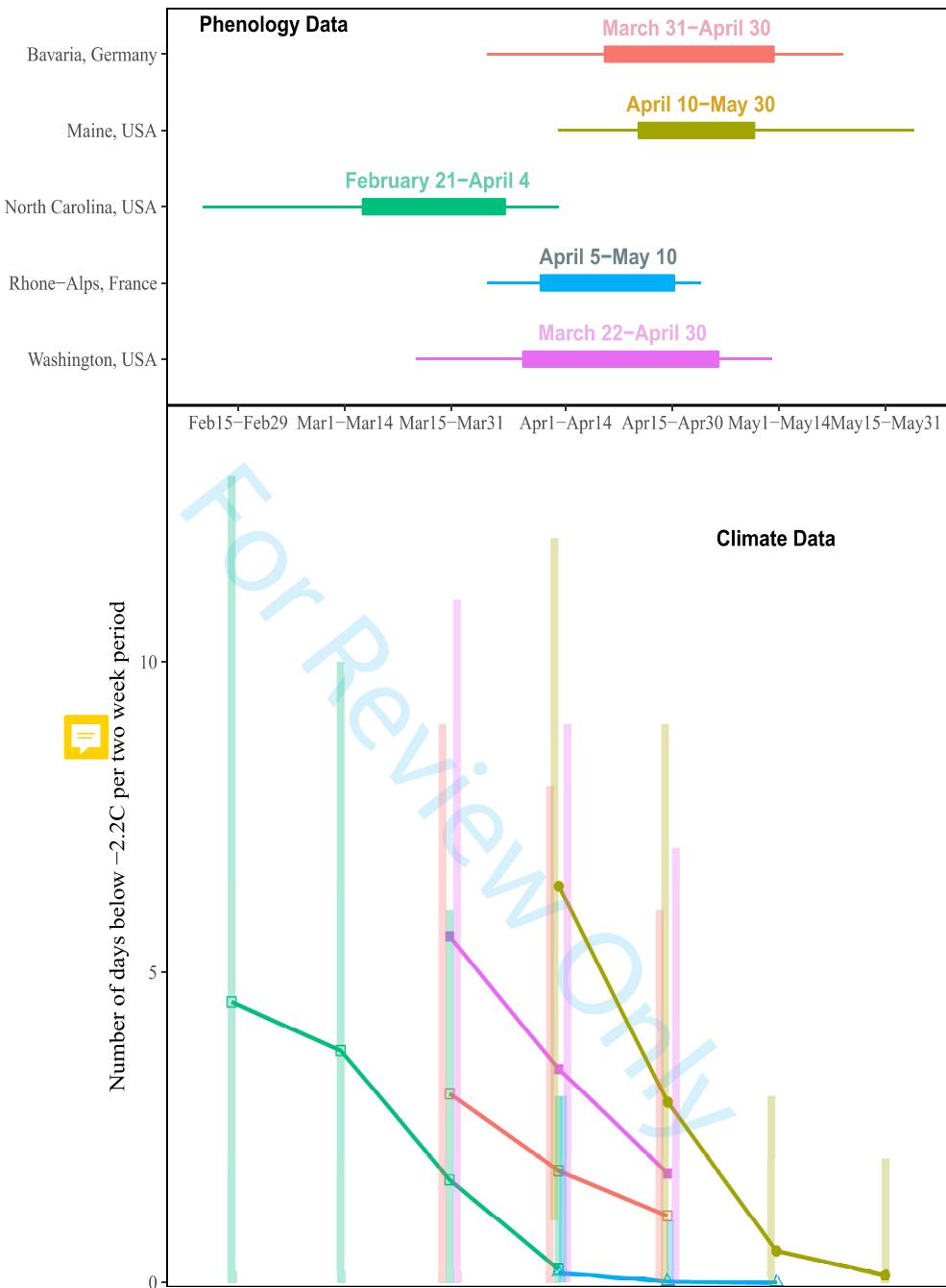


Figure 5: False spring risk can vary dramatically across regions. Here we show the period when plants are most at risk to tissue loss – between budburst and leafout (upper, lines represent the range with the thicker line representing the interquartile range) and the variation in the number of freeze 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 (Schaber & Badeck, 2005; Soudani et al., 2012; USA-NPN, 2016; White et al., 2009) and NOAA Climate Data Online tool for climate (from 1950–2016).



192 How a single species phenological cues varies across space is not yet well predicted. Some studies have
193 investigated how phenological cues for budburst vary across space, including variation across populations, by
194 using latitudinal gradients (Gauzere *et al.*, 2017; Søgaard, Gunnhild and Johnsen, Øystein and Nilsen, Jarle
195 and Junntila, Olavi, 2008; Way & Montgomery, 2015; Zohner *et al.*, 2016). Fewer, however, have integrated
196 distance from the coast (but see Aitken & Bemmels, 2015; Harrington & Gould, 2015; Myking & Skrooppa,
197 2007) or regional effects. Some studies assert that the distance from the coast is a stronger indicator of
198 budburst timing than latitude (Myking & Skrooppa, 2007), with populations further inland initiating budburst
199 first, whereas those closer to the coast budburst later in the season. Therefore, to better understand the
200 interplay between duration of vegetative risk and climatic variation it is important to recognize how climate
201 regime extremes (e.g. seasonal trends, annual minima and annual maxima) vary across regions and how
202 they will shift in the future: as climatic regimes are altered by climate change false spring risk could vary
203 in intensity across regions and time (i.e. regions currently at high-risk of false spring damage could become
204 low-risk regions in the future and vice versa).

205 Conclusion

206 Temperate forest trees are most at risk to frost damage in the spring due to the stochasticity of spring freezes.
207 With warm temperatures advancing in the spring but last spring freeze dates advancing at a slower rate,
208 there could be more damaging false spring events in the future, especially in high-risk regions (Gu *et al.*, 2008;
209 Inouye, 2008; Liu *et al.*, 2018). Current equations for evaluating false spring damage (e.g. Equation 1) largely
210 simplify the myriad complexities involved in assessing false spring damage and risks. More studies aimed
211 at understanding relationships between species avoidance and tolerance strategies, climatic regimes, and
212 physiological cue interactions with the duration of vegetative risk would improve predictions. Additionally,
213 research to establish temperature thresholds for damage across functional types and phenophases will help
214 effectively predict false spring risk in the future. An integrated approach to assessing past and future spring
215 freeze damage would provide novel insights into plant strategies, and offer more robust predictions as climate
216 change progresses, which is essential for mitigating the adverse ecological and economic effects of false springs.

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