Rethinking False Spring Risk

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Abstract

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

Introduction

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

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

Current metrics for estimating false springs events are generally simple, often requiring an estimate for the start of biological 'spring' (i.e., budburst) and whether temperatures below a particular threshold occurred in the following week. Such estimates inherently assume consistency of damage across species, functional group, life stages, and other climatic regimes, ignoring that such factors can greatly impact plants' false spring risk. As a result, such indices may lead to inaccurate estimates and predictions.

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

Cold Hardiness and Risk of Frost Damage

Cold hardiness (i.e. freezing tolerance) is an essential process for temperate plants to survive cold winters and hard freezes (Vitasse *et al.*, 2014). During the cold acclimation phase, cold hardiness increases rapidly as temperate plants begin to enter dormancy. Once buds reach the dormancy phase, buds are able to tolerate temperates as low as -25°C to -40°C or lower (Charrier *et al.*, 2011; Vitasse *et al.*, 2014). Freezing tolerance diminishes again during the cold deacclimation phase, when metabolism and development start to increase. Once buds begin to swell and deharden, freezing tolerance greatly diminishes (often around -8°C for many temperate plants) but is lowest between budburst (i.e., -2°C) to leafout (i.e., -3°C).

Thus, temperate forest plants experience elevated risk of frost damage during the spring due to the stochastic timing of frosts and the rapid decrease in freezing tolerance. Freezing temperatures following a warm spell can result in plant damage or even death (Ludlum, 1968; Mock *et al.*, 2007). Many temperate species exhibit flexible spring phenologies, which help them minimize spring freezing risk, but freeze damage can still occur. There is high variability in defining a damaging temperature threshold across species, including between agricultural and ecological studies (Figure 1).

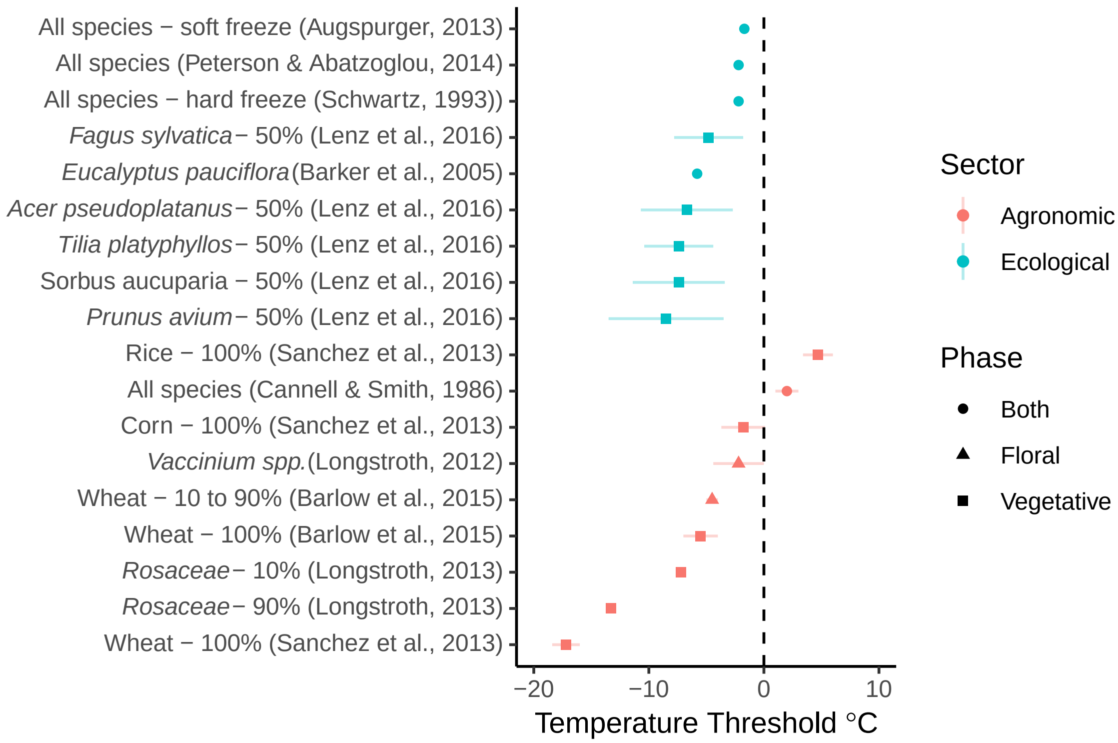

Figure 1: A comparison of damaging spring freezing temperature thresholds across ecological and agronomic studies. Each study is listed on the vertical axis along with the taxonomic group of focus. Next to the species name is the freezing definition used within that study (e.g., 100% is 100% whole plant lethality). Each point is the best estimate recorded for the temperature threshold with standard deviation if indicated in the study.

The flowering and fruiting phenophases are generally more sensitive to freezing temperatures than vegetative phases (Inouye, 2000; Augspurger, 2009; CaraDonna, Paul J and Bain, Justin A, 2016; Lenz *et al.*, 2013), but false spring events that occur during the vegetative growth phenophases may impose the greatest freezing threat to deciduous plant species. It can take 16-38 days for trees to refoliate after a spring freeze (Gu *et al.*, 2008; Augspurger, 2009, 2013; Menzel *et al.*, 2015), which can detrimentally affect crucial processes such as carbon updake and nutrient cycling (Hufkens *et al.*, 2012; Richardson *et al.*, 2013; Klosterman *et al.*, 2018). Additionally, plants will suffer greater long-term effects from the loss of photosynthetic tissue, which could impact multiple years of growth, reproduction, and canopy development (Vitasse *et al.*, 2014; Xie *et al.*, 2015). For this reason, we will focus primarily on spring freeze risk for the vegetative phases, specifically between budburst and leafout, when vegetative tissues are most at risk of damage.

Defining False Spring

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):

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

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.

Measuring False Spring: An example in one temperate plant community

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 applied three, commonly used methodologies to calculate spring onset (i.e., intial green up and budburst): long-term ground observational data (O'Keefe, 2014), PhenoCam data (Richardson, 2015), and USA National Phenology Network's (USA-NPN) Extended Spring Index (SI-x) "First Leaf - Spring Onset" data (USA-NPN, 2016). These spring onset values that were calculated for this particular site were then inputted into the FSI equation (Equation 1) to determine the FSI from 2008 to 2014 (Figure 2).

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 and observational data indicate a false spring year, whereas the PhenoCam data does 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 determined in Figure 2 exemplify the differences in functional group spring onset dates and illustrate variations in forest demography and phenology. While the SI-x data (based on observations of early-active shrub species, including lilac, *Syringa vulgaris*) may best capture understory dynamics, the PhenoCam and observational FSI data integrate over larger canopy species and can be more site-specific in regards to species. Such differences are visible each year, as the canopy-related metrics show lower risk, but are especially apparent in 2012. In 2012, a false spring event was reported through many regions of the US due to warm temperatures occurring in March (Ault *et al.*, 2015). These high temperatures would most likely have been too early for larger canopy species to initiate budburst but they would have affected smaller understory species, as is seen by the high risk of the SI-x FSI in Figure 2.

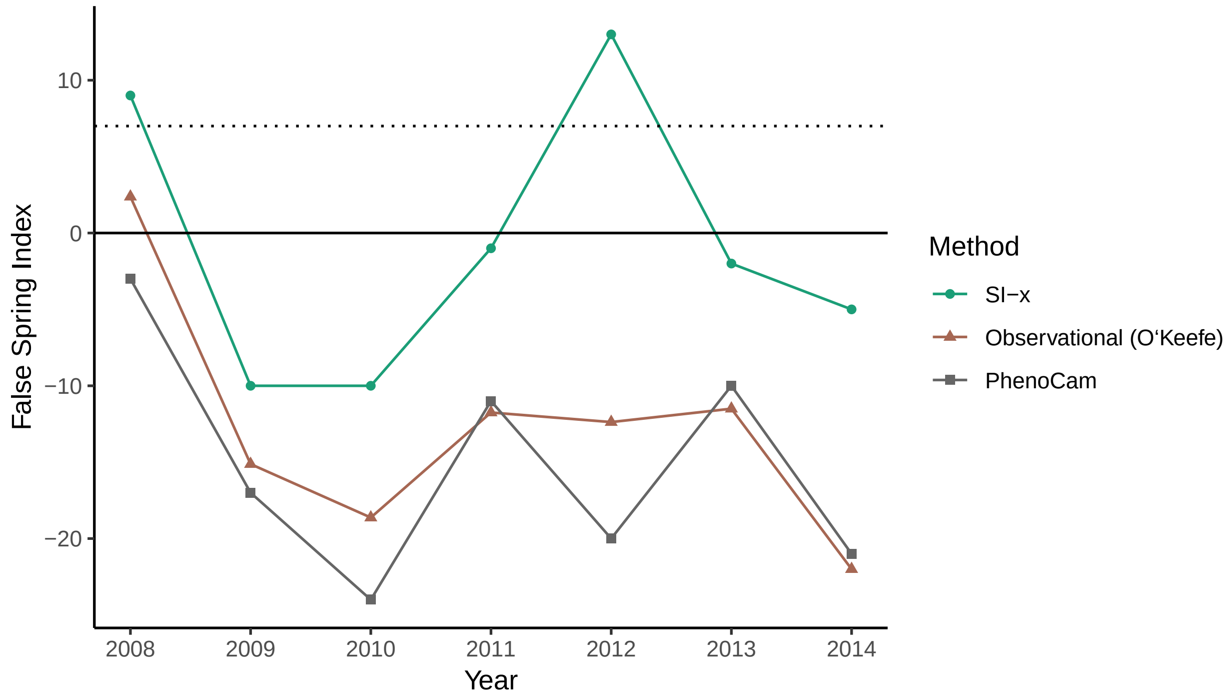

Figure 2: False Spring Index (FSI) values from 2008 to 2014 vary across methodologies. To calculate spring onset, we used the USA-NPN Extended Spring Index tool for the USA-NPN FSI values, which are in red (USA-NPN, 2016), long-term ground observational data for the observed FSI values, which are in green (O'Keefe, 2014), and near-surface remote-sensing canopy data for the PhenoCam FSI values, which are in blue (Richardson, 2015). See supplemental information for extended details. 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.

Yet, in contrast to our three metrics of spring onset for one site, most FSI work currently ignores variation across functional groups — instead using one metric (often from SI-x data) of spring onset and assuming it applies to the whole community of plants (Allstadt *et al.*, 2015; Marino *et al.*, 2011; Mehdipoor & Zurita-Milla, 2017; Peterson & Abatzoglou, 2014). The risk of a false spring varies across habitats and with species composition since spring onset is not consistent across functional groups (Martin *et al.*, 2010). Therefore, one spring onset date cannot be used as an effective proxy for all species.

Rather than use any metric to evaluate spring onset, we encourage researchers to first assess the forest demographics and functional groups relevant to the study question. From there, researchers can choose the most appropriate method to estimate the date of budburst to determine if a false spring could have occurred. However, as we outline below, considering different functional groups is unlikely to be enough for robust predictions in regards to level of damage from a false spring, especially when trying to determine how frosts are shaping the life history of plants. In such cases, it will also be important to integrate species differences within functional groups and to consider the various interspecific tolerance and avoidance strategies that species have evolved against false springs.

Plant Physiology and Strategies against False Springs

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

Rather than being more tolerant of spring freezing temperatures, some temperate forest species have evolved to avoid frosts via their phenologies. Most temperate deciduous tree species optimize growth and minimize spring freeze damage by using three cues to initiate budburst: low winter temperatures (chilling), warm spring temperatures (forcing), and increasing photoperiods (Chuine, 2010). The evolution of these three cues and their interactions have permitted temperate plant species to occupy more northern ecological niches (Kollas *et al.*, 2014) and decrease the risk of false spring damage (Charrier *et al.*, 2011). One avoidance strategy, for example, is the interaction between over-winter chilling and spring forcing temperatures. Warm temperatures too early in the winter (i.e. in February, or even January in the Mediterranean) will not result in early budburst due to insufficient chilling (Basler & Körner, 2012), thus reducing the risk of false spring damage. Likewise, photoperiod sensitivity is a common false spring avoidance strategy: species that respond strongly to photoperiod cues in addition to warm spring temperatures are unlikely to have large advances in budburst, and thus may evade false spring events as warming continues (Basler & Korner, 2014), and with climate-change induced shifts, photoperiod limitations may become even more important.

Defining Vegetative Risk

Phenology and false spring avoidance are clearly intertwined — with important variation occurring across different phenological phases. There is also important variation within certain phenological phases. Most noteably, within the vegetative phases of spring leafout, plants that have initiated budburst but have not fully leafed out are more likely to sustain damage from a false spring than individuals past the leafout phase. This is because freezing tolerance is lowest 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 the level of damage from a false spring event. We will refer to the timing between these phenophases — budburst to leafout — as the duration of vegetative risk. (Figure 3)

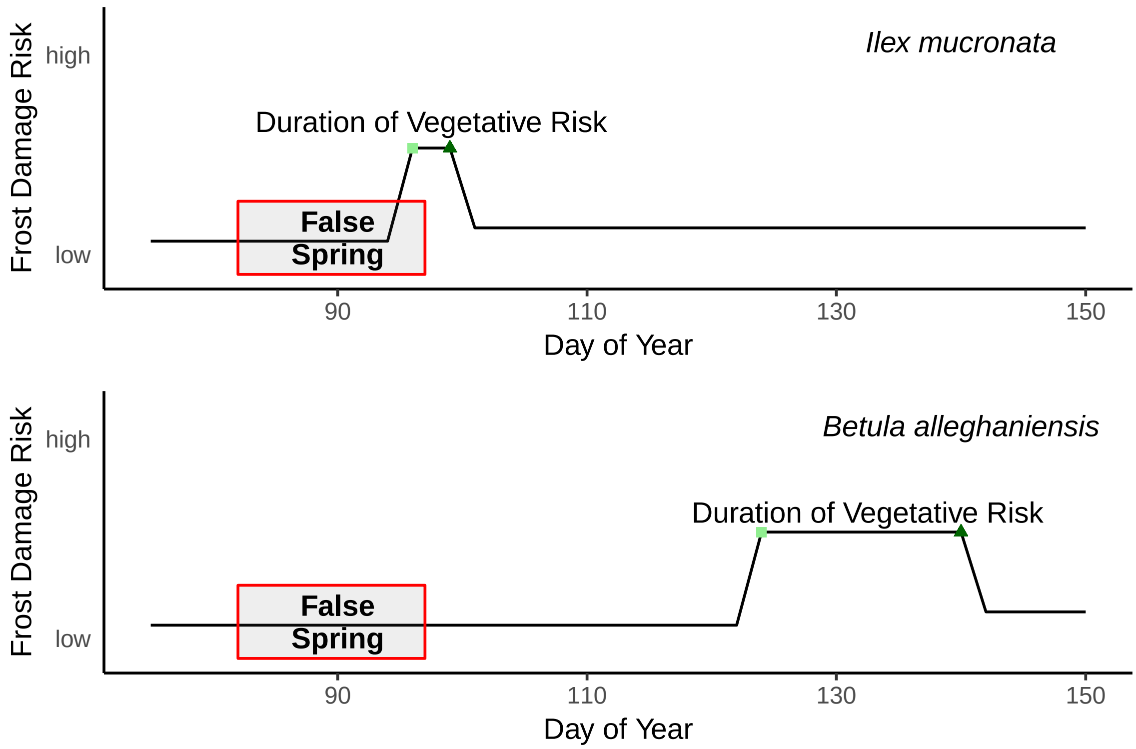

Figure 3: Differences in spring phenology and false spring risk across two species: *Ilex mucronata* (L.) and *Betula alleghaniensis* (Marsh.). We mapped a hypothetical false spring event based on historical weather data and long-term observational phenological data collected at Harvard Forest (O'Keefe, 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.

With spring advancing, species that have shorter durations of vegetative risk may avoid false springs more successfully than species that have much longer durations of vegetative risk. Understanding the various physiological and phenological mechanisms across species are crucial for species- or site-specific studies as well as ecosystem-wide models. By simply using one day of budburst for an entire site rather than multiple budburst dates across species and additionally failing to include leafout data in our predictions, we will be unable to forecast false spring risk as climate change progresses.

How Species Phenological Cues Shape Vegetative Risk

Predictions of false spring critically depend on understanding what controls the duration of vegetative risk across species. For temperate species, the three major cues that control budburst (e.g., low winter temperatures, warm spring temperatures, and increasing photoperiods, Chuine, 2010) play a dominant role. Most phenological studies currently focus on one phenophase (i.e., budburst or leafout) but, to examine false spring risk, it is important to examine the effects of the three phenological cues and their interactions on the duration of vegetative risk—that is, researchers must collect data on both budburst and leafout timing.

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

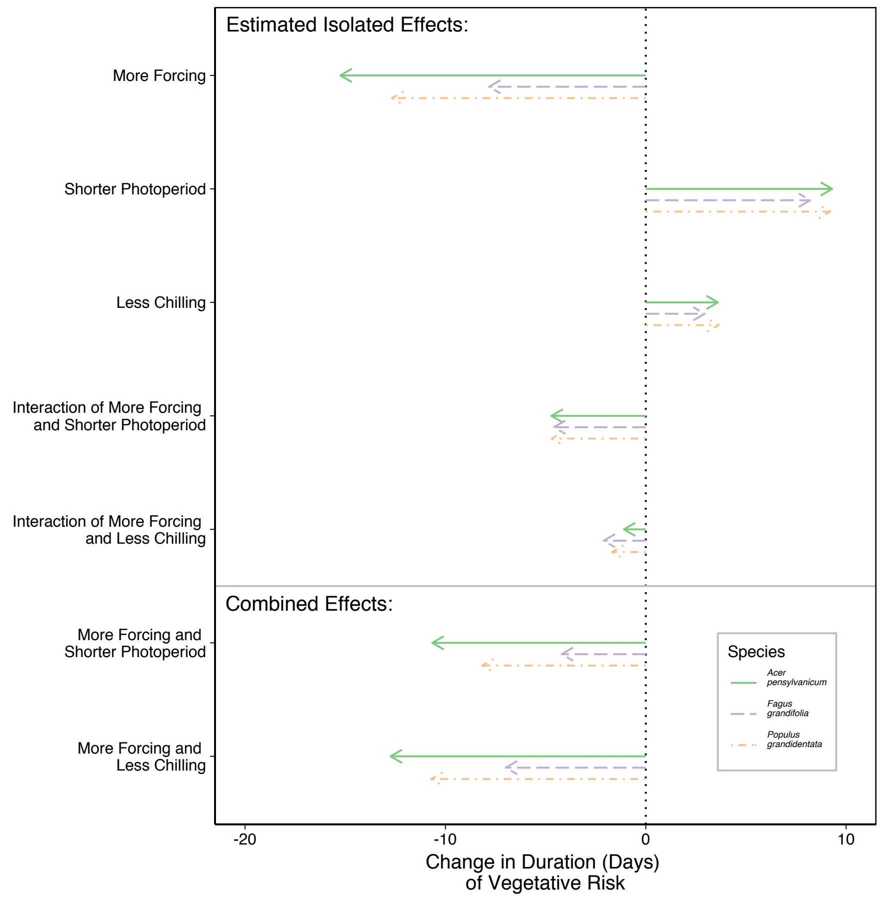

Figure 4: We examine the effects of phenological cues on the duration of vegetative risk across three species: *Acer pensylvanicum*, *Fagus grandifolia*, and *Populus grandidentata* (see supplemental information for futher details). 'More Forcing' is a 5°C increase in spring warming temperatures, 'Shorter 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 the 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 among 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.

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

Robust predictions at a bigger scale must consider the interplay of species cues with a specific location's climate. Climate and thus false spring risk vary across regions. We analyzed five archetypal regions across North America and Europe. Through the use of both phenology (USA-NPN, 2016; Soudani *et al.*, 2012; Schaber & Badeck, 2005; White *et al.*, 2009) and climate data (from the NOAA Climate Data Online tool NOAA, 2017) we determined the number of false springs (i.e., temperatures at -2.2°C or below) for each region. We found that some regions experienced harsher winters and greater temperature variability throughout the year (Figure 5 e.g., Maine, USA), and these more variable regions often have a much higher risk of false spring than others (Figure 5 e.g., Lyon, France).

Understanding and integrating spatiotemporal effects and regional differences when investigating false spring risk and duration of vegetative risk across continents would help improve predictions as climate change progresses. Such differences depend both on the local climate, the local species and the cues for each species at that location, as a single species may have varying cues across space. Therefore, based on cues alone, different regions may have different durations of vegetative risk for the same species (Caffarra & Donnelly, 2011; Partanen, 2004; Vihera-aarnio *et al.*, 2006). Studies also show that different species within the same location can exhibit different sensitivities to the three cues (Basler & Körner, 2012; Laube *et al.*, 2013), further amplifying the myriad of climatic and phenological shifts that determine false spring risk in a region.

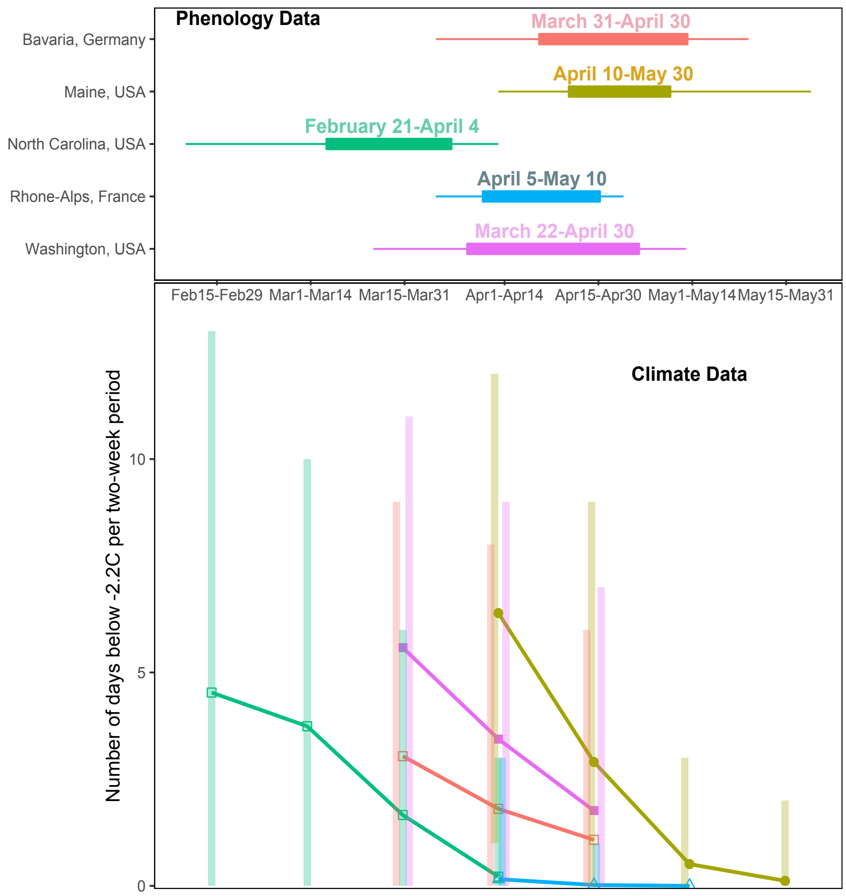

Figure 5: False spring risk can vary dramatically across regions. Here we show the period when plants are most at risk to tissue loss – between budburst and leafout (upper, lines represent the range with the thicker line representing the interquartile range) and the variation in the number of freeze 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). See supplemental information for futher details on methods.

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

The Future of False Spring Research

FSI has its merit: For most ecosystem-dynamic models, using the FSI approach would be better than not including spring frost potential at all. The ED model already has some sort of phenological model within it (Kim *et al.*, 2015; Moorcroft *et al.*, 2001), if they use that prediction for budburst and also include a last freeze date, then they could use FSI to better predict false spring occurence and intensity with predicted shifts in climate. As well as integrates functional groups to some degree! So very close. The ultimate goal would be to also include some sort of proxy for false spring risk, which should help better inform range shifts with predicted shifts in climate.

At the next level, models such as PHENOFIT, incorporate abiotic stresses to assess predicted range shifts (Gritti *et al.*, 2013; Chuine & Beaubien, 2001)

For studies looking to understand community shifts in species range shifts, it is important to recognize the limitations of using FSI:... Limitations: non-native, small shrub species. No estimate or measure for actual damage just simply a vague assessment of possible damage.

PhenoCam data is a way to bridge gap between on the ground observations and satellite images. It is possible for researchers to look through every image or to simply use a specific greeness parameter to identify greenup (Richardson, 2018). Issue with this parameter is that often, if greenup initiates and then a false spring hits, the canopy defoliates and then refoliates. The greenup measure can sometimes miss that green. Often misses that initial start of greenup. Therefore, if the PhenoCam is the best choice, then should be aware of the fact it often misses false spring damage. Better than NDVI, captures the shift in greenness (i.e., if greenup occurs, then defoliates due to herbivory or frost then refoliates, can capture that shift and flux) (Richardson *et al.*, 2018). Best option for canopy-specific studies and for evaluating level of damage to a certain degree.

But, sometimes using FSI will not work at all: Observational data is the best to capture on different functional types and life stages. But for studies that are looking to understand life-history theory, more is crucial. FSI will not provide enough meaningful information. Observational phenology data is the best path forward or using PhenoCam images and screening each image individually. Also good to look at different life stages to understand how false springs can be limiting. Therefore, false spring events could have large scale consequences on forest recruitment, potentially impacting juvenile growth and forest diversity. Plants suffer long-term effects from the loss of photosynthetic tissues, which could impact multiple years of growth, reproduction, and canopy development (Sakai & Larcher, 1987; Vitasse *et al.*, 2014) and these effects could vary by life stage. Adult trees, especially individuals from the canopy layer, typically initiate budburst later in the season than juvenile trees of the same species (Augspurger & Bartlett, 2003). Juvenile trees that leaf out earlier in the season have enhanced growth and, subsequently, are more likely to survive into maturity (Augspurger, 2008), as long as there aren't damaging false spring events that occur.

Conclusion

With warm temperatures advancing in the spring but last spring freeze dates advancing at a slower rate, there could be more damaging false spring events in the future, especially in high-risk regions (Gu *et al.*, 2008; Inouye, 2008; Liu *et al.*, 2018). Current equations for evaluating false spring damage (e.g., Equation 1) largely simplify the myriad complexities involved in assessing false spring damage and risks. More studies aimed at understanding relationships among species tolerance and avoidance strategies, climatic regimes, and physiological cue interactions with the duration of vegetative risk would improve predictions and ecosystem models that will hopefully replace our current metric. Additionally, research to establish temperature thresholds for damage across functional types and phenophases will help effectively predict false spring risk in the future. An integrated approach to assessing past and future spring freeze damage would provide novel insights into plant strategies, and offer more robust predictions as climate change progresses, which is essential for mitigating the adverse ecological and economic effects of false springs.

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