Rethinking False Spring Risk

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Introduction

1. Introduce False Spring Concept
   (a) Plants growing in temperate environments are at risk of being exposed to late spring freezes, which can be detrimental to growth.
   (b) Individuals that leaf out before the last frost are at risk of leaf loss, damaging wood tissue, and slowed or stalled canopy development (Gu *et al.*, 2008; Hufkens *et al.*, 2012).
   (c) Therefore, temperate deciduous tree species must have plastic phenological responses in the spring in order to optimize photosynthesis and minimize frost or drought risk (Polgar & Primack, 2011).
   (d) 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).
2. Introduce Climate Change and Importance of False Spring Studies
   (a) Climate change is expected to increase 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).
   (b) Temperate forest species around the world are initiating leaf out about 4.6 days earlier per degree Celsius (Wolkovich *et al.*, 2012; Polgar *et al.*, 2014).
   (c) 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).
   (d) 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).

(e) 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.

3. Introduce Current False Spring Index Equation

    (a) Different species respond differently to late spring freezing events.

    (b) The level of damage sustained by plants from a false spring also varies across phenophases.

    (c) Various studies have assessed the risk of damage or the intensity of particular false spring events but at this time false spring studies fail to incorporate all potential factors that could affect the level of frost damage risk.

    (d) A False Spring Index (FSI) signifies the likelihood of a damage to occur from a late spring freeze.

    (e) Currently, FSI evaluates day of budburst, number of growing degree days, and day of last spring freeze through a simple equation as seen below (Marino *et al.*, 2011).

$$FSI = JulianDate(LastSpringFreeze) - JulianDate(Budburst) \tag{1}$$

    (f) False spring studies largely simplify the various ecological elements that could predict the level of plant damage from late spring freezing events.

    (g) In contrast to these simplifications, we argue that a wealth of factors greatly impacts plants' frost spring risk such that simple indices will most likely lead to inaccurate predictions and ultimately do little to advance the field.

4. State the Purpose of the Paper

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

    (b) 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?), proximity to water (Gu *et al.*, 2008), level of precipitation prior to the freezing event (Anderegg *et al.*, 2013), freeze duration/intensity, and range limits of the species (Martin *et al.*, 2010) unhinge simple metrics of false spring.

    (c) The ultimate intent is to demonstrate how an integrated view of false spring that incorporates these factors would rapidly advance progress in this field.

Defining False Spring

1. Definition and Threat

(a) Temperate forest plants are most at risk to frost damage from episodic spring frosts (Sakai & Larcher, 1987).

(b) Abnormally warm conditions in the late winter or early spring can cause budburst to initiate early in trees and shrubs.

(c) Freezing temperatures following a warm spell could result in plant damage or even death (Ludlum, 1968; Mock *et al.*, 2007).

(d) False springs are defined by two phases: rapid vegetative growth prior to a freeze and a post freeze setback (Gu *et al.*, 2008).

(e) Freeze and thaw fluctuations can cause defoliation, xylem embolism and decreased xylem conductivity which can result in crown dieback (Gu *et al.*, 2008).

(f) Species that are better able to phenologically track the shifts in spring advancement due to climate change are more likely to sustain damaging events such as false springs (Scheifinger *et al.*, 2003).

2. Define Chilling requirements to specify timing of damaging false spring events

(a) Deciduousness and the evolution of two dormancy phases (i.e. endodormancy and ecodormancy) in temperate forest trees has permitted species to occupy more northern ecological niches (Samish, 1954).

(b) Endodormancy is the period of winter when temperate trees are inhibited from growing, regardless of the outdoor environment.

(c) Ecodormancy is the period of time when growth can occur but the external environment is not conducive to growth (e.g. too cold) (Basler & Körner, 2012).

(d) Therefore, warm temperatures earlier in the year (i.e. in February) do not seem to affect species, most likely because trees have not yet left the endodormancy phase.

(e) 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).

(f) 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).

(g) The 7 day parameter exposes less resistant foliate phenophases to a false spring, thus putting the plant at a higher risk of damage.

(h) 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).

(i) There are two types of freezes: a "hard freeze" at -2.2°C and a "soft freeze" at -1.7°C (Vavrus *et al.*, 2006; Kodra *et al.*, 2011; Augspurger, 2013).

(j) However, the definition is still largely under debate.

3. Damage and drought

    (a) Freezing damage can occur directly via intracellular ice formation or indirectly via freezing dehydration (Pearce, 2001; Beck *et al.*, 2004; Hofmann & Bruelheide, 2015).

    (b) Intracellular ice formation often results in defoliaiton and increased xylem cavitation or embolism in the stem.

    (c) Freezing tolerance in plants is usually against extracellular freezing or freezing dehydration (Burke *et al.*, 1976).

    (d) Drought and desiccation within the xylem mimick the adverse effects of false spring events (Cavender-Bares *et al.*, 2015).

    (e) 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).

    (f) Therefore, 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), although long-term drought stress can lead to accumulated xylem damage and decreased false spring tolerance (Anderegg *et al.*, 2013).

    (g) More studies are needed to investigate the interplay between false spring events and precipiation and how that relationship impacts the level and type of damage a plant sustains and what the long-term implications may be.

Determining Spring Onset

1. Elucidate the difference between spring onset and study species

    (a) Spring forest phenology essentially progresses through successional stages: understory species, seedlings and saplings typically initiate budburst first in order to exploit open canopies and early growth, whereas late successional species may start later in the season to avoid frost or drought risk (Richardson & O'Keefe, 2009; Xin, 2016).

    (b) Therefore, habitat type plays a large role in the overall spring onset of a specific ecological region.

    (c) Pure grasslands or young forest will, overall, have earlier budburst dates than large stands of canopy trees and mixed forests may have a spring onset date somewhere between the two.

(d) 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.

2. Methodologies

   (a) A suitable methodology for determining spring onset is crucial in order to establish an effective model for false spring risk, especially since the current false spring equation only uses two inputs: date of spring onset and date of last freeze (Equation 1).

   (b) If the date of spring onset is inaccurate, the level of risk determined by the current equation (Equation 1) could render erroneous results.

   (c) There are many methods available to ascertain the first day of spring.

   (d) Spring onset can be calculated through observational data, PhenoCam or remote-sensing data, or through the USA National Phenology Network's (USA-NPN) Extended Spring Index (SI-x) tool (USA-NPN, 2016).

   (e) Studies often use observation data to evaluate spring onset to target budburst more precisely, however, it can be difficult or even impossible for large-scale studies.

   (f) PhenoCam and remote-sensing data is suitable for canopy tree species, whereas USA-NPN SI-x is more applicable for understory species.

   (g) The three methodologies to determine spring onset were compared using observational data from Harvard Forest (O'Keefe, 2014), PhenoCam data from Harvard Forest (Richardson, 2015), and USA-NPN SI-x (USA-NPN, 2016) and then inputted into the FSI equation (Equation 1) to calculate FSI values from 2008 to 2014 (Figure 1).

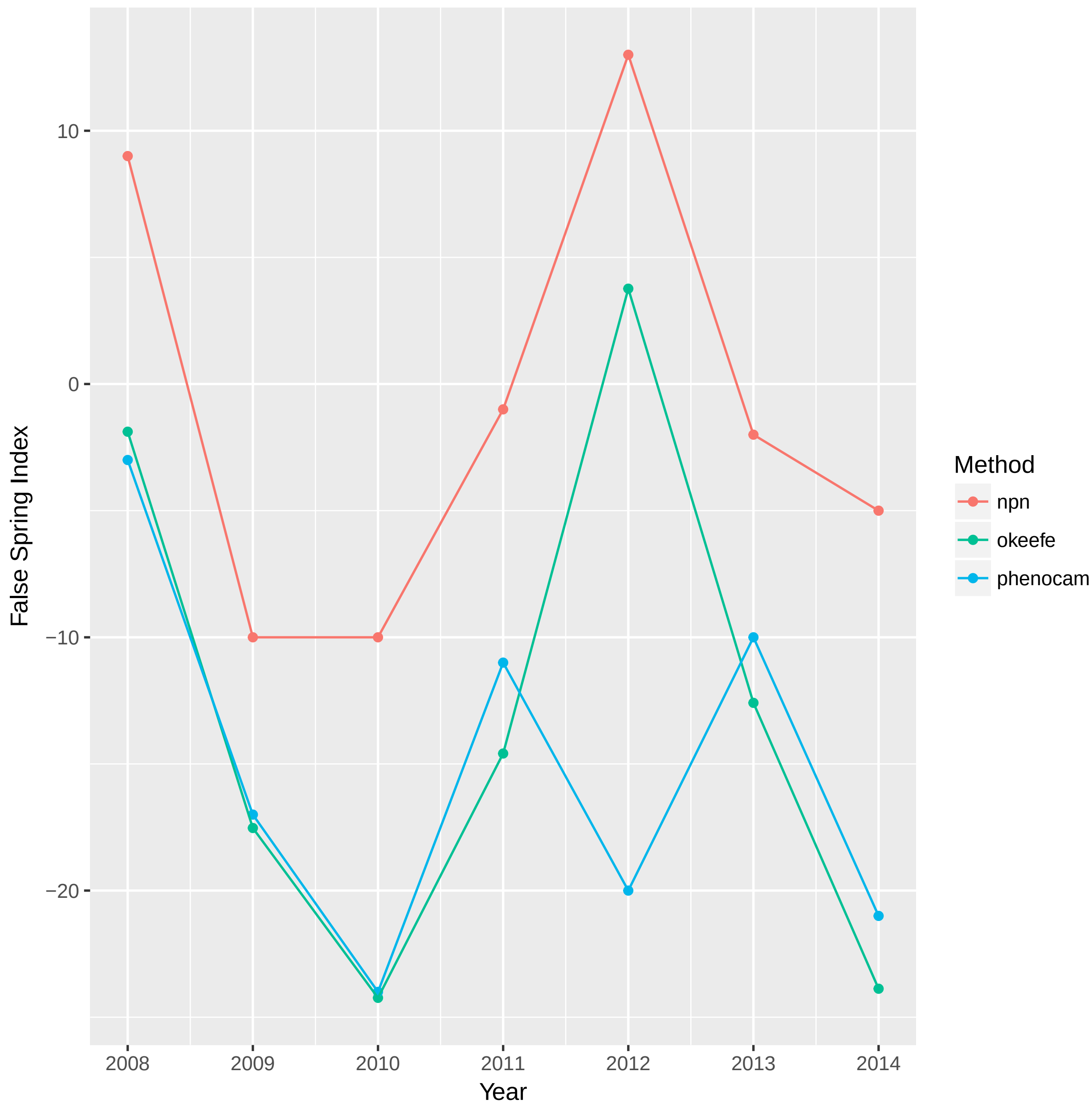

Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methdology used in this study. PhenoCam FSI values are red, Observed FSI values are blue, and USA-NPN FSI values are green.

(h) Observational FSI values and USA-NPN FSI values are highly comparable and are justifiable methods for determining potenial false spring risk.

(i) PhenoCam data is also comparable to the other two methods, however, it would be more useful for canopy species, which is evident from the results seen in 2012 (Figure 1).

(j) In 2012, a false spring event was reported through many regions of the US due to warm temperatures occuring in March (Ault *et al.*, 2015).

(k) 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 discrepany in results for 2012 (Figure 1).

(l) Researchers should use the USA-NPN dataset for understory species, PhenoCam or remote-sensing data for late successional species, and observational data for a wide array of plant functional types.

Defining Vegetative Risk

1. Define Vegetative Risk

   (a) 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.

   (b) Frost tolerance steadily decreases after budburst begins until the leaf is fully unfolded, with leafout being the most susceptible to frost damage (Lenz *et al.*, 2016).

   (c) 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.

   (d) We will refer to the timing of these collective phenophases (i.e. budburst to leafout) as the duration of vegetative risk.

2. Phenophases and Life Stage

   (a) Reproductive phases are generally more sensitive to false spring events than vegetative phases and developing leaves are more susceptible to damage than opening buds or expanding shoots (Augspurger, 2009; Lenz *et al.*, 2013).

   (b) However, trees that suffer severe vegetative growth damage will suffer greater long-term effects from the loss of photosynthetic tissue than trees that lose one year of reproductive growth.

   (c) Spring freezing events that occur during the vegetative growth phenophases impose the greatest freezing threat to deciduous tree and shrub species (Sakai & Larcher, 1987).

   (d) Therefore, phenophase is a crucial indicator for how much damage a plant will sustain from a freezing event.

   (e) Seedlings and saplings initiate budburst before canopy closure in order to benefit from the increased light levels (Augspurger, 2008), which puts them at greater risk to false spring damag than adult trees (Vitasse *et al.*, 2014).

(f) Younger plants are mre likely to sustain lasting damage to the leaf buds and vegetative growth, whereas adult trees are at risk of xylem embolism.

(g) For xylem embolism to occur, extreme cavitation must first be present.

(h) Extensive cavitation in the xylem requires more intensive freezing events than freezing events that damage seedling and sapling leaf buds.

(i) Especially strong freezing events (i.e. $>$-8.6°C), could result in meristemic tissue, wood parenchyma and phloem damage (Sakai & Larcher, 1987; Augspurger, 2011; Lenz *et al.*, 2013).

3. Species Differences

(a) Different species respond differently to anthropogenic climate change.

(b) 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).

(c) 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).

(d) Similarly, late successional species exhibit greater photoperiod sensitivies than pioneer 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).

(e) It is anticipated that these more opportunistic individuals that initiate budburst earlier in the spring with the shifts in climate would attempt to limit freezing risk by decreasing the duration of vegetative risk and progress to full leaf expansion faster.

(f) The duration of vegetative risk is usually extended if a freezing event occurs during the phenophases between budburst and full leafout and species with short durations of vegetative risk often sustain higher levels of damage (Augspurger, 2009).

(g) It is hypothesized that if the duration of vegetative risk is longer, then the buds and leaves will be heartier against frosts, however this still has yet to be tested thoroughly.

(h) We assess the interaction between duration of vegetative risk and false spring events using two datasets: from a growth chamber chilling experiment and long-term observational data.

4. Dan's Data

(a) Deciduous trees and shrubs require a certain number of chilling units in order to leave the endodormancy phase.

(b) This helps protect temperate plants against stochastic warm spells in the winter so that they do not break dormancy too early in the season.

(c) Chilling units differ across species and across habitats.

(d) Species growing at higher latitudes are more likely to have lower chilling requirements to break dormancy (Myking & Heide, 1995; Howe *et al.*, 2003) due to the shorter growing season and selective pressure to initiate budburst as soon as temperatures are conducive to growth (Prevéy *et al.*, 2017).

(e) With anthropogenic climate change, it is possible that certain species will have insufficient winter chilling (especially at lower latitudes) resulting in higher spring forcing requirements (McCreary *et al.*, 1990; Morin *et al.*, 2009; Fu *et al.*, 2012; Polgar *et al.*, 2014; Chuine, 2010).

(f) Similarly, spring forcing temperature and photoperiod length requirements for budburst to occur vary among species and habitats.

(g) This is evident throught he high levels of genetic diversity for spring budburst to occur across temperate forest tree species (Chuine *et al.*, 2001).

(h) 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?).

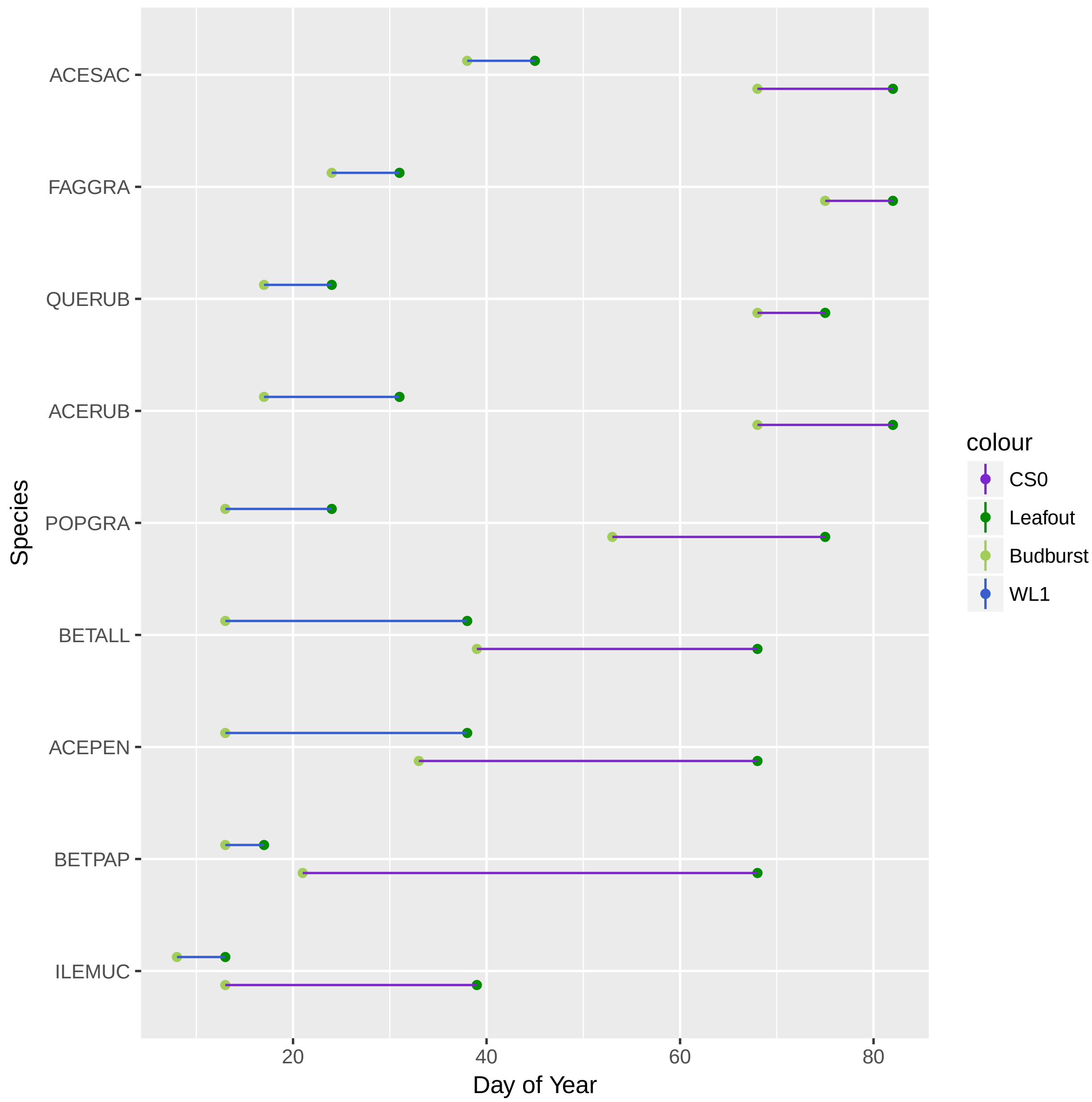

Figure 2: Day of budburst and the day of leaf out for native tree species in New England. Data was collected from a growth chamber experiment using any combination of two photoperiod treatments, two forcing treatments, and three chilling treatments. The standard deviation is represented in blue for budburst and green for leaf out.

(i) According to the results, individuals that initiate budburst earlier in the season (i.e. *Betula papyrifera* (Marsh.) and *Ilex mucronata* (L.)) tend to begin budburst early regardless of treatment, but the treatment does affect the duration of vegetative risk significantly (Figure 2).

(j) As the season progresses, treatment does not affect the duration of vegetation as much, however, the day of budburst tends to initiate later in the season with the weaker treatment effects (i.e. CS0).

(k) Anova results indicate forcing temperatures and photoperiod length determine the duration of vegetative risk more than chilling requirements, which may be due to studying species within similar latitudinal range limits.

(l) Further studies are essential to investigate the interplay between chilling, forcing, and photoperiod effects on the duration of vegetative risk, especially for species occupying habitats more susceptible to false spring events.

5. Harvard Forest Data

   (a) 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).

   (b) It is therefore expected that high variation in spring temperatures (i.e. oscillating above and below the development threshold) may result in longer durations of vegetative risk.

   (c) 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).

   (d) 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).

   (e) This could potentially be due to photoperiodic effects.

   (f) Forcing temperature requirements, like chilling requirements, are key phenotypic traits for many temperate tree species (Kramer *et al.*, 2017), which may explain the similarity in growing degree days and budburst date between the two years.

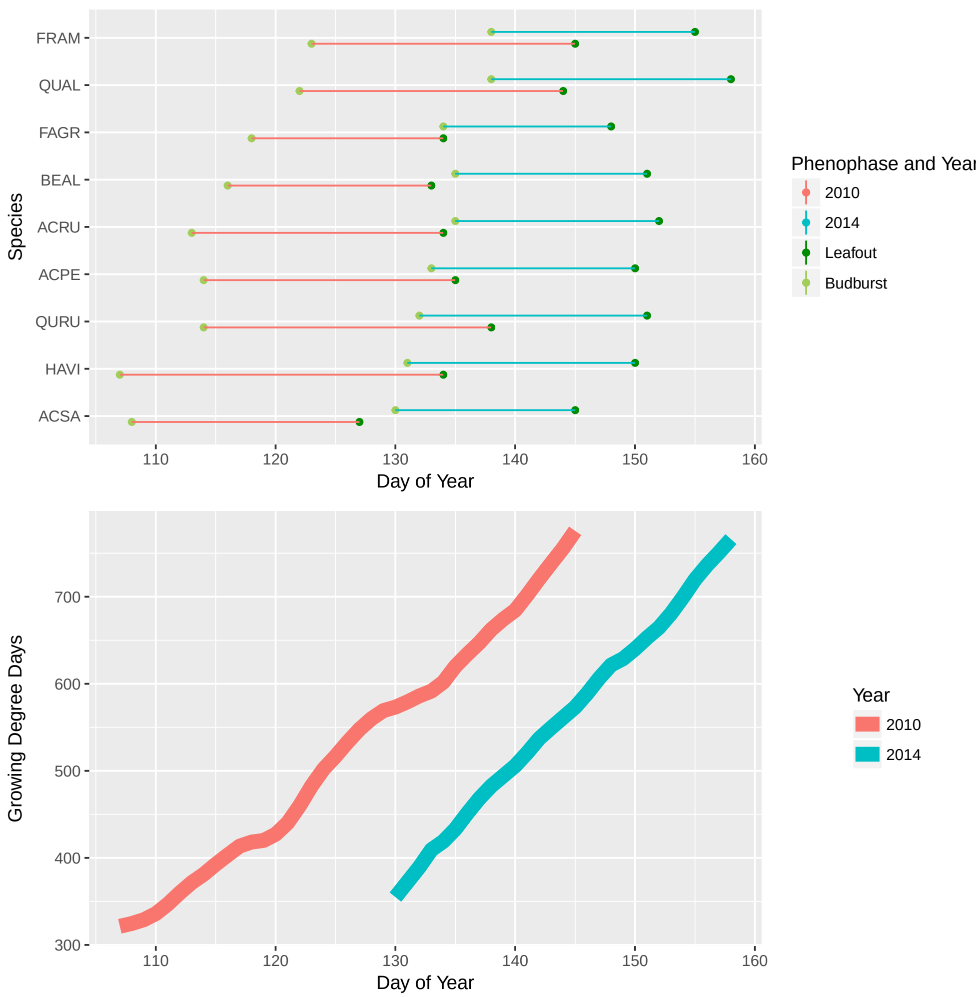

Figure 3: A comparison of two years of observational data investigating the effects of growing degree days on the duration of vegetative risk. The average duration of vegetative risk for 2010 was 21 +/- 3.39 days versus 17.1 +/- 1.96 days in 2014.

Regional Differences in False Spring Risk and Temperature Thresholds

1. Introduce concept of regional differences

    (a) Statement about varying durations of vegetative risk because of forest tree species demographics and climatic regimes.

    (b) Species distributions are largely driven by phenology (Chuine *et al.*, 2001) and photoinsensitive species are likely to outcompete photosensitive species as spring forcing temperatures continue to increase Vitasse *et al.* (2011); Gauzere *et al.* (2017).

(c) However, the climatic implications of increasing forcing temperatures could potentially lead to earlier dates of budburst and enhance the risk for frost or drought risk.

(d) 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).

(e) There are discrepancies in defining a false spring event, especially with understanding damaging freezing temperatures.

(f) Some regions and species may be more able to tolerate lower temperature thresholds than others (Table 1).

(g) It is crucial to gain an understanding on which climatic parameters result in false spring events, what habitats are at risk now, and what habitats will be at risk in the future.

(h) It is anticipated that most habitats will trend towards earlier spring onsets, however, the dates of last freezes will not occur at the same rate, rendering some regions to be more susceptible to false spring events in the future (Labe *et al.*, 2016).

(i) By determining the range of budburst dates for the dominant species in five archetypal climate regions, we were able to elucidate the current spatial variation of false spring risk (Figure 4).

(j) We assessed the number of freezing days (Schwartz, 1993) that occurred on average over the past 50 years within those range of dates and found that Maine has the highest risk for frost damage and Lyon, France as the lowest.

(k) Current studies focus on latitudinal and photoperiodic effects (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011; Gauzere *et al.*, 2017), however, future research should aim to integrate spatiotemporal effects more when investigating false spring risk.

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

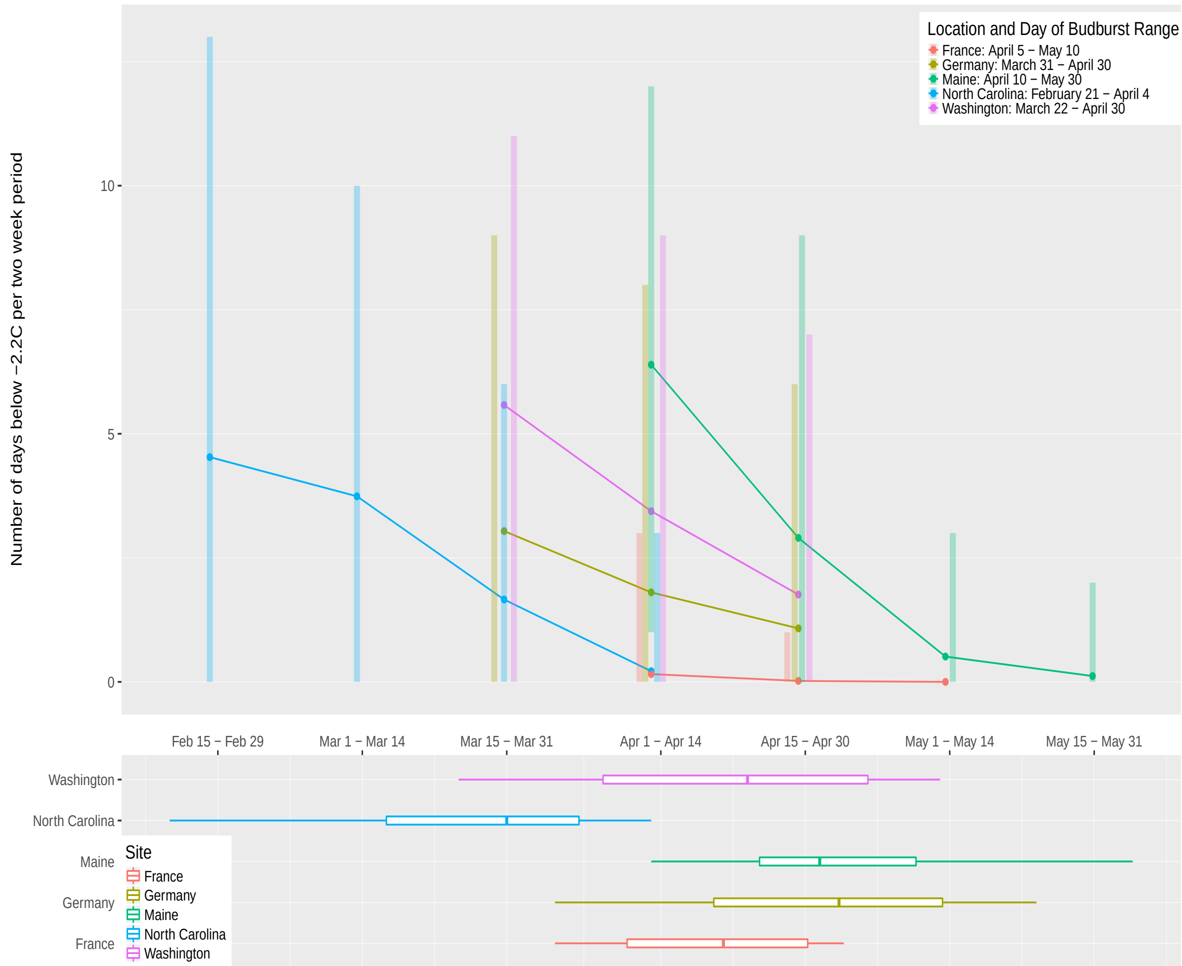

Figure 4: A comparison of false spring risk across five climate regions. The data was subsetted for each region based on earliest historical spring onset date to the latest historical leafout date and was divided into biweekly time periods (Schaber & Badeck, 2005; White *et al.*, 2009; Soudani *et al.*, 2012; USA-NPN, 2016).

Conclusion

1. Phenology is closely linked to climatic regimes (Pau *et al.*, 2011) and is therefore a key indicator for the phenotypic variation for cold adpated traits and false spring risk avoidance.

2. Understanding the variation of spring onset across regions and within habitats as well as the rate of budburst will permit greater insight into false spring risk.

3. Tree species with smaller and more fragemented distribution ranges are more prone to genetic drift due

to geographic barriers and higher susceptibility to stochastic events (i.e. frost and drought) (Alberto *et al.*, 2013) so gathering data on species at risk is essential.

4. Climate change could increase the level of damage from spring frost events, especially in certain regions or for particular species, due to earlier spring onset and greater fluctuations in temperature (Martin *et al.*, 2010).

5. Therefore, it is essential that temperate forest tree species maintain continuous ranges in order to successfully track the changes in climate and to utilize photoperiodic and temperature cues simultaneously rather than rely strickly on photoperiodism especially along range edges (Zohner *et al.*, 2016; Gauzere *et al.*, 2017).

6. Ecosystem dynamics and risk of damage can vary from year to year and the timing of the last spring freeze in relation to higher spring forcing temperatures may become less consistent.

7. Fewer freezing events does not necessarily mean there will be less false spring damage.

8. 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).

9. As global change progresses and atmospheric CO_2 increases, false spring damage will likely be intensified and low temperature thresholds will decrease (Table 1) (Beerling *et al.*, 2001; Barker *et al.*, 2005).

10. Plants have higher freeze tolerance after exposure to low temperatures over a period of time (Thomashow, 1999) so shorter dormancy lengths coupled with elevated CO_2 levels could result in highly adverse effects.

11. Global change will also likely result in less snow accumulation and decreased snowpack in the early spring, which could cause increased exposure of fine roots to freezing temperatures, further augmenting the detrimental effects of false spring events.

12. Future studies are necessary to investigate the relationship between anthropogenic climate change, phenological plasticity, the level of damage sustained from false spring events, and the duration of vegetative risk.

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Supplemental Information

ACEPEN	Sum.Sq	Df	F value	Pr(>F)
chilling	149.41	2	1.20	0.30
forcing	4909.59	1	78.94	0.00
photoperiod	1309.59	1	21.06	0.00
Residuals	6654.56	107		

ACERUB	Sum.Sq	Df	F value	Pr(>F)
chilling	0.62	2	0.00	1.00
forcing	1731.00	1	25.92	0.00
photoperiod	462.78	1	6.93	0.01
Residuals	6611.17	99		

ACESAC	Sum.Sq	Df	F value	Pr(>F)
chilling	65.41	2	0.46	0.64
forcing	259.14	1	3.61	0.06
photoperiod	231.41	1	3.22	0.08
Residuals	4524.88	63		

BETALL	Sum.Sq	Df	F value	Pr(>F)
chilling	525.95	2	5.00	0.01
forcing	1463.30	1	27.81	0.00
photoperiod	632.83	1	12.03	0.00
Residuals	6944.50	132		

BETPAP	Sum.Sq	Df	F value	Pr(>F)
chilling	6.00	2	0.04	0.96
forcing	1776.23	1	21.47	0.00
photoperiod	1105.08	1	13.35	0.00
Residuals	10509.00	127		

FAGGRA	Sum.Sq	Df	F value	Pr(>F)
chilling	144.41	2	1.66	0.20
forcing	611.20	1	14.04	0.00
photoperiod	1.05	1	0.02	0.88
Residuals	2829.78	65		

ILEMUC	Sum.Sq	Df	F value	Pr(>F)
chilling	26.49	2	0.54	0.59
forcing	2262.34	1	91.61	0.00
photoperiod	1035.85	1	41.94	0.00
Residuals	3334.05	135		

POPGRA	Sum.Sq	Df	F value	Pr(>F)
chilling	54.63	2	0.39	0.68
forcing	2405.73	1	34.52	0.00
photoperiod	1019.78	1	14.63	0.00
Residuals	6760.98	97		

QUERUB	Sum.Sq	Df	F value	Pr(>F)
chilling	35.61	2	0.45	0.64
forcing	680.83	1	17.34	0.00
photoperiod	369.53	1	9.41	0.00
Residuals	4946.29	126		

ACEPEN	Sum.Sq	Df	F value	Pr(>F)
chilling	104.66	2	0.87	0.42
forcing	4745.38	1	79.18	0.00
photoperiod	1306.03	1	21.79	0.00
chilling:forcing	63.31	2	0.53	0.59
chilling:photoperiod	181.96	2	1.52	0.22
forcing:photoperiod	257.63	1	4.30	0.04
Residuals	6113.18	102		

ACERUB	Sum.Sq	Df	F value	Pr(>F)
chilling	1.53	2	0.01	0.99
forcing	1721.25	1	26.13	0.00
photoperiod	381.81	1	5.80	0.02
chilling:forcing	358.58	2	2.72	0.07
chilling:photoperiod	37.69	2	0.29	0.75
forcing:photoperiod	17.35	1	0.26	0.61
Residuals	6191.98	94		

ACESAC	Sum.Sq	Df	F value	Pr(>F)
chilling	65.78	2	0.45	0.64
forcing	204.31	1	2.83	0.10
photoperiod	267.24	1	3.70	0.06
chilling:forcing	76.27	2	0.53	0.59
chilling:photoperiod	164.28	2	1.14	0.33
forcing:photoperiod	0.05	1	0.00	0.98
Residuals	4194.28	58		

BETALL	Sum.Sq	Df	F value	Pr(>F)
chilling	526.41	2	5.57	0.00
forcing	1463.33	1	30.95	0.00
photoperiod	632.83	1	13.38	0.00
chilling:forcing	66.32	2	0.70	0.50
chilling:photoperiod	226.18	2	2.39	0.10
forcing:photoperiod	612.56	1	12.95	0.00
Residuals	6005.50	127		

BETPAP	Sum.Sq	Df	F value	Pr(>F)
chilling	6.07	2	0.04	0.96
forcing	1765.57	1	21.22	0.00
photoperiod	1101.18	1	13.24	0.00
chilling:forcing	71.38	2	0.43	0.65
chilling:photoperiod	62.92	2	0.38	0.69
forcing:photoperiod	233.62	1	2.81	0.10
Residuals	10148.80	122		

FAGGRA	Sum.Sq	Df	F value	Pr(>F)
chilling	145.37	2	1.64	0.20
forcing	595.26	1	13.40	0.00
photoperiod	0.42	1	0.01	0.92
chilling:forcing	39.45	2	0.44	0.64
chilling:photoperiod	83.56	2	0.94	0.40
forcing:photoperiod	35.33	1	0.80	0.38
Residuals	2665.38	60		

ILEMUC	Sum.Sq	Df	F value	Pr(>F)
chilling	28.03	2	0.60	0.55
forcing	2277.73	1	97.37	0.00
photoperiod	1033.49	1	44.18	0.00
chilling:forcing	16.09	2	0.34	0.71
chilling:photoperiod	106.28	2	2.27	0.11
forcing:photoperiod	171.89	1	7.35	0.01
Residuals	3041.00	130		

POPGRA	Sum.Sq	Df	F value	Pr(>F)
chilling	50.56	2	0.37	0.69
forcing	2390.66	1	35.16	0.00
photoperiod	1016.39	1	14.95	0.00
chilling:forcing	45.72	2	0.34	0.72
chilling:photoperiod	152.02	2	1.12	0.33
forcing:photoperiod	296.37	1	4.36	0.04
Residuals	6254.69	92		

QUERUB	Sum.Sq	Df	F value	Pr(>F)
chilling	35.70	2	0.46	0.63
forcing	668.59	1	17.39	0.00
photoperiod	364.39	1	9.48	0.00
chilling:forcing	174.11	2	2.26	0.11
chilling:photoperiod	110.91	2	1.44	0.24
forcing:photoperiod	15.92	1	0.41	0.52
Residuals	4652.62	121		