# 1 Rethinking False Spring Risk

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16

17 **Abstract**

18 Temperate plants are at risk of being exposed to late spring freezes — often called false springs — which can

19 be damaging ecologically and economically. As climate change may alter the prevalence and severity of false

20 springs, our ability to accurately forecast such events has become more critical. Currently, many false spring

21 studies simplify the ecological and physiological information needed for accurate predictions of the level of

22 plant damage from late spring freezes. Here we review the complexity of factors driving a plant’s false spring

23 risk. We highlight how species, life stage, and habitat differences contribute to the damage potential of false

24 springs. Integrating these complexities could rapidly advance forecasting of false spring events in climate

25 change and ecological studies.

# 26 The Complexities of Spring Freeze

27 Plants from temperate environments time their growth each spring to follow rising temperatures alongside

28 increasing light and soil resource availability. While tracking spring resource availability, individuals that

29 budburst before the last freeze date are at risk of leaf loss, damaged wood tissue, and slowed canopy develop-

30 ment [1, 2]. These damaging late spring freezes are also known as false springs, and are widely documented

31 to result in adverse ecological and economic consequences [3, 4].

32 Climate change is expected to cause an increase in damage from false spring events due to earlier spring

33 onset and potentially greater fluctuations in temperature in some regions [5, 6]. Already, multiple studies

34 have documented false springs in recent years [1, 7, 8, 9] and some have linked these events to climate change

35 [4, 10, 11, 12, 13]. This increasing interest in false springs has led to a growing body of research investigating

36 the effects on temperate forests. For this research to produce accurate predictions, however, researchers need

37 methods that properly evaluate the effects of false springs across diverse species and climate regimes.

### 38 Measuring False Spring

39 Current metrics for estimating false springs events are generally simple, often requiring an estimate for the

40 start of biological ‘spring’ (i.e. budburst) and whether temperatures below a particular threshold occurred

41 in the following week. Such estimates inherently assume consistency of damage across species, functional

42 group, life stages, and other climatic regimes, ignoring that such factors can greatly impact plants’ false

43 spring risk. As a result, such indices may lead to inaccurate estimates and predictions, slowing our progress

44 in understanding false spring events and how they may shift with climate change.

45 In this paper we highlight the complexity of factors driving a plant’s false spring risk and provide a road map

46 for improved metrics. We show how location within a forest or canopy, interspecific variation in avoidance

47 and tolerance strategies, freeze temperature thresholds, and regional effects unhinge simple metrics of false

48 spring. We argue that a new approach that integrates these and other crucial factors would help accurately

49 determine current false spring damage and improve predictions of spring freeze risk under a changing climate

50 — while potentially providing novel insights to how plants respond to and are shaped by spring frost.

# 51 Defining False Spring: An example in one temperate plant commu-

52 **nity**

53 Temperate forest plants experience elevated risk of frost damage during the spring due to the stochastic timing

54 of frosts. Freezing temperatures following a warm spell can result in plant damage or even death [14, 15].

55 Many temperate species exhibit flexible spring phenologies, which help them minimize spring freezing risk,

56 but freeze damage can still occur. Once buds exit the dormancy phase, they are less freeze tolerant and less

57 resistant to ice formation [16, 17, 18]. An effective and consistent definition of false spring would accurately

58 determine the amount and type of ice formation to properly evaluate the level of damage that could occur.

59 There are several definitions currently used to define a false spring. A common definition describes a false

60 spring as having two phases: rapid vegetative growth prior to a freeze and a post freeze setback [1]. Other

61 definitions instill more precise temporal parameters, specific to certain regions [e.g., in 8, false spring for the

62 Midwestern United States is defined as a warmer than average March, a freezing April, and enough growing

63 degree days between budburst and the last freeze date]. A widely used definition integrates a mathematical

64 equation to quantify a false spring event. This equation, known as a False Spring Index (FSI), signifies the

65 likelihood of damage to occur from a late spring freeze. Currently, FSI is evaluated annually by the day of

66 budburst and the day of last spring freeze [often calculated at -2.2*◦*C, 19] through the simple equation [20]:

*F SI* = Day of Year(*LastSpringF reeze*) *−* Day of Year(*Budburst*) (1)

67 Negative values indicate no risk situations, whereas a damaging FSI is currently defined to be 7 or more days

68 between budburst and the last freeze date (Equation 1) [21]. This 7 day threshold captures the reality that

69 leaf tissue is at high risk of damage from frost in the period after budburst, with later vegetative phases (e.g.,

70 full leafout) being more resistant to such damage.

71 To demonstrate how the FSI definition works, we applied it to data from the Harvard Forest Long-term

72 Ecological Research program in Massachusetts. We used three separate methodologies to calculate spring

73 onset: long-term ground observational data [22], PhenoCam data from Harvard Forest [23], and USA National

74 Phenology Network’s (USA-NPN) Extended Spring Index (SI-x) data [24]. These spring onset values were

75 then inputted into the FSI equation (Equation 1) to calculate FSI from 2008 to 2014 (Figure 1).

76 Each methodology rendered different FSI values, suggesting different false spring damage for the same site

77 and same year. For most years, the observational FSI and PhenoCam FSI are about 10-15 days lower than

78 the SI-x data. This is especially important for 2008, when the SI-x data indicates a false spring year, whereas

79 the other two datasets do not. In 2012, the observational data and PhenoCam data diverge slightly and the

80 PhenoCam FSI is over 30 days less than the SI-x value.

81 The reason for these discrepancies is that each method evaluates spring onset by integrating different at-

82 tributes such as age, species or functional group. Spring phenology in temperate forests typically progresses

83 by functional group: understory species and young trees tend to initiate budburst first, whereas larger canopy

84 species start later in the season [25, 12]. The different FSI values determined in Figure 1 exemplify the dif-

85 ferences in functional group spring onset dates and illustrate variations in forest demography and phenology.

86 While the SI-x data (based on observations of early-active shrub species, including lilac, *Syringa vulgaris*)

87 may best capture understory dynamics, the PhenoCam and observational FSI data integrate over larger

88 canopy species. Such differences are visible each year, as the canopy-related metrics show lower risk, but are

89 especially apparent in 2012. In 2012, a false spring event was reported through many regions of the US due

90 to warm temperatures occurring in March [26]. These high temperatures would most likely be too early for

91 larger canopy species to initiate budburst but they would have affected smaller understory species, as is seen

92 by the high risk of the SI-x FSI in Figure 1.

93 Yet, in contrast to our three metrics of spring onset for one site, most FSI work currently ignores variation

94 across functional groups — instead using one metric of spring onset and assuming it applies to the whole

95 community of plants [20, 21, 10, 27]. The risk of a false spring varies across habitats and with species compo-

96 sition since spring onset is not consistent across functional groups. Therefore, one spring onset date cannot

97 be used as an effective proxy for all species. False spring studies should first assess the forest demographics

98 and functional groups relevant to the study question in order to effectively estimate the date of spring onset.

99 However, as we outline below, considering different functional groups is unlikely to be enough for robust

100 predictions. It is also crucial to integrate species differences within functional groups and to consider the

101 various interspecific avoidance and tolerance strategies that species have evolved against false springs.

# 102 Plant Physiology and Diversity versus the Current False Spring

103 **Definition**

104 Plants have evolved to minimize false spring damage through two strategies: avoidance and tolerance. Many

105 temperate forest plants utilize various morphological strategies to be more frost tolerant: some have toothed

106 leaves to increase ‘packability’ in winter buds, which permits more rapid leafout [28] and minimizes the

107 exposure time of less resistant tissues. Other species have young leaves with more trichomes to act as a

108 buffer against spring frosts [29, 30]. These strategies are probably only a few of the many ways plants work

109 to morphologically avoid frost damage, and more studies are needed to investigate the interplay between

110 morphological traits and false spring tolerance.

111 Rather than being more tolerant of spring freezing temperatures, some temperate forest species have evolved

112 to avoid frosts via their phenologies. Effective avoidance strategies require well-timed spring phenologies.

113 Most temperate deciduous tree species optimize growth and minimize spring freeze damage by using three

114 cues to initiate budburst: low winter temperatures (chilling), warm spring temperatures, and increasing pho-

115 toperiods [31]. The evolution of these three cues and their interactions has permitted temperate plant species

116 to occupy more northern ecological niches [32] and decrease the risk of false spring damage [33]. One avoid-

117 ance strategy, for example, is the interaction between over-winter chilling and spring forcing temperatures.

118 Warm temperatures earlier in the winter will not result in early budburst due to insufficient chilling [34].

119 Likewise, photoperiod sensitivity is a common false spring avoidance strategy: species that respond strongly

120 to photoperiod cues in addition to warm spring temperatures are unlikely to have large advances in budburst

121 with warming, and thus may evade false spring events as warming continues [35].

# 122 Defining Vegetative Risk

123 Phenology and frost tolerance are intertwined — with important variation occurring across different phe-

124 nological phases. Flowering and fruiting are generally more sensitive to false spring events than vegetative

125 phases [7, 17], but false spring events that occur during the vegetative growth phenophases may impose the

126 greatest freezing threat to deciduous plant species. Plants will suffer greater long-term effects from the loss of

127 photosynthetic tissue, which could impact multiple years of growth, reproduction, and canopy development

128 [36, 37]. However, there is high variability in defining a damaging temperature threshold across species,

129 including between agricultural and ecological studies (Figure 2).

130 There is also important variation within certain phenological phases. Most notably, within the vegetative

131 phases of spring leafout, plants that have initiated budburst but have not fully leafed out are more likely to

132 sustain damage from a false spring than individuals past the leafout phase. This is because freezing tolerance

133 is lowest after budburst begins until the leaf is fully unfolded [38]. Therefore, the rate of budburst and the

134 length of time between budburst and leafout is essential for predicting the level of damage from a false spring

135 event. We will refer to the timing between these phenophases — budburst to leafout — as the duration of

136 vegetative risk (Figure 3). The duration of vegetative risk can be extended if a freezing event occurs during

137 the phenophases between budburst and full leafout [7], which could result in exposure to multiple frost events

138 in one season.

# 139 How Species Phenological Cues Shape Vegetative Risk

140 Predictions of false spring critically depend on understanding what controls the duration of vegetative risk

141 across species. For temperate species, the three major cues (winter chilling temperatures, spring warm

142 temperatures and photoperiod) that control budburst [31] probably play a dominant role. One study, which

143 examined how these cues impact budburst and leafout, shows that the duration of vegetative risk can vary

144 by 21 days or more depending on the suite of cues a plant experiences (Figure 4) [39]. The experiment

145 examined 9 temperate trees and shrubs using a fully crossed design of three levels of chilling (field chilling,

146 field chilling plus 30 days at either 1 or 4 *◦*C), two levels of forcing (20*◦*C/10*◦*C or 15*◦*C/5*◦*C day/night

147 temperatures) and two levels of photoperiod (8 versus 12 hour days) resulting in 12 treatment combinations.

148 Increased forcing, photoperiod and chilling all decreased the duration of vegetative risk, with forcing causing

149 the greatest decrease (10 days), followed by daylength (9 days), and chilling (2-3 days depending on the

150 temperature), but the full effect of any one cue depended on the other cues due to important interactions—

151 for example, the combined effect of warmer temperatures and longer days would be 14 days, because of -5

152 days interaction between the forcing and photoperiod cues (Figure 4A).

153 Such cues may provide a starting point for predicting how climate change will alter the duration of vegetative

154 risk. Robust predictions will require much more information, especially the emissions scenario realized over

155 coming decades [40], but one potential outcome is that higher temperatures will increase forcing and decrease

156 chilling in many locations. Under this scenario experimental results suggest a 2-10 day increase in duration

157 of vegetative risk depending on the species, except for *Betula alleghaniensis* which had a 6 day decrease in

158 duration of vegetative risk (Figure 4B). This cue interaction could thus expose at-risk plants to more intense

159 false spring events or even multiple events in one year.

160 Considering the interaction of cues and climate change further complicates understanding species future

161 vulnerabilities to false spring events. Most species are expected to begin leafout earlier in the season with

162 warming spring temperatures but some species may have the opposite response due to less winter chilling or

163 decreased photoperiod cues [41, 42, 12]. Individuals that initiate budburst earlier in the spring may attempt

164 to limit freezing risk by decreasing the duration of vegetative risk in order to minimize the exposure of

165 less frost tolerant phenophases [7]. But with a changing climate and thus shifts in phenological cues, this

166 relationship may change [43]. Further studies are essential to understand the interplay between chilling,

167 forcing, and photoperiod cues and the duration of vegetative risk, especially for species occupying ecological

168 niches more susceptible to false spring events.

### 169 Predictable Regional Differences in Climate, Species Responses and False Spring

170 **Risk**

171 Robust predictions must consider the full interplay of species cues and a specific location’s climate. Climate

172 and thus false spring risk vary across regions. For example, consider five different regions within a temper-

173 ate climate (Figure S1). Some regions may experience harsher winters and greater temperature variability

174 throughout the year, and these more variable regions often have a much higher risk of false spring than

175 others (i.e. compare Maine versus Lyon in Figure S1). Understanding and integrating such spatiotemporal

176 effects and regional differences when investigating false spring risk and duration of vegetative risk would help

177 improve predictions as climate change progresses. Such differences depend both on the local climate, the

178 local species and the cues for that species at that location, as a single species may have varying cues across

179 space. Therefore, based on cues alone, different regions may have different durations of vegetative risk for

180 the same species [44, 45, 46]. Studies also show that different species within the same location can exhibit

181 different sensitivities to the three cues [34, 47], further amplifying the myriad of climatic and phenological

182 shifts that determine false spring risk in a region.

183 How a single species phenological cues varies across space is not yet well predicted. Some studies have

184 investigated how phenological cues for budburst vary across space, including variation across populations,

185 by using latitudinal gradients [48, 49]. Fewer, however, have integrated distance from the coast [but see

186 50, 51, 52] or regional effects. Some studies indicate that populations further inland will initiate budburst

187 first, whereas those closer to the coast will initiate budburst later in the season and that the distance from

188 the coast is a stronger indicator of budburst timing than latitude [50]. It is therefore important to recognize

189 climate regime extremes (e.g. seasonal trends, annual minima and annual maxima) across regions to better

190 understand the interplay between duration of vegetative risk and climatic variation. The climatic implications

191 of advancing forcing temperatures could potentially lead to earlier dates of budburst and enhance the risk of

192 frost. These shifts in climatic regimes could vary in intensity across regions (i.e. regions currently at high-risk

193 of false spring damage could become low-risk regions over time).

# 194 Concluding Remarks and Future Perspectives

195 Temperate forest trees are most at risk to frost damage in the spring due to the stochasticity of spring freezes.

196 With warm temperatures advancing in the spring but last spring freeze dates advancing at a slower rate,

197 there could be more damaging false spring events in the future, especially in high-risk regions [1, 5, 53]. Cur-

198 rent equations for evaluating false spring damage (e.g. Equation 1) largely simplify the myriad complexities

199 involved in assessing false spring damage and risks. More studies aimed at understanding relationships be-

200 tween species avoidance and tolerance strategies, climatic regimes, and physiological cue interactions with the

201 duration of vegetative risk would improve predictions (see ‘Outstanding Questions’). Additionally, research

202 to establish temperature thresholds for damage across functional types and phenophases will help effectively

203 predict false spring risk in the future. An integrated approach to assessing past and future spring freeze dam-

204 age would provide novel insights into plant strategies, and offer more robust predictions as climate change

205 progresses, which is essential for mitigating the adverse ecological and economic effects of false springs.

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## Calculating False Spring Risk

10

0

False Spring Index

−10

−20

#### Method

SI−x



O‘Keefe Phenocam

#### Method

SI−x

Observational (O‘Keefe) Phenocam

2008 2009 2010 2011 2012 2013 2014

#### Year

Figure 1: FSI values from 2008 to 2014 vary across methdologies. 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 dotted line at y=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 y=7 indicates the 7 day threshold frequently used in false spring definitions, which suggests years with FSI values greater than 7 very likely had false spring events.

All species − soft freeze (Augspurger, 2013) All species (Peterson & Abatzoglou, 2014) All species − hard freeze (Schwartz, 1993)) *Fagus sylvatica*− 50% (Lenz et al., 2016) *Eucalyptus pauciflora*(Barker et al., 2005)

*Acer pseudoplatanus*− 50% (Lenz et al., 2016) *Tilia platyphyllos*− 50% (Lenz et al., 2016) Sorbus aucuparia − 50% (Lenz et al., 2016) *Prunus avium*− 50% (Lenz et al., 2016) Rice − 100% (Sanchez et al., 2013)

All species (Cannell & Smith, 1986) Corn − 100% (Sanchez et al., 2013) *Vaccinium spp.*(Longstroth, 2012)

Wheat − 10 to 90% (Barlow et al., 2015) Wheat − 100% (Barlow et al., 2015) *Rosaceae*− 10% (Longstroth, 2013)

*Rosaceae*− 90% (Longstroth, 2013) Wheat − 100% (Sanchez et al., 2013)

## Descrepancies in Defining False Spring Temperatures

−20 −10 0 10

#### Temperature Threshold °C

Sector

Agronomic Ecological

#### Phase

Both Floral Vegetative

Figure 2: 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.

high

Frost Damage Risk

## Defining the Duration of Vegetative Risk

low

90 110 130 150

**False Spring**

*Ilex mucronata*

Duration of Vegetative Risk

#### Day of Year

high

*Betula alleghaniensis*

Duration of Vegetative Risk

Frost Damage Risk

low

**False Spring**

90 110 130 150

#### Day of Year

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 histori- cal 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 be- tween budburst (light green squares) and leafout (dark green triangles), would be exposed to a false spring event during it’s duration of vegetative risk (i.e. from budburst to leafout), whereas *Betula alleghaniensis* would avoid it entirely, due to later budburst. Budburst is indicated by the light green squares and leafout is indicated by the dark green triangles.

#### A. B.

Forcing



Change in Duration of Vegetative Risk (days)

10

Photoperiod

Chilling 1.5°C

5

Chilling 4°C

Forcing x Photoperiod

0

Forcing x Chilling 1.5°C

Forcing x Chilling 4°C

-5

Photoperiod x Chilling 1.5°C

Photoperiod x Chilling 4°C

-20 -10 0 10

Figure 4: How major cues of spring phenology alter vegetative risk. (A) Model estimates of changes in the duration of vegetative risk due to varying cues from a full-factorial experiment (means *±* 95% credible intervals, slightly larger blue circles represent the overall mean estimate, while each species estimate is shown below and colored as shown in B). Higher forcing temperatures decreased the period of vegetative risk the most (by 10 days overall given a 10 degree difference), as did photoperiod (by 9 days overall given a 4 hour increase). However, together these effects offset, thus the combined effect of greater forcing and longer photoperiod would be a reduction in duration of vegetative risk of 14 days due to a 5 day delay through their interaction. (B) A comparison of the durations of vegetative risk (raw data means *±* 1 standard error) across two treatments (high chilling and high forcing temperatures vs. low chilling and low forcing, in both photoperiod was 12 hr) for each species in the experiment. Species along the x-axis are ordered by day of budburst.