

¹ **Rethinking False Spring Risk**

² Authors:

³ C. J. Chamberlain ^{1,2}, B. I. Cook ³, I. Garcia de Cortazar Atauri ⁴ & E. M. Wolkovich ^{1,2}

⁴ *Author affiliations:*

⁵ ¹Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

⁶ ²Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

⁷ ³NASA Goddard Institute for Space Studies, New York, New York, USA;

⁸ ⁴French National Institute for Agricultural Research, INRA, US1116 AgroClim, F-84914 Avignon, France

⁹ *Keywords:* false spring, phenology, freezing tolerance, climate change, forest communities *Paper type:* Opinion
¹⁰ ion

¹¹ *Counts:* Total word count for the main body of the text: 2985; Abstract: 120; 6 figures (all in color).

¹²

¹³ **1 Abstract**

¹⁴ Temperate plants are at risk of being exposed to late spring freezes — often called false springs — which
¹⁵ can be damaging ecologically and economically. As climate change may alter the prevalence and severity
¹⁶ of false springs, our ability to accurately forecast such events has become more critical. Currently, many
¹⁷ false spring studies simplify the various ecological elements needed for accurate predictions of the level of
¹⁸ plant damage from late spring freezing events. Here we review the complexity of factors driving a plant's
¹⁹ false spring risk. We highlight how species, life stage, and habitat differences contribute to the likelihood of
²⁰ occurrence and damage potential of false springs. Integrating some of these complexities could help rapidly
²¹ advance forecasting of false springs in climate change and ecological studies.

²² **2 Introduction**

²³ Plants growing in temperate environments time their growth each spring to follow rising temperatures along-
²⁴ side increasing light and soil resource availability. While tracking spring resource availability, temperate
²⁵ plants are at risk of late spring freezes, which can be detrimental to growth. Individuals that leaf out before
²⁶ the last freeze date are at risk of leaf loss, damaged wood tissue, and slowed canopy development (Gu *et al.*,
²⁷ 2008; Hufkens *et al.*, 2012). These damaging late spring freezes are also known as false springs, and are widely
²⁸ documented to result in adverse ecological and economic consequences (Knudson, 2012; Ault *et al.*, 2013).

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

38 Current metrics for estimating false springs events are generally simple, often requiring an estimate for the
39 start of biological ‘spring’ (i.e. budburst) and whether temperatures occurred below a particular temperature
40 threshold in the following week. Such estimates inherently assume consistency of damage across species,
41 functional group, life stages, and other climatic regimes, ignoring that such factors can greatly impact plants’
42 false spring risk. As a result, such indices may lead to inaccurate current estimates as well as poor future
43 predictions, slowing our progress in understanding false spring events and how they may shift with climate
44 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 **3 Defining False Spring: An example in one temperate plant com- 52 munity**

53 Temperate forest plants experience elevated risk of frost damage during the spring due to the stochastic
54 timing of spring frosts. Plants must therefore exhibit flexible spring phenologies to minimize freezing risk.
55 Freezing temperatures following a warm spell could result in plant damage or even death (Ludlum, 1968; Mock
56 *et al.*, 2007). Intracellular ice formation from false spring events often results in severe leaf and stem damage
57 (Burke *et al.*, 1976; Sakai & Larcher, 1987). Ice formation can also occur indirectly (i.e. extracellularly), which
58 results in freezing dehydration and mimics drought conditions (Pearce, 2001; Beck *et al.*, 2004; Hofmann &
59 Bruelheide, 2015). Both forms of ice formation can cause defoliation and crown dieback (Gu *et al.*, 2008).

60 Once buds exit the dormancy phase, they are less freeze tolerant and resistance to bud ice formation is greatly
61 reduced (Taschler *et al.*, 2004; Lenz *et al.*, 2013; Vitasse *et al.*, 2014b). An effective and consistent definition
62 of false spring would accurately determine the amount and type of ice formation to properly evaluate the
63 level of damage that could occur.

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

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

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

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

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

88 The reason for these discrepancies is that each method evaluates spring onset by integrating different at-
89 tributes such as age, species or functional group. Spring phenology in temperate forests typically progresses
90 by functional group (e.g. deciduous broadleaf trees). Understory species and young trees tend to initiate

91 budburst first, whereas larger canopy species may start later in the season (Richardson & O'Keefe, 2009;
92 Xin, 2016). The different FSI values determined in Figure 1 exemplify the differences in functional group
93 spring onset dates and illustrate variations in forest demography and phenology, which is most apparent in
94 2012. In 2012, a false spring event was reported through many regions of the US due to warm temperatures
95 occurring in March (Ault *et al.*, 2015). These high temperatures would most likely be too early for larger
96 canopy species to initiate budburst but they would affect smaller understory species as is seen in Figure 1.

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

107 4 Plant Physiology and Diversity versus the Current False Spring 108 Definition

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

115 Rather than being more tolerant of spring freezing temperatures, some temperate forest species have evolved
116 to avoid frosts via more flexible phenologies. Effective avoidance strategies require well-timed spring phenolo-
117 gies. Temperate deciduous tree species optimize growth and minimize spring freeze damage by using three
118 cues to initiate budburst: low winter temperatures, warm spring temperatures, and increasing photoperi-
119 ods (Chuine, 2010). The evolution of these three cues and their interactions has permitted temperate plant
120 species to occupy more northern ecological niches (Kollas *et al.*, 2014) and decrease the risk of false spring
121 damage, which is crucial for avoidance strategies. One avoidance strategy, for example, is the interaction

122 between over-winter chilling and spring forcing temperatures. Warm temperatures earlier in the year (i.e. in
123 February, or even January in the Mediterranean) will not result in early budburst due to insufficient chilling
124 (Basler & Körner, 2012). Likewise, photoperiod sensitivity is a common false spring avoidance strategy:
125 species that respond strongly to photoperiod cues in addition to warm spring temperatures will likely delay
126 budburst and evade false spring events as spring continues to advance earlier in the year (Basler & Korner,
127 2014).

128 5 Defining Vegetative Risk

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

136 There is also important variation within certain phenological phases. Most notably, within the vegetative
137 phases of spring leafout, plants that have initiated budburst but have not fully leafed out are more likely to
138 sustain damage from a false spring than individuals past the leafout phase. This is because freezing tolerance
139 is lowest after budburst begins until the leaf is fully unfolded (Lenz *et al.*, 2016) (Box 1). Therefore, the rate
140 of budburst and the length of time between budburst and leafout is essential for predicting level of damage
141 from a false spring event. We will refer to the timing of these phenophases — budburst to leafout — as the
142 duration of vegetative risk (Figure 2). The duration of vegetative risk is usually extended if a freezing event
143 occurs during the phenophases between budburst and full leafout (Augspurger, 2009), which could result in
144 exposure to multiple frost events in one season.

145 6 How Species' Phenological Cues Shape Vegetative Risk

146 Predictions of false spring critically depend on understanding what controls the duration of vegetative risk
147 across species. For temperate species, the three major cues that control budburst (Chuine, 2010) probably
148 play a dominant role. One study, which examined how these cues impact budburst and leafout, shows that
149 the duration of vegetative risk can vary by 21 days or more depending on the suite of cues a plant experiences
150 (Figure 5). The experiment examined 9 temperate trees and shrubs using a fully crossed design of three levels

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

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

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

173 6.1 Predictable Regional Differences in Climate, Species Responses and False 174 Spring Risk

175 Robust predictions must consider the full interplay of species cues and a specific location's climate. A single
176 species may have varying cues across space: various studies that investigate latitudinal effects indicate that
177 species and individuals growing further north respond to a different interaction of cues than those growing
178 further south and, subsequently, species across different regions may have different durations of vegetative
179 risk (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011). Studies also suggest that
180 species within the same system can exhibit different sensitivities to the three cues (Basler & Körner, 2012;
181 Laube *et al.*, 2013) thus further amplifying the myriad of climatic and phenological shifts as well as the
182 varying species-level effects. We assessed climate data across North America and Europe to gain a better

¹⁸³ understanding of the interaction between duration of vegetative risk and false spring events in an attempt to
¹⁸⁴ unravel these complexities.

¹⁸⁵ Numerous studies have investigated how the relationship between budburst and major phenological cues
¹⁸⁶ varies across space and the genetic variations that occur between populations by using latitudinal gradients
¹⁸⁷ (Partanen, 2004; Vihera-aarnio *et al.*, 2006; Caffarra & Donnelly, 2011; Zohner *et al.*, 2016; Gauzere *et al.*,
¹⁸⁸ 2017). Few, however, have integrated longitudinal variation or regional effects. Yet climate and thus false
¹⁸⁹ spring risk and phenological cues vary across regions. For example, consider five different regions within
¹⁹⁰ a temperate climate (Figure 3). Some regions may experience harsher winters and greater temperature
¹⁹¹ variability throughout the year, and these more variable regions often have a much higher risk of false spring
¹⁹² (i.e. Maine) than others (i.e. Lyon) (Figure 3). Understanding and integrating such spatiotemporal effects
¹⁹³ and regional differences when investigating false spring risk and duration of vegetative risk would help improve
¹⁹⁴ predictions as climate change progresses.

¹⁹⁵ Accurate predictions need to carefully consider how chilling and forcing cues vary across a longitudinal gra-
¹⁹⁶ dient. Climatic variation across regions and at different distances from the coast results in varying durations
¹⁹⁷ of vegetative risk due to different chilling and forcing temperatures (Myking & Skroppa, 2007). It is therefore
¹⁹⁸ important to recognize climate regime extremes (e.g. seasonal trends, annual minima and annual maxima)
¹⁹⁹ across regions in future studies in order to better understand the interplay between duration of vegetative
²⁰⁰ risk and climatic variation. The climatic implications of advancing forcing temperatures could potentially
²⁰¹ lead to earlier dates of budburst and enhance the risk of frost. These shifts in climatic regimes could vary in
²⁰² intensity across regions (i.e. habitats currently at risk of false spring damage could become low risk regions
²⁰³ over time).

²⁰⁴ There are also discrepancies in defining a false spring event related to understanding the temperature threshold
²⁰⁵ for damage. Some regions and species may tolerate lower temperature thresholds than others (Figure 4). It
²⁰⁶ is crucial to gain an understanding on which climatic parameters result in false spring events and how these
²⁰⁷ parameters may vary across regions. It is anticipated that most regions will have earlier spring onsets,
²⁰⁸ however, last freeze dates will not advance at the same rate (Inouye, 2008; Martin *et al.*, 2010; Labe *et al.*,
²⁰⁹ 2016; Sgubin *et al.*, 2018), rendering some regions and species to be more susceptible to false spring events
²¹⁰ in the future.

²¹¹ 7 Conclusion

²¹² Temperate forest trees are most at risk to frost damage in the spring due to the stochasticity of spring freezes.
²¹³ With warm temperatures advancing in the spring but last spring freeze dates advancing at a slower rate,

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

223 References

- 224 Agrawal, A.A., Conner, J.K. & Stinchcombe, J.R. (2004) Evolution of plant resistance and tolerance to frost
225 damage. *Ecology Letters* **7**, 1199–1208.
- 226 Allstadt, A.J., Vavrus, S.J., Heglund, P.J., Pidgeon, A.M., Wayne, E. & Radeloff, V.C. (2015) Spring plant
227 phenology and false springs in the conterminous U. S. during the 21st century. *Environmental Research
228 Letters (submitted)* **10**, 104008.
- 229 Augspurger, C.K. (2009) Spring 2007 warmth and frost: Phenology, damage and refoliation in a temperate
230 deciduous forest. *Functional Ecology* **23**, 1031–1039.
- 231 Augspurger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124
232 years: Spring damage risk is increasing. *Ecology* **94**, 41–50.
- 233 Ault, T.R., Henebry, G.M., de Beurs, K.M., Schwartz, M.D., Betancourt, J.L. & Moore, D. (2013) The False
234 Spring of 2012, Earliest in North American Record. *Eos, Transactions American Geophysical Union* **94**,
235 181–182.
- 236 Ault, T.R., Zurita-Milla, R. & Schwartz, M.D. (2015) A Matlab \odot toolbox for calculating spring indices from
237 daily meteorological data. *Computers & Geosciences* **83**, 46–53.
- 238 Barker, D., Loveys, B., Egerton, J., Gorton, H., Williams, W. & Ball, M. (2005) Co2 enrichment predisposes
239 foliage of a eucalypt to freezing injury and reduces spring growth. *Plant, Cell and Environment* **28**, 1506–
240 1515.
- 241 Barlow, K., Christy, B., O'Leary, G., Riffkin, P. & Nuttall, J. (2015) Simulating the impact of extreme heat
242 and frost events on wheat crop production: A review. *Field Crops Research* **171**, 109–119.

- ²⁴³ Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species.
²⁴⁴ *Agricultural and Forest Meteorology* **165**, 73–81.
- ²⁴⁵ Basler, D. & Korner, C. (2014) Photoperiod and temperature responses of bud swelling and bud burst in
²⁴⁶ four temperate forest tree species. *Tree Physiology* **34**, 377–388.
- ²⁴⁷ Beck, E.H., Heim, R. & Hansen, J. (2004) Plant resistance to cold stress: Mechanisms and environmental
²⁴⁸ signals triggering frost hardening and dehardening. *Journal of Biosciences* **29**, 449–459.
- ²⁴⁹ Burke, M., Gusta, L., Quamme, H., Weiser, C. & Li, P. (1976) Freezing and injury in plants. *Annual Review*
²⁵⁰ *of Plant Physiology* **27**, 507–528.
- ²⁵¹ Caffarra, A. & Donnelly, A. (2011) The ecological significance of phenology in four different tree species:
²⁵² Effects of light and temperature on bud burst. *International Journal of Biometeorology* **55**, 711–721.
- ²⁵³ Cannell, M. & Smith, R. (1986) Climatic Warming , Spring Budburst and Forest Damage on Trees. *Journal*
²⁵⁴ *of Applied Ecology* **23**, 177–191.
- ²⁵⁵ Charrier, G., Bonhomme, M., Lacointe, A. & Améglio, T. (2011) Are budburst dates, dormancy and cold ac-
²⁵⁶ climation in walnut trees (*Juglans regia* L.) under mainly genotypic or environmental control? *International*
²⁵⁷ *Journal of Biometeorology* **55**, 763–774.
- ²⁵⁸ Chuine, I. (2010) Why does phenology drive species distribution? *Philosophical Transactions of the Royal*
²⁵⁹ *Society B: Biological Sciences* **365**, 3149–3160.
- ²⁶⁰ Cleland, E., Chiariello, N., Loarie, S., Mooney, H. & Field, C. (2006) Diverse responses of phenology to global
²⁶¹ changes in a grassland ecosystem. *PNAS* **103**, 13740–13744.
- ²⁶² Edwards, E.J., Chatelet, D.S., Spriggs, E.L., Johnson, E.S., Schlutius, C. & Donoghue, M.J. (2017) Correla-
²⁶³ tion, causation, and the evolution of leaf teeth: A reply to Givnish and Kriebel. *Am J Bot* **104**, 509–515.
- ²⁶⁴ Gauzere, J., Delzon, S., Davi, H., Bonhomme, M., Garcia de Cortazar-Atauri, I. & Chuine, I. (2017) Inte-
²⁶⁵ grating interactive effects of chilling and photoperiod in phenological process-based models. A case study
²⁶⁶ with two European tree species: *Fagus sylvatica* and *Quercus petraea*. *Agricultural and Forest Meteorology*
²⁶⁷ pp. 9–20.
- ²⁶⁸ Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008)
²⁶⁹ The 2007 Eastern US Spring Freeze: Increased Cold Damage in a Warming World. *BioScience* **58**, 253.
- ²⁷⁰ Hofmann, M. & Bruelheide, H. (2015) Frost hardiness of tree species is independent of phenology and macro-
²⁷¹ climatic niche. *Journal of Biosciences* **40**, 147–157.

- 272 Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J. & Richardson, A.D. (2012)
273 Ecological impacts of a widespread frost event following early spring leaf-out. *Global Change Biology* **18**,
274 2365–2377.
- 275 Inouye, D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane
276 wildflowers. *Ecology* **89**, 353–362.
- 277 IPCC (2015) *Climate change 2014: mitigation of climate change*, vol. 3. Cambridge University Press.
- 278 Knudson, W. (2012) The economic impact of the spring's weather on the fruit and vegetable sectors. *The
279 Strategic Marketing Institute Working Paper*.
- 280 Kollas, C., K??rner, C. & Randin, C.F. (2014) Spring frost and growing season length co-control the cold
281 range limits of broad-leaved trees. *Journal of Biogeography* **41**, 773–783.
- 282 Labe, Z., Ault, T. & Zurita-Milla, R. (2016) Identifying anomalously early spring onsets in the CESM large
283 ensemble project. *Climate Dynamics* **48**, 3949–3966.
- 284 Laube, J., Sparks, T.H., Estrella, N., Höfler, J., Ankerst, D.P. & Menzel, A. (2013) Chilling outweighs
285 photoperiod in preventing precocious spring development. *Global Change Biology* **20**, 170–182.
- 286 Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of freezing
287 damage in temperate trees. *Functional Ecology* pp. 1–11.
- 288 Lenz, A., Hoch, G., Vitasse, Y. & Körner, C. (2013) European deciduous trees exhibit similar safety margins
289 against damage by spring freeze events along elevational gradients. *New Phytologist* **200**, 1166–1175.
- 290 Longstroth, M. (2012) Protect blueberries from spring freezes by using sprinklers. url.
- 291 Longstroth, M. (2013) Assessing frost and freeze damage to flowers and buds of fruit trees. url.
- 292 Ludlum, D.M. (1968) *Early American Winters: 1604-1820*. 3, Boston: American Meteorological Society.
- 293 Marino, G.P., Kaiser, D.P., Gu, L. & Ricciuto, D.M. (2011) Reconstruction of false spring occurrences over
294 the southeastern United States, 1901–2007: an increasing risk of spring freeze damage? *Environmental
295 Research Letters* **6**, 24015.
- 296 Martin, M., Gavazov, K., Körner, C., Hattenschwiler, S. & Rixen, C. (2010) Reduced early growing season
297 freezing resistance in alpine treeline plants under elevated atmospheric CO₂. *Global Change Biology* **16**,
298 1057–1070.
- 299 Mehdipoor, H. & Zurita-Milla, E.I.V.R. (2017) Continental-scale monitoring and mapping of false spring: A
300 cloud computing solution .

- 301 Mock, C.J., Mojzisek, J., McWaters, M., Chenoweth, M. & Stahle, D.W. (2007) The winter of 1827–1828 over
302 eastern North America: a season of extraordinary climatic anomalies, societal impacts, and false spring.
303 *Climatic Change* **83**, 87–115.
- 304 Muffler, L., Beierkuhnlein, C., Aas, G., Jentsch, A., Schweiger, A.H., Zohner, C. & Kreyling, J. (2016) Dis-
305 tribution ranges and spring phenology explain late frost sensitivity in 170 woody plants from the northern
306 hemisphere. *Global Ecology and Biogeography* **25**, 1061–1071.
- 307 Myking, T. & Skroppa, T. (2007) Variation in phenology and height increment of northern *Ulmus glabra*
308 populations: Implications for conservation. *Scandinavian Journal of Forest Research* **22**, 369–374.
- 309 O'Keefe, J. (2014) Phenology of Woody Species at Harvard Forest since 1990. Tech. rep.
- 310 Partanen, J. (2004) Dependence of photoperiodic response of growth cessation on the stage of development
311 in *Picea abies* and *Betula pendula* seedlings. *Forest Ecology and Management* **188**, 137–148.
- 312 Pearce, R. (2001) Plant freezing and damage. *Annals of Botany* **87**, 417–424.
- 313 Peterson, A.G. & Abatzoglou, J.T. (2014) Observed changes in false springs over the contiguous United
314 States. *Geophysical Research Letters* **41**, 2156–2162.
- 315 Prozherina, N., Freiwald, V., Rousi, M. & Oksanen, E. (2003) Interactive effect of springtime frost and
316 elevated ozone on early growth, foliar injuries and leaf structure of birch (*Betula pendula*). *New Phytologist*
317 **159**, 623–636.
- 318 Richardson, A. & O'Keefe, J. (2009) *Phenological differences between understory and overstory: a case*
319 *study using the long-term harvard forest records*, pp. 87–117. A. Noormets (Ed.), *Phenology of Ecosystem*
320 *Processes*, Springer, New York.
- 321 Richardson, A.D. (2015) PhenoCam images and canopy phenology at Harvard Forest since 2008.
- 322 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants*. Springer-Verlag.
- 323 Sánchez, B., Rasmussen, A. & Porter, J.R. (2013) Temperatures and the growth and development of maize
324 and rice: a review. *Global Change Biology* **20**, 408–417.
- 325 Schaber, J. & Badeck, F.W. (2005) Plant phenology in germany over the 20th century. *Regional Environmental*
326 *Change* **5**, 37–46.
- 327 Schwartz, M.D. (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography* **14(6)**,
328 536–550.

- 329 Sgubin, G., Swingedouw, D., Dayon, G., de Cortázar-Atauri, I.G., Ollat, N., Pagé, C. & van Leeuwen, C.
330 (2018) The risk of tardive frost damage in french vineyards in a changing climate. *Agricultural and Forest
331 Meteorology* **250-251**, 226 – 242.
- 332 Soudani, K., Hmimina, G., Delpierre, N., Pontailler, J.Y., Aubinet, M., Bonal, D., Caquet, B., de Grandcourt,
333 A., Burban, B., Flechard, C. & et al. (2012) Ground-based network of ndvi measurements for tracking
334 temporal dynamics of canopy structure and vegetation phenology in different biomes. *Remote Sensing of
335 Environment* **123**, 234–245.
- 336 Taschler, D., Beikircher, B. & Neuner, G. (2004) Frost resistance and ice nucleation in leaves of five woody
337 timberline species measured in situ during shoot expansion. *Tree Physiology* **24**, 331–337.
- 338 USA-NPN (2016) USA National Phenology Network Extended Spring Indices.
- 339 Vihera-aarnio, A., Hakkinen, R. & Junntila, O. (2006) Critical night length for bud set and its variation in
340 two photoperiodic ecotypes of *Betula pendula*. *Tree Physiology* **26**, 1013–1018.
- 341 Vitasse, Y., Lenz, A., Hoch, G. & Körner, C. (2014a) Earlier leaf-out rather than difference in freezing
342 resistance puts juvenile trees at greater risk of damage than adult trees. *Journal of Ecology* **102**, 981–988.
- 343 Vitasse, Y., Lenz, A. & Körner, C. (2014b) The interaction between freezing tolerance and phenology in
344 temperate deciduous trees. *Frontiers in plant science* **5**, 541.
- 345 White, M.A., De Beurs, K.M., Didan, K., Inouye, D.W., Richardson, A.D., Jensen, O.P., O'Keefe, J., Zhang,
346 G., Nemani, R.R., Van Leeuwen, W.J.D. & Al., E. (2009) Intercomparison, interpretation, and assessment
347 of spring phenology in north america estimated from remote sensing for 1982-2006. *Global Change Biology*
348 **15**, 2335–2359.
- 349 Xin, Q. (2016) A risk-benefit model to simulate vegetation spring onset in response to multi-decadal climate
350 variability: Theoretical basis and applications from the field to the Northern Hemisphere. *Agriculture and
351 Forest Meteorology* pp. 139–163.
- 352 Yu, H., Luedeling, E. & Xu, J. (2010) Winter and spring warming result in delayed spring phenology on the
353 Tibetan Plateau. *Proceedings of the National Academy of Sciences of the United States of America* **107**,
354 22151–6.
- 355 Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to constrain climate-
356 driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123.

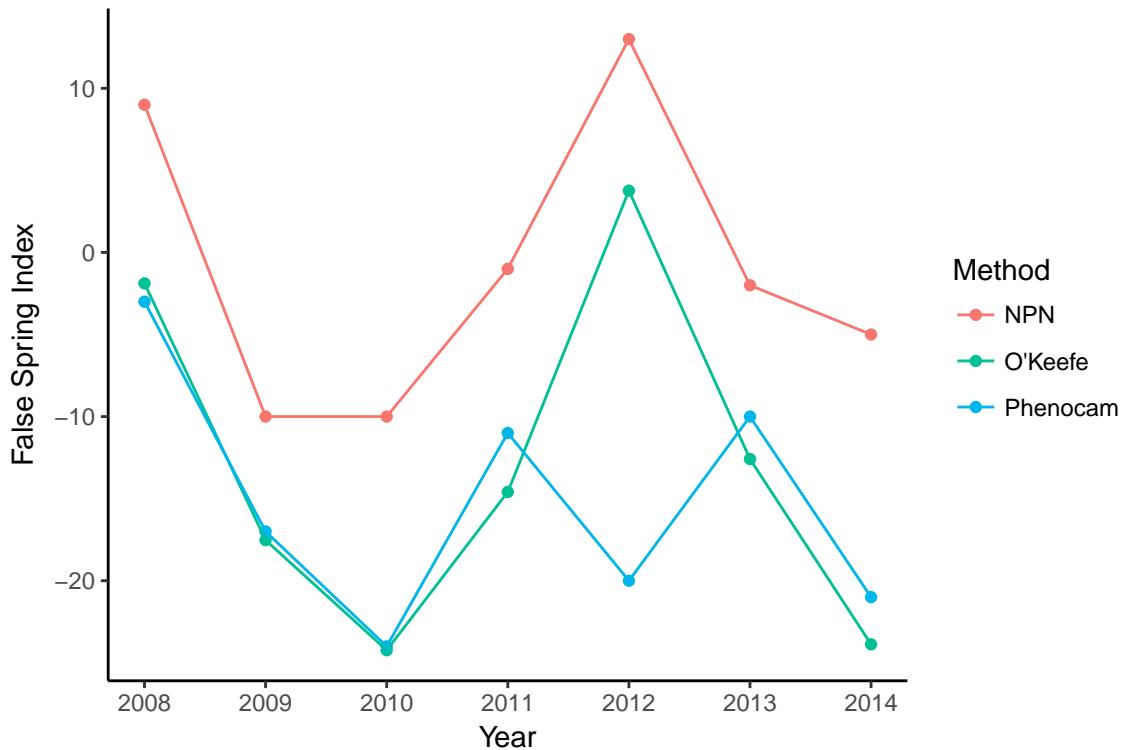


Figure 1: A scatterplot indicating FSI values from 2008 to 2014 for each methodology used in this study. To calculate spring onset, we used the USA-NPN Extended Spring Index tool for the USA-NPN FSI values, which are in red (USA-NPN, 2016), long-term ground observational data for the observed FSI values,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

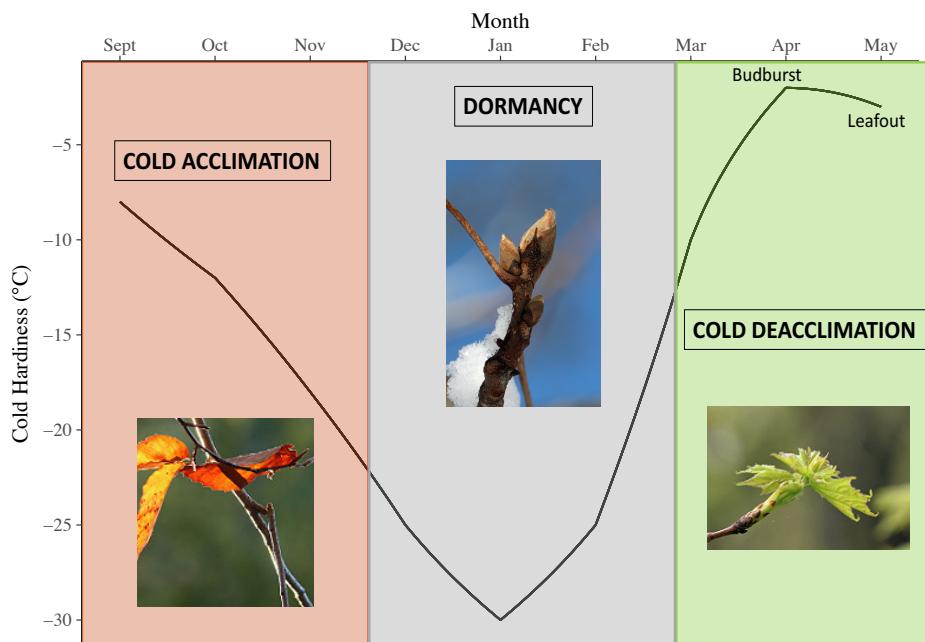
Box 1:

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

Cold Hardiness: Ability to resist injury to low temperatures

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

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



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

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

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

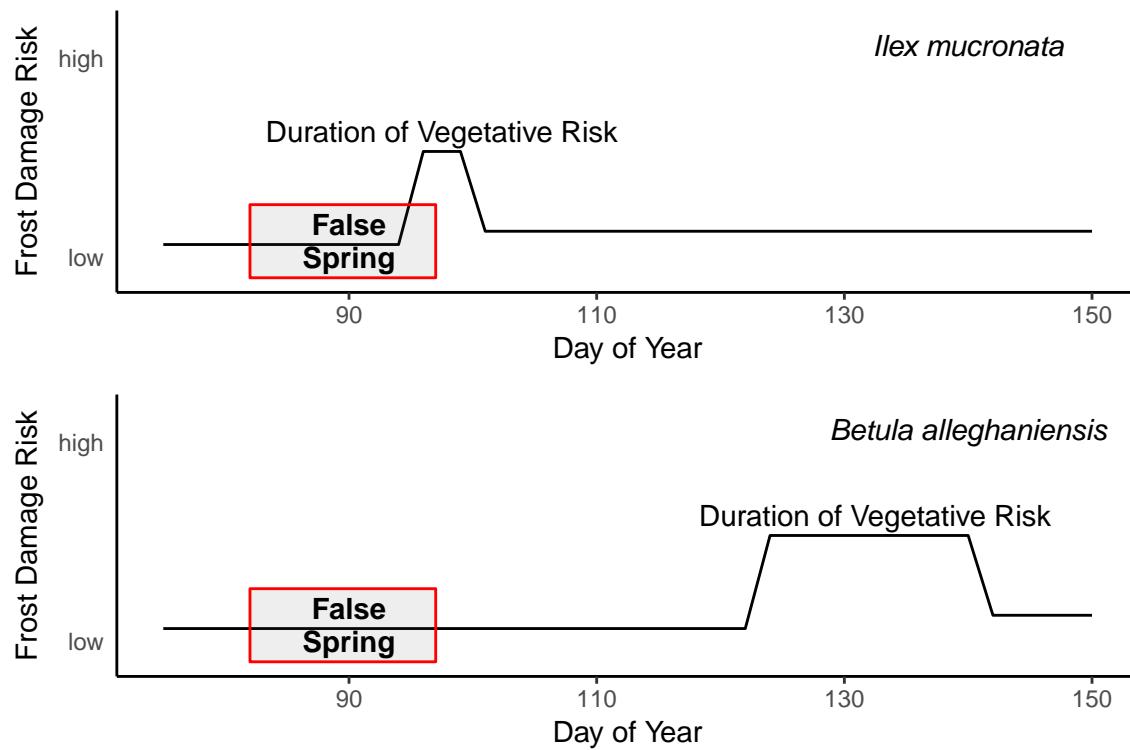


Figure 2: A figure showing the differences in spring phenology and false spring risk across two species: *Ilex mucronata* (L.) and *Betula alleghaniensis* (Marsh.). We mapped a possible false spring event based on historic weather data and compared it to the observational data collected at Harvard Forest (O'Keefe, 2014). In this scenario, the *Ilex mucronata* would be exposed to a false spring event, whereas the *Betula alleghaniensis* would avoid it entirely.

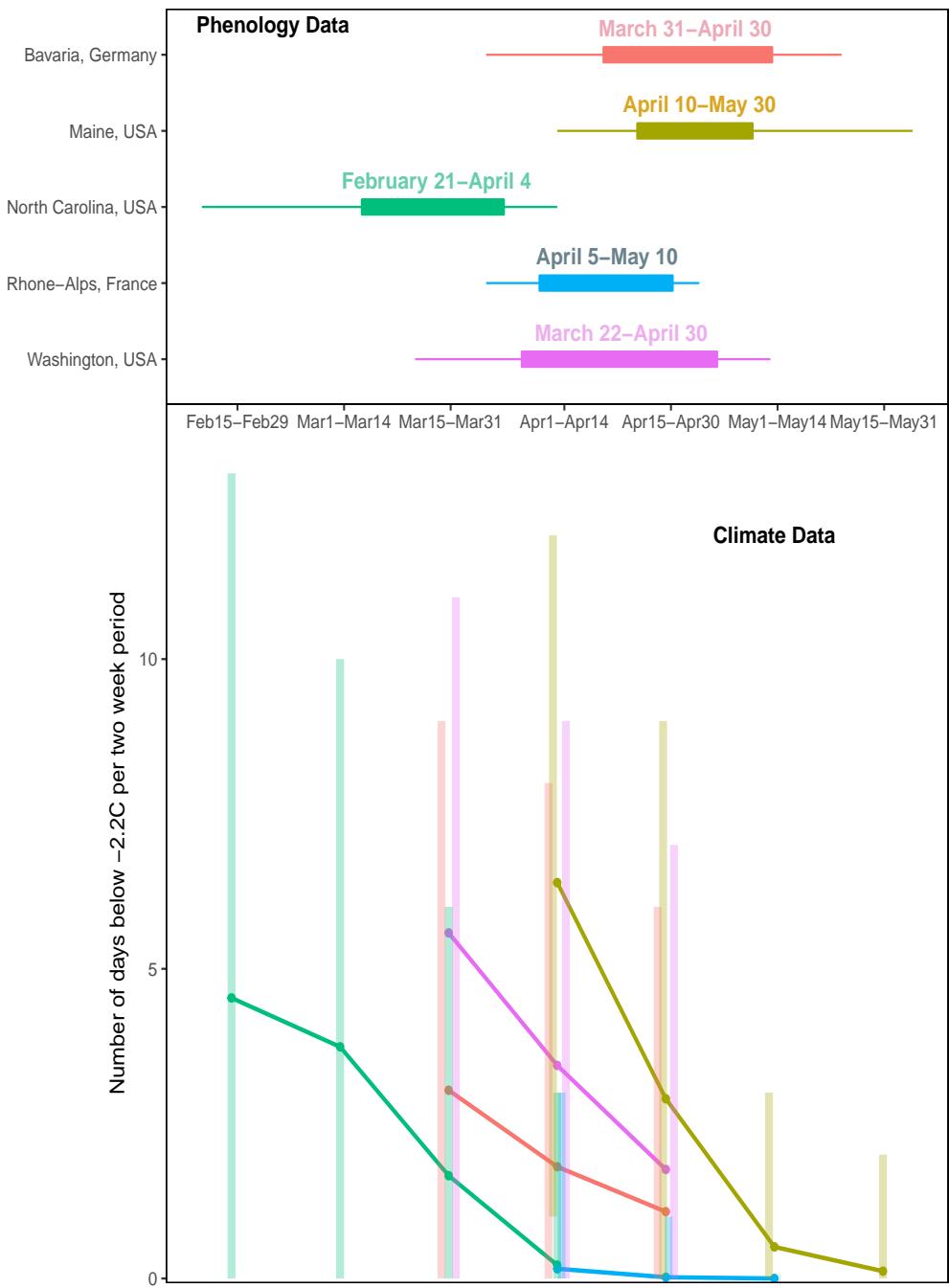


Figure 3: False spring risk can vary dramatically across regions. Here we show the period when plants are most at risk to tissue loss – between budburst and leafout (upper, lines represent the range with the thicker line representing the interquartile range) and the variation in the number of freeze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

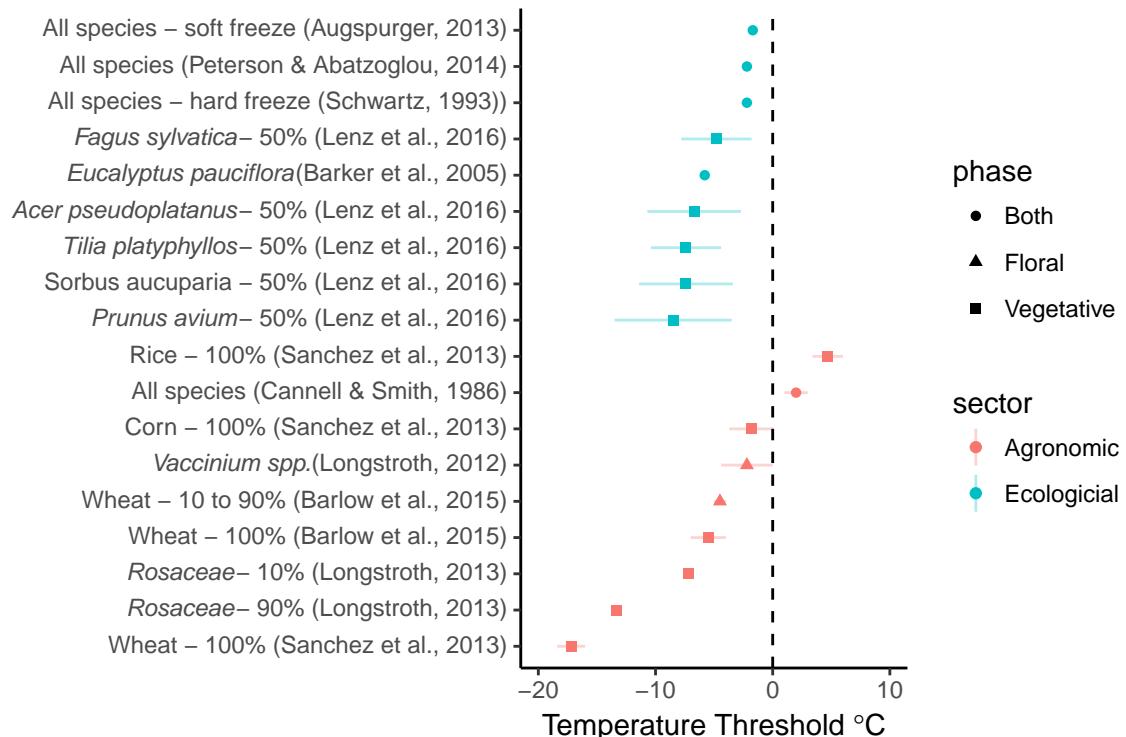


Figure 4: A comparison of damaging spring freezing temperature thresholds across ecological and agronomic studies. Each study is listed on the y axis along with the taxonomic group of focus. Next to the species name is the freezing definition used within that study (e.g. 100% is 100% lethality). Each point is the best estimate recorded for the temperature threshold with standard deviation if indicated in the study. The shape of the point represents the phenophases of interest and the colors indicate the type of study (i.e. agronomic or ecological).

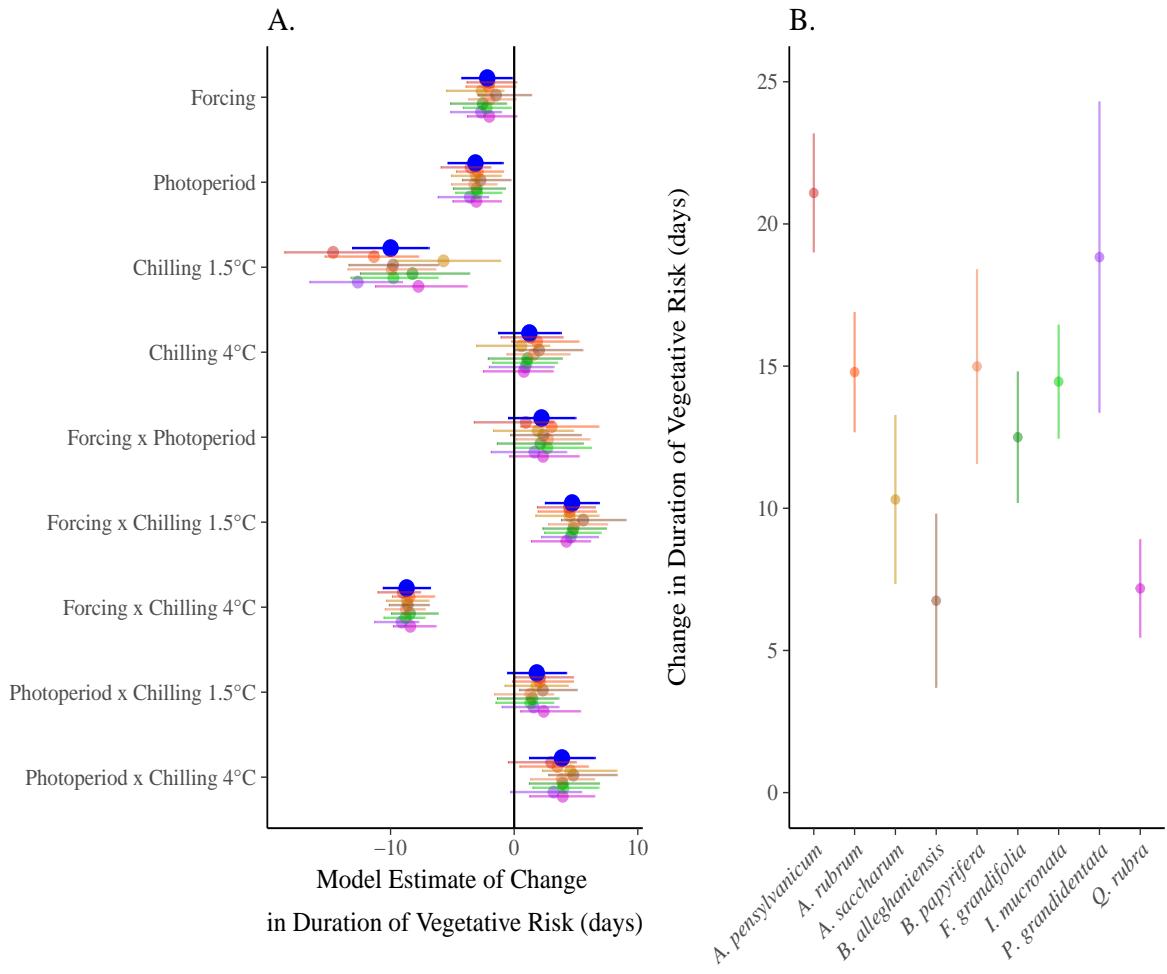


Figure 5: Results from the growth chamber experiment. (A) A plot of the model parameter estimates on the duration of vegetative risk. Spring forcing temperatures had the largest effect on the rate of leafout, with photoperiod also being a critical factor. Thus, while greater forcing or longer photoperiods alone will shorten the duration of vegetative risk by 10 and 9 days respectively, their combined effect would be 14 days due to a 5 day delay through their interaction ($10 + 9 - 5 = 14$). Data was collected from a growth chamber experiment where one treatment had no additional overwinter chilling, low spring forcing temperatures, and shorter spring daylengths and the other had additional overwinter chilling, high spring forcing temperatures, and longer spring daylengths. (B) A comparison of the durations of vegetative risk across two treatments for each species collected for the experiment. Species along the x-axis are ordered by day of budburst. The standard error is represented by the bars around each point.