## 1 Regional Risk Outline

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## Abstract

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Late spring freezing events, also known as false springs, can be ecologically damaging to many temperate and boreael plants. A number of studies have found evidence that false springs have become more frequent with climate change, while others have found the reverse. These diverging results could be due to the location of the study and/or to the differing uses of regional and climatic effects linked to false spring risk, which have shifted with climate change. To date, no other study has compared multiple regional and climatic factors at once. Using PEP725 leafout data for six tree species across 11,648 sites in Europe, we assessed the effects of the North Atlantic Oscillation (NAO), mean spring temperature, elevation and distance from the coast to determine which factors were the strongest predictors of false spring risk and how these predictors shifted with climate change. Species varied in their risk of false springs but, overall, false spring risk increased with climate change for all species. Mean spring temperature and distance from the coast were the strongest predictors of false spring risk, with higher mean spring temperatures having fewer false springs and sites further from the coast experiencing more false springs. Our results suggest that considering multiple regional and climatic factors is essential for predicting false spring risk — especially as these events are increasing with climate change.

## 26 Introduction

Temperate tree and shrub species are at risk of damage from late spring freezing events, also known as false 27 springs, and this risk may shift with climate change. With earlier springs due to warming, the growing season is lengthening across many regions in the northern hemisphere (Chen et al., 2005; Kukal & Irmak, 2018; Liu et al., 2006), but late spring frosts still pose a threat in many of these regions (Wypych et al., 2016b). Spring onset is advancing, with temperate tree and shrub species initiating leafout 4-6 days on average earlier per 31 °C of warming (IPCC, 2015; Wolkovich et al., 2012). Last spring freeze dates are not predicted to advance at the same rate (Inouye, 2008; Labe et al., 2016; Martin et al., 2010; Sgubin et al., 2018), potentially amplifying 33 the effects of false spring events in these regions. In Germany, for example, the last freeze date has advanced by 2.6 days per decade since 1955 (Zohner et al., 2016) but budburst is advancing around twice as fast. Major false spring events have been recorded in recent years and have found it can take 16-38 days for trees to refoliate (Augspurger, 2009, 2013; Gu et al., 2008; Menzel et al., 2015), which can detrimentally affect crucial processes such as carbon updake and nutrient cycling (Hufkens et al., 2012; Klosterman et al., 2018; Richardson et al., 2013). Episodic spring frosts are one of the largest limiting factors in species range limits and have shaped plant life history strategies (Kollas et al., 2014). Temperate plants are exposed to freezing temperatures numerous times throughout the year, however, individuals are most at risk to damage from spring frosts, when frost tolerance is lowest (Sakai & Larcher, 1987). Plants can avoid damage by carefully timing budburst each year. Indeed, trees and shrubs in temperate regions optimize growth and minimize frost risk by using a complex mix of cues to initiate budburst: low winter temperatures, warm spring temperatures, and increasing spring daylengths. With climate change advancing, this interaction of cues may shift spring phenologies both across and within 46 species, making some species less – or more — vulnerable to false springs than before. Early-leafout species may be especially at risk as warm spring temperatures increase. Plants are least frost resistant during certain phenophases, especially early season phases such as budburst and flowering. Freeze damage during flowering or fruiting damage has fewer long-term consequences than 50 damage to photosynthetic material, therefore we will focus on budburst and leafout, when frost tolerance is lowest. Frost tolerance greatly diminishes once individuals exit the dormancy phase (i.e. processes leading 52 to budburst) through full leaf expansion (Lenz et al., 2016; Vitasse et al., 2014). Individuals that initiate budburst and have not fully leafed out before the last spring freeze are at risk of leaf tissue loss, damage to the xylem, and slowed canopy development (Gu et al., 2008; Hufkens et al., 2012). Thus, It is important

to consider the length of time between budburst and leafout — when individuals are most at risk to spring freeze damage (Lenz *et al.*, 2016) — in order to better predict false spring risk. We will refer to this timing between budburst and leafout as the duration of vegetative risk (Rethinking).

Given its importance to plant performance and survival, understanding how false spring is shifting with 59 climate change has been a major topic in the literature. There is large debate over whether or not spring freeze damage will increase (Augspurger, 2013; Hänninen, 1991; Labe et al., 2016), remain the same (Scheifinger 61 et al., 2003) or even decrease (Kramer, 1994; Vitra et al., 2017) with climate change and there is also great 62 variation within studies. Some research suggests false spring incidence has already begun to decline in many regions (i.e. across parts of North America and Asia), however the prevalence of spring frosts has consistently increased across Europe since 1982 (Liu et al., 2018). Furthermore, recent studies have demonstrated site effects may be more closely related to false spring risk: whether via altitudinal variation (Ma et al., 2018; Vitra et al., 2017) or distance from the coast (Ma et al., 2018; Wypych et al., 2016b). By better understanding these regional climatic implications and which factors are most crucial for predicting risk, we may be able to determine which regions may be at risk currently and which regions may become more at risk in the future. The majority of false spring studies assess the effects of one predictor (e.g. temperature, elevation or distance 70 from the coast) on false spring prevalence but most fail to incorporate multiple effects. Our primary aim is to investigate the known regional factors on false spring risk and compare the effect of them and their interaction with climate change. The key regional factors we identify for this study are: mean spring temperature, elevation and distance from the coast. Given our focus on Europe, we additionally examine the North Atlantic Oscillation (NAO) index, which is tied to winter and spring circulation across Europe. More positive NAO phases tend to result in higher than average winter and spring temperatures. With climate-change induced shifts, higher NAO phases has correlated to even earlier budburst dates since the late 1980s in some regions (Chmielewski & Rötzer, 2001), however it is unclear if more positive NAO phases also translates to more false springs.

By refining and identifying budburst and climate trends in recent years, we could improve future projections in false springs. For this purpose, we assessed the number of false springs that occured across 11,648 sites around Europe, spanning altitudinal and coastal gradients, using observed phenological data (754,786 observations) for six temperate, deciduous trees and combined that with daily gridded climate data for each site that extended from 1951-2016. In this study, a false spring was tallied when temperatures fell below -2.2° (Schwartz, 1993) between budburst and leafout (CITE Rethinking here?). Since the primary aim of the study

is to predict false spring incidence in a changing climate, we split our data to before and after 1983 to capture reported temporal shifts in temperature trends (Kharouba *et al.*, 2018; Stocker *et al.*, 2013). We predicted that: (1) Earlier budburst species would experience more false springs, especially after 1983, (2) there would be different regional effects (i.e. mean spring temperature, NAO index, elevation, distance from the coast) on false spring incidence and those trends would shift when coupled with the effects of climate change.

## $_{\scriptscriptstyle{91}}$ Methods

#### Phenological Data and Calculating Vegetative Risk

We obtained phenological data from the Pan European Phenology network (PEP725, www.pep725.edu),
which provides open access phenology records across Europe (Templ et al., 2018). Since plants are most
susceptible to damage from frost between budburst and full leafout, we selected only leafout data (i.e., in
Meier, 2001, BBCH 11, which is defined as the point of leaf unfolding and the first visible leaf stalk) from
the PEP725 dataset. The species used in the study were Aesculus hippocastanum Poir., Alnus glutinosa
(L.) Gaertn., Betula pendula Roth., Fagus sylvatica Ehrh., Fraxinus excelsior L., Quercus robur L. Selection
criteria for the species were as follows: (1) to be temperate, deciduous species that were not cultivars or
used for crops, (2) there were at least 90,000 observations of BBCH 11 (leafout), (3) to represent over half
of the total number of sites available (11,684), and (4) there were observations for at least 65 out of the 66
years of the study (1951-2016) (Table S1). We then subtracted 12 days from the leafout date to establish a
standardized estimate for day of budburst (Donnelly et al., 2017).

#### 04 Climate Data

We collected daily gridded climate data from the European Climate Assessment & Dataset (ECA&D) and used the E-OBS 0.25 degree regular latitude-longitude grid from version 16. We used the daily minimum temperature dataset to determine if a false spring occurred. False springs in this study were defined as temperatures at or below -2.2°C (Schwartz, 1993) during the duration of vegetative risk. In order to capture regional climatic effects we calculated the mean spring temperature by using the daily mean temperature from March 1 through May 31. Mean spring temperature was calculated – likely after chilling was accummulated – in an attempt to incorporate the general effects of spring forcing temperatures in our Bayesian model and

to compare differences in spring across sites (Basler & Körner, 2012; Körner et al., 2016). We collected NAOindex data from the KNMI Climate Explorer CPC daily NAO time series and selected the NAO indices from
November until April to best capture the effects of NAO on budburst for each region and then took the mean
NAO index during these months (KNMI, 2018). Since the primary aim of the study is to predict false spring
incidence in a changing climate, we split the data: before temperature trends increased (1951-1983) and after
trends increased (1984-2016, Kharouba et al., 2018; Stocker et al., 2013) to represent climate change.

#### 118 Data Analysis

A false spring was determined if temperatures fell below -2.2°C at least once between budburst and leafout.

We scaled all of the predictors and used a z-score following the binary predictor approach in order to best
compare the effects of each climate variable to each other (Gelman & Hill, 2006). We used a space parameter, rather than a more traditional latitude parameter, to adjust for spatial autocorrelation issues using a
minimization of Moran's *I* of the residuals (David *et al.*, 2017) (Figure S1). We then took the calculated
eigenvectors determined from the MIR approach and regressed these against the number of false springs for
each datapoint to establish a spatial parameter (space).

We used a Bayesian hierarchical model approach to analyze our data to best estimate the number of false springs across-species levels. We fit a bernoulli distribution model using mean spring temperature, NAO, elevation, distance from the coast, space, and climate change as predictors and all two-way interactions (fixed effects) and species as two-way interactions to simulate modeled groups on the main effects. The Bayesian model was fit using the brms package (Bürkner, Paul-Christian, 2017), version 2.3.1, in R (R Development Core Team, 2017), version 3.3.1, and was written as follows:

$$y_{i} \sim N(\alpha_{(i)}) + \beta_{NAO_{(i)}} + \beta_{MeanSpringTemp_{(i)}} + \beta_{Elevation_{(i)}} + \beta_{DistanceCoast_{(i)}} + \beta_{Space_{(i)}}$$
 
$$+ \beta_{ClimateChange_{(i)}} + \beta_{NAO \times Species_{(i)}} + \beta_{MeanSpringTemp \times Species_{(i)}} + \beta_{Elevation \times Species_{(i)}}$$
 
$$+ \beta_{DistanceCoast \times Species_{(i)}} + \beta_{Space \times Species_{(i)}} + \beta_{ClimateChange \times Species_{(i)}}$$
 
$$+ \beta_{NAO \times ClimateChange_{(i)}} + \beta_{MeanSpringTemp \times ClimateChange_{(i)}} + \beta_{Elevation \times ClimateChange_{(i)}}$$
 
$$+ \beta_{DistanceCoast \times ClimateChange_{(i)}} + \beta_{Space \times ClimateChange_{(i)}} + \sigma_{sp_{(i)}}$$

We ran two chains, each with 2,500 warm-up iterations and 4,000 sampling iterations for a total of 8,000 posterior samples for each predictor. We evaluated our model performance on  $\hat{R}$  values that were close to

one and assessed chain convergence and posterior predictive checks (Gelman & Hill, 2006).

## Testing the rate of budburst on false spring incidence

The definition of a false spring has been established to be freezing temperatures of -2.2°C (Schwartz, 1993) 130 after budburst but plants are most susceptible to damage during the duration of vegetative risk (Augspurger, 2013; Lenz et al., 2016). Different species have different durations of vegetative risk, which is also shifting with climate change (Cleland et al., 2006; Fu et al., 2015; Xin, 2016). We tested our original model by 133 making a different — more biologically relevant — model with different durations of vegetative risk for each species. Due to insufficient budburst data from PEP725, we calculated budburst by subtracting 11 days 135 from leafout for Aesculus hippocastanum and Betula pendula, 12 days for Alnus glutinosa, 5 days for Faqus sylvatica, and 7 days for both Frazinus excelsior and Quercus robur based on growth chamber experiment 137 data from phylogenetically related species (Buerki et al., 2010; Wang et al., 2016; Hipp et al., 2017; Flynn & 138 Wolkovich, 2018). 139

#### Testing the temperature threshold on false spring incidence

Plants have varying temperature thresholds in frost tolerance during the duration of vegetative risk (Lenz et al., 2013) (AND Rethinking). We tested our original model by changing the definition of a freezing temperature from -2.2°C (Schwartz, 1993) to -5°C (Lenz et al., 2013; Sakai & Larcher, 1987) to examine variation in the false spring defintion.

## 5 Discussion

Climate change has increased false spring risk by 0.35 across our data. But this average hides many important complexities as our models show that species and climate combine to predict false spring. Species are really different, however all species are at risk of false springs. Fraxinus excelsior had the lowest number of false springs across our data and generally had the latest budburst dates but, regardless of budburst time, all species had a heightened risk of damage after 1983. Mean spring temperature, distance from the coast and climate change were the strongest predictors for false springs, however, NAO and elevation also affected the risk of false spring incidence. These effects have changed — with significantly fewer false springs with higher

NAO indices and more false springs with warmer mean spring temperature sites — since the major onset of climate change.

#### Species differences

There is robust evidence for advancing budburst with climate change (Cleland et al., 2007; IPCC, 2015; Wolkovich et al., 2012) and some studies indicate earlier budburst species are more at risk of false spring damage (Ma et al., 2018). After 1983, all of our species initiated budburst earlier in the spring and there was a increase overall in false spring risk. Additionally, some of the early bursting species were more susceptible to false spring risk (i.e. Betula pendula and Aesuculus hippocastanum) but all species were susceptible frost damage. Thus, simply looking at budburst time is not a sufficient proxy to forecast false spring risk and other climatic and regional factors must be evaluated.

# 163 Climatic and regional effects

Past studies using single predictors for false spring events has lead to contradicting predictions in future false spring risk. Through our holistic approach, we were able to assess the myriad of climatic and regional effects on false spring risk – and how the magnitude of those effects compare to one another – by incorporating the space parameter, thus erasing the collinearity issues of certain effects (i.e., elevation and distance from the coast). This was an essential step in forecasting false spring risk.

Our study supports findings from previous studies: higher elevations tend to experience more false springs (Vitra et al., 2017) and sites that are generally warmer have lower risks of false springs (Wypych et al., 2016a) and that risk is increasing with climate change (Liu et al., 2018). However, we also discovered that effects of elevation and distance from the coast cannot be assumed to be the same, which contradicts previous studies (Ma et al., 2018). Our results suggest that sites further from the coast had a higher risk of false springs than sites at higher elevations and, with shifts in climate, sites further from the coast experienced fewer false springs whereas there was little change for sites at higher elevations.

Overall, mean spring temperature and distance from the coast are the best predictors for false spring risk: sites
that are warmer generally have fewer false springs and sites that are at further from the coast generally have
more false springs. Across our study sites, budburst initiated earlier after 1983 due to warming temperatures.
False spring risk is increasing across our study species, even with increasing minimum temperatures during

the duration of vegetative risk. Recent studies have also found that sites experiencing warming with climate change are experiencing more false springs, especially in Europe (Liu *et al.*, 2018). This may suggest a shifting relationship between spring warming and budburst. Plants at certain regions could be responding more strongly to increased spring warming with climate change and, thus, are at an increased risk of exposure to false springs.

#### Forecasting future false springs

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Our study fails to assess the intensity or severity of the false spring events. It is possible that with increasing false spring risk, the events after 1983 could be lasting longer or could at be at even harsher temperatures. 187 Additionally, there is sufficient evidence that different species are able to tolerate different minimum temperature extremes (Körner et al., 2016; Lenz et al., 2013; Zhuo et al., 2018). Some species or individuals may be 189 less tolerant of low temperatures (i.e., are damaged from higher temperatures than -2.2°C), whereas other 190 species or individuals may be able to tolerate temperatures as low as -8.5°C (Lenz et al., 2016). Thus, species 191 that are typically found in low risk sites but have early budburst (i.e. Alnus qlutinosa) may be less tolerant 192 of low temperatures and they may be at sites that are experiencing an increased risk with climate change. 193 For this reason, models should ideally incorporate species-specific temperature thresholds to best capture the 194 shifts in false spring risk over time and space.

Biological spring is advancing with climate change-induced shifts but few studies have assessed the effects of climate change on the duration of vegetative risk: is leafout advancing at the same rate or is the duration of vegetative risk lengthening? For false spring studies, it is important to consider the effects of climate change on both budburst and leafout, the timing when individuals are most at risk to spring freeze damage (Lenz et al., 2016) (AND RETHINKING). With less chilling, shorter photoperiods but warmer spring temperatures, the duration of vegetative risk could change, thus altering the predicted outcome of false spring risk. And with changing rates of budburst, the regional and climatic effects will impact the number of false springs an individual experiences differently. Incorporating observed durations of vegetative risk across sites, years and species would greatly enhance model predictions.

Our integrated approach may help direct future modelling advancements in false spring research. We show
here the importance of using all regional factors in predicting false spring risk and how that risk varies across
species. By using phenology data to provide a better estimate for budburst and leafout, predictions for false
springs will be more accurate. We also show that choosing the appropriate temperature threshold is more

important than including accurate durations of vegetative risk. Range studies and management regimes will
benefit from the integration of false spring risk in a changing climate.

# Conclusion

False spring risk is influenced by numerous climatic and regional factors and all of these factors must be 212 incorporated into models to best predict spatiotemporal shifts in false springs. Some factors are better at 213 predicting risk than others (i.e., mean spring temperature and distance from the coast), however it is essential 214 to additionally assess the effects of NAO and elevation, which contribute to an individual's risk of false spring. 215 Individuals that initiate budburst earlier in the season aren't necessarily exposed to more false springs, thus, investigating site effects is a more consistent proxy for false spring risk than budburst time. Overall, the 217 frequency of false spring events is increasing with climate change so it is essential to additionally understand how the intensity and duration of these events are shifting. Furthermore, incorporating both budburst and 219 leafout data as well as species-specific temperature thresholds will advance our knowledge of false spring risk in a changing climate. Our results bolster the argument for heightened risk of false springs with climate 221 change and suggest complex responses to warming in the future, which could in turn, have escalating impacts on plant community dynamics.

## 224 References

- Augspurger CK (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. Functional Ecology, 23, 1031–1039. doi:10.1111/j.1365-2435.2009.01587.x.
- Augspurger CK (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years:

  Spring damage risk is increasing. *Ecology*, **94**, 41–50. doi:10.1890/12-0200.1.
- Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. Agricultural and Forest Meteorology, 165, 73-81. doi:10.1016/j.agrformet.2012.06.001. URL http://dx.doi.org/10.
  1016/j.agrformet.2012.06.001.
- Buerki S, Lowry II P, Alvarez N, Razafimandimbison S, Kupfer P, Callmander M (2010) Phylogeny and circumscription of Sapindaceae revisited: Molecular sequence data, morphology and biogeography support

- recognition of a new family, Xanthoceraceae. *Plant Ecology and Evolution*, **143**, 148–159. doi:10.5091/plecevo.2010.437.
- Bürkner, Paul-Christian (2017) brms: An R Package for Bayesia Multilevel Models. Journal of Statistical
   Software, 80, 1–28.
- Chen X, Hu B, Yu R (2005) Spatial and temporal variation of phenological growing season and climate change impacts in temperate eastern China. *Global Change Biology*, **11**, 1118–1130. doi:10.1111/j.1365-2486.2005.00974.x.
- Chmielewski FM, Rötzer T (2001) Response of tree phenology to climate change across Europe. Agricultural
  and Forest Meteorology, 108, 101 112. doi:https://doi.org/10.1016/S0168-1923(01)00233-7. URL http:
  //www.sciencedirect.com/science/article/pii/S0168192301002337.
- Cleland E, Chiariello N, Loarie S, Mooney H, Field C (2006) Diverse responses of phenology to global changes
   in a grassland ecosystem. PNAS, 103, 13740–13744.
- <sup>246</sup> Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to <sup>247</sup> global change. *Trends in Ecology and Evolution*, **22**, 357–365. doi:10.1016/j.tree.2007.04.003.
- David B, Thomas D, Stéphane D, Jason V (2017) Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography*, **0**. doi:10.1111/ecog.03380. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/ecog.03380.
- Donnelly A, Yu R, Caffarra A, et al. (2017) Interspecific and interannual variation in the duration of spring
  phenophases in a northern mixed forest. Agricultural and Forest Meteorology, 243, 55–67.
- Flynn DFB, Wolkovich EM (2018) Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*. doi:10.1111/nph.15232. URL http://dx.doi.org/10.

  1111/nph.15232.
- Fu YH, Piao S, Vitasse Y, et al. (2015) Increased heat requirement for leaf flushing in temperate woody species over 1980-2012: effects of chilling, precipitation and insolation. Global Change Biology, 21, 2687–2697. doi:10.1111/gcb.12863. URL http://dx.doi.org/10.1111/gcb.12863.
- Gelman A, Hill J (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge university press.

- Gu L, Hanson PJ, Post WM, et al. (2008) The 2007 Eastern US spring freeze: Increased cold damage in a warming world. BioScience, 58, 253. doi:10.1641/B580311.
- Hänninen H (1991) Does climatic warming increase the risk of frost damage in northern trees? Plant, Cell
- & Environment, 14, 449-454. doi:10.1111/j.1365-3040.1991.tb01514.x. URL https://onlinelibrary.
- wiley.com/doi/abs/10.1111/j.1365-3040.1991.tb01514.x.
- Hipp A, S Manos P, González-Rodríguez A, et al. (2017) Sympatric parallel diversification of major oak clades
- in the Americas and the origins of Mexican species diversity. New Phytologist, 217. doi:10.1111/nph.14773.
- Hufkens K, Friedl MA, Keenan TF, Sonnentag O, Bailey A, O'Keefe J, Richardson AD (2012) Ecological
- impacts of a widespread frost event following early spring leaf-out. Global Change Biology, 18, 2365–2377.
- doi:10.1111/j.1365-2486.2012.02712.x.
- 271 Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane
- wildflowers. *Ecology*, **89**, 353–362.
- <sup>273</sup> IPCC (2015) Climate change 2014: mitigation of climate change, vol. 3. Cambridge University Press.
- Kharouba HM, Ehrlén J, Gelman A, Bolmgren K, Allen JM, Travers SE, Wolkovich EM (2018) Global shifts in
- the phenological synchrony of species interactions over recent decades. Proceedings of the National Academy
- of Sciences, 115, 5211-5216. doi:10.1073/pnas.1714511115. URL http://www.pnas.org/content/115/
- 20/5211.
- <sup>278</sup> Klosterman S, Hufkens K, Richardson AD (2018) Later springs green-up faster: the relation between onset
- and completion of green-up in deciduous forests of North America. International Journal of Biometeorology.
- doi:10.1007/s00484-018-1564-9.
- 281 KNMI (2018) Daily CPC NAO data. URL https://climexp.knmi.nl/getindices.cgi?WMO=NCEPData/
- cpc\_nao\_daily&STATION=NAO&TYPE=i&id=someone@somewhere&NPERYEAR=366.
- Kollas C, Körner C, Randin CF (2014) Spring frost and growing season length co-control the cold range
- limits of broad-leaved trees. Journal of Biogeography, 41, 773–783. doi:10.1111/jbi.12238.
- <sup>285</sup> Körner C, Basler D, Hoch G, et al. (2016) Where, why and how? Explaining the low-temperature range
- limits of temperate tree species. Journal of Ecology, 104, 1076–1088. doi:10.1111/1365-2745.12574. URL
- 287 http://dx.doi.org/10.1111/1365-2745.12574.

- 288 Kramer K (1994) A modelling analysis of the effects of climatic warming on the probability of spring frost
- damage to tree species in the netherlands and germany. Plant, Cell & Environment, 17, 367–377. doi:10.
- 290 1111/j.1365-3040.1994.tb00305.x. URL https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-
- <sup>291</sup> 3040.1994.tb00305.x.
- <sup>292</sup> Kukal MS, Irmak S (2018) U.S. Agro-Climate in 20th century: growing degree days, first and last frost,
- growing season length, and impacts on crop yields. Scientific Reports, 8. doi:10.1038/s41598-018-25212-2.
- Labe Z, Ault T, Zurita-Milla R (2016) Identifying anomalously early spring onsets in the CESM large ensemble
- project. Climate Dynamics, 48, 3949–3966. doi:10.1007/s00382-016-3313-2.
- <sup>296</sup> Lenz A, Hoch G, Körner C, Vitasse Y (2016) Convergence of leaf-out towards minimum risk of freezing
- damage in temperate trees. Functional Ecology, **30**, 1–11. doi:10.1111/1365-2435.12623.
- <sup>298</sup> Lenz A, Hoch G, Vitasse Y, Körner C (2013) European deciduous trees exhibit similar safety margins against
- damage by spring freeze events along elevational gradients. New Phytologist, 200, 1166–1175. doi:10.1111/
- nph.12452.
- Liu Q, Piao S, Janssens IA, et al. (2018) Extension of the growing season increases vegetation exposure to
- frost. Nature Communications, 9. doi:10.1038/s41467-017-02690-y. URL http://dx.doi.org/10.1038/
- s41467-017-02690-y.
- Liu X, Yin Z, Shao X, Qin N (2006) Temporal trends and variability of daily maximum and minimum,
- extreme temperature events, and growing season length over the eastern and central Tibetan Plateau
- during 1961–2003. Journal of Geophysical Research: Atmospheres, 111. doi:10.1029/2005JD006915.
- Ma Q, Huang JG, Hänninen H, Berninger F (2018) Divergent trends in the risk of spring frost damage to
- trees in europe with recent warming. Global Change Biology, 0. doi:10.1111/gcb.14479. URL https:
- //onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14479.
- Martin M, Gavazov K, Körner C, Hattenschwiler S, Rixen C (2010) Reduced early growing season freezing
- resistance in alpine treeline plants under elevated atmospheric  $CO_2$ . Global Change Biology, 16, 1057–1070.
- doi:10.1111/j.1365-2486.2009.01987.x.
- Meier U (2001) Growth stages of mono-and dicotyledonous plants BBCH Monograph Edited by Uwe Meier
- Federal Biological Research Centre for Agriculture and Forestry. Agriculture, 12, 141—147 ST Geo-
- chemical study of the organic mat. doi:10.5073/bbch0515. URL http://pub.jki.bund.de/index.php/
- BBCH/article/view/515/464.

- Menzel A, Helm R, Zang C (2015) Patterns of late spring frost leaf damage and recovery in a European beech
- (Fagus sylvatica L.) stand in south-eastern Germany based on repeated digital photographs. Frontiers in
- Plant Science, 6, 110. doi:10.3389/fpls.2015.00110.
- 320 R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation
- for Statistical Computing, Vienna, Austria.
- 222 Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phe-
- nology, and phenological control of vegetation feedbacks to the climate system. Agricultural and Forest
- 324 Meteorology, **169**, 156 173. doi:https://doi.org/10.1016/j.agrformet.2012.09.012.
- Sakai A, Larcher W (1987) Frost Survival of Plants. Springer-Verlag.
- Scheifinger H, Menzel A, Koch E, Peter C (2003) Trends of spring time frost events and phenological dates
- in Central Europe. Theoretical and Applied Climatology, 74, 41–51. doi:10.1007/s00704-002-0704-6. URL
- http://dx.doi.org/10.1007/s00704-002-0704-6.
- Schwartz MD (1993) Assessing the onset of spring: A climatological perspective. Physical Geography, 14(6),
- <sub>330</sub> 536–550.
- 331 Sgubin G, Swingedouw D, Dayon G, de Cortázar-Atauri IG, Ollat N, Pagé C, van Leeuwen C (2018) The risk
- of tardive frost damage in French vineyards in a changing climate. Agricultural and Forest Meteorology,
- 250-251, 226 242. doi:https://doi.org/10.1016/j.agrformet.2017.12.253.
- 334 Stocker TF, Qin D, Plattner GK, et al. (2013) Climate Change 2013: The Physical Science Basis. Contribution
- of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,
- 336 1535 pp.
- Templ B, Koch E, Bolmgren K, et al. (2018) Pan European Phenological database (PEP725): a single point
- of access for European data. International Journal of Biometeorology, 62, 1109–1113. doi:10.1007/s00484-
- 339 018-1512-8. URL https://doi.org/10.1007/s00484-018-1512-8.
- <sup>340</sup> Vitasse Y, Lenz A, KÄÄűrner C (2014) The interaction between freezing tolerance and phenology in
- temperate deciduous trees. Frontiers in Plant Science, 5. doi:10.3389/fpls.2014.00541. URL http:
- 342 //dx.doi.org/10.3389/fpls.2014.00541.

- Vitra A, Lenz A, Vitasse Y (2017) Frost hardening and dehardening potential in temperate trees from winter
- to budburst. New Phytologist, **216**, 113–123. doi:10.1111/nph.14698. URL http://dx.doi.org/10.1111/
- nph.14698.
- Wang N, McAllister HA, Bartlett PR, Buggs RJA (2016) Molecular phylogeny and genome size evolution
- of the genus Betula (Betulaceae). Annals of Botany, 117, 1023–1035. doi:10.1093/aob/mcw048. URL
- 348 http://dx.doi.org/10.1093/aob/mcw048.
- Wolkovich EM, Cook BI, Allen JM, et al. (2012) Warming experiments underpredict plant phenological
- responses to climate change. Nature, 485, 18–21. doi:10.1038/nature11014.
- Wypych A, Sulikowska A, Ustrnul Z, Czekierda D (2016a) Variability of growing degree days in Poland
- in response to ongoing climate changes in Europe. International Journal of Biometeorology, 61, 49–59.
- doi:10.1007/s00484-016-1190-3. URL http://dx.doi.org/10.1007/s00484-016-1190-3.
- Wypych A, Ustrnul Z, Sulikowska A, Chmielewski FM, Bochenek B (2016b) Spatial and temporal variability of
- the frost-free season in Central Europe and its circulation background. *International Journal of Climatology*,
- 37, 3340–3352. doi:10.1002/joc.4920.
- <sup>357</sup> Xin Q (2016) A risk-benefit model to simulate vegetation spring onset in response to multi-decadal climate
- variability: Theoretical basis and applications from the field to the Northern Hemisphere. Agriculture and
- Forest Meteorology, **228-229**, 139–163.
- 250 Zhuo X, Zheng T, Zhang Z, et al. (2018) Genome-wide analysis of the NAC transcription factor gene family
- reveals differential expression patterns and cold-stress responses in the woody plant Prunus mume. Genes,
- 9. doi:10.3390/genes9100494. URL http://www.mdpi.com/2073-4425/9/10/494.
- Zohner CM, Benito BM, Svenning JC, Renner SS (2016) Day length unlikely to constrain climate-driven
- shifts in leaf-out times of northern woody plants. Nature Climate Change, 6, 1120–1123. doi:10.1038/
- nclimate 3138.

# Tables and Figures

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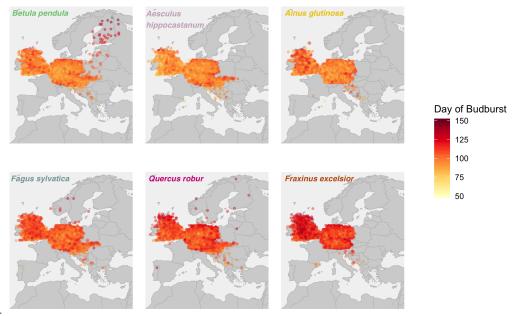


Figure 1: The average day of budburst is mapped by site for each species. Species are ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*. Earlier budburst dates are yellow and later budburst dates are in red.

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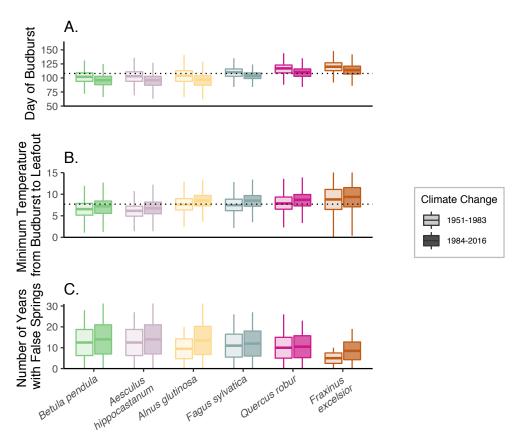


Figure 2: Budburst, minimum temperatures and false springs were compared before and after 1983 for each species. We plotted the day of budburst (A.) before and after 1983 for each species across all sites. We then compared the average minimum temperatures (B.) between budburst and leafout for all species across all sites. The bottom panel (C.), shows the total number of years there was a false spring before and after 1983 at each site across all species. Species are ordered by day of budburst.

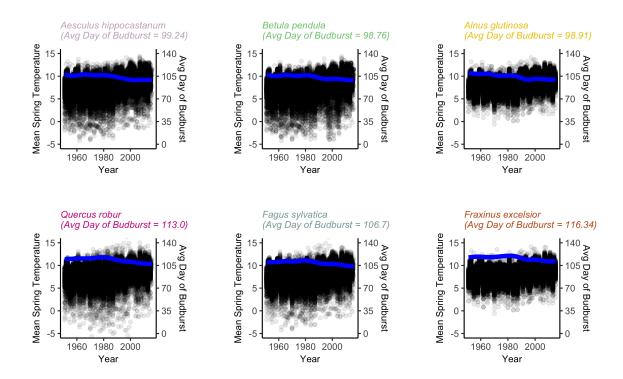


Figure 3: Mean spring temperatures are plotted for each site over time (from 1951-2016) for each species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula pendula* and the latest being *Fraxinus excelsior*.

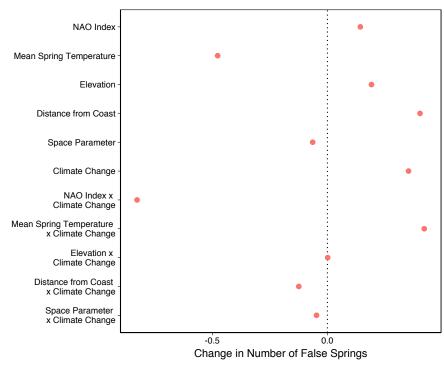


Figure 4: Model output with standardized durations of vegetative risk for each species. More positive parameter effects indicate an increased probability of a false spring whereas more negative effects suggest a lower probability of a false spring. Uncertainly intervals are at 50%. Parameter effects closer to zero have less of an effect on false springs.

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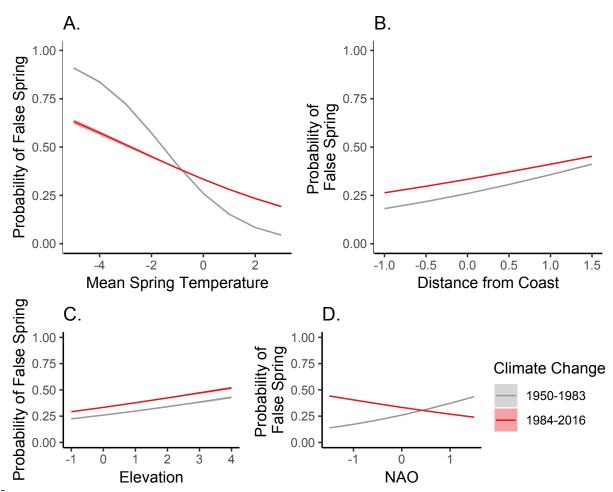


Figure 5: Plots showing the interaction effects on false spring risk for each predictor coupled with climate change. (A.) As mean spring temperature increases, there were fewer false springs but there were fewer false springs after 1983 at sites with lower mean spring temperatures. (B.) There were more false springs further from the coast and the rate of increase was consistent, however, there were fewer false springs in total after 1983. (C.) As elevation increased, false spring risk increased but the relationship remained consistent after 1983. (D.) As NAO indices increased, there were more false springs before 1983 but fewer after 1983. Since we found the z-score for each predictor, the x-axis for each panel does not reflect the raw data.

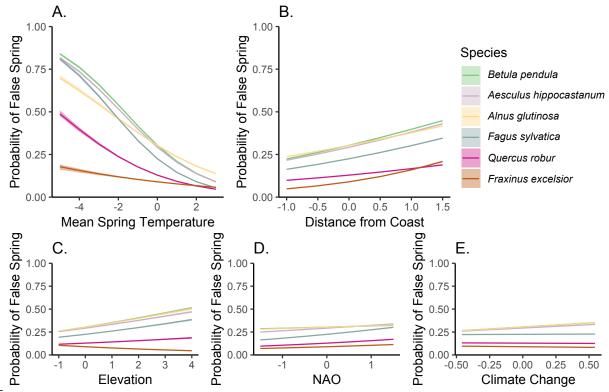


Figure 6: Plots showing the interaction effects of each predictor with species. (A.) As mean spring temperature increases, the probability of a false spring decreases for each species but *Fraxinus excelsior* always has the lowest risk of false spring. (B.) There's an increase in false spring risk for individuals further from the coast, especially for *Fraxinus excelsior*. (C.) The risk of a false spring increases with increasing elevation but the relationship is strongest for *Aesculus hippocastanum* and *Betula pendula*. (D.) There are slightly more false springs in years with higher NAOs, especially for *Fagus sylvatica*. (E.) There are more false springs after 1983, especially for *Aesculus hippocastanum* and *Betula pendula*. Since we found the z-score for each predictor, the x-axis for each panel does not reflect the raw data.