

Regional Risk Outline

Authors:

C. J. Chamberlain^{1,2}, B. I. Cook³, I. Morales Castilla^{1,4} & E. M. Wolkovich^{1,2}

Author affiliations:

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

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

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

⁴Edificio Ciencias, Campus Universitario 28805 Alcalá de Henares, Madrid, Spain

*Corresponding author: 248.953.0189; cchamberlain@g.harvard.edu

Abstract

Late spring freezing events, also known as false springs, can be ecologically damaging to many temperate and boreal 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.

Introduction

Temperate tree and shrub species are at risk of damage from late spring freezing events, also known as false 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; Kukul & 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 °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 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 refoamate (Augspurger, 2009, 2013; Gu *et al.*, 2008; Menzel *et al.*, 2015), which can detrimentally affect crucial processes such as carbon uptake 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 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 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 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 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 *et al.*, 2003) or even decrease (Kramer, 1994; Vitra *et al.*, 2017) with climate change and there is also great 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 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 occurred 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.

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).

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 accumulated – 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 NAO-index 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.

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, 2017), version 2.3.1, in R (R Development Core Team, 2017), version 3.3.1, and was written as follows:

$$\begin{aligned}
y_i \sim N(\alpha(i)) &+ \beta_{NAO(i)} + \beta_{MeanSpringTemp(i)} + \beta_{Elevation(i)} + \beta_{DistanceCoast(i)} + \beta_{Space(i)} \\
&+ \beta_{ClimateChange(i)} + \beta_{NAO \times Species(i)} + \beta_{MeanSpringTemp \times Species(i)} + \beta_{Elevation \times Species(i)} \\
&+ \beta_{DistanceCoast \times Species(i)} + \beta_{Space \times Species(i)} + \beta_{ClimateChange \times Species(i)} \\
&+ \beta_{NAO \times ClimateChange(i)} + \beta_{MeanSpringTemp \times ClimateChange(i)} + \beta_{Elevation \times ClimateChange(i)} \\
&+ \beta_{DistanceCoast \times ClimateChange(i)} + \beta_{Space \times ClimateChange(i)} + \sigma_{sp(i)}
\end{aligned}$$

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) 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 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 from leafout for *Aesculus hippocastanum* and *Betula pendula*, 12 days for *Alnus glutinosa*, 5 days for *Fagus sylvatica*, and 7 days for both *Fraxinus excelsior* and *Quercus robur* based on growth chamber experiment data from phylogenetically related species (Buerki *et al.*, 2010; Wang *et al.*, 2016; Hipp *et al.*, 2017; Flynn & Wolkovich, 2018).

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 definition.

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 *Aesculus hippocastanum*) but all species were susceptible to 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.

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

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. 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 less tolerant of low temperatures (i.e., are damaged from higher temperatures than -2.2°C), whereas other species or individuals may be able to tolerate temperatures as low as -8.5°C (Lenz *et al.*, 2016). Thus, species that are typically found in low risk sites but have early budburst (i.e. *Alnus glutinosa*) may be less tolerant of low temperatures and they may be at sites that are experiencing an increased risk with climate change. For this reason, models should ideally incorporate species-specific temperature thresholds to best capture the 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 incorporated into models to best predict spatiotemporal shifts in false springs. Some factors are better at predicting risk than others (i.e., mean spring temperature and distance from the coast), however it is essential to additionally assess the effects of NAO and elevation, which contribute to an individual's risk of false spring. 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 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 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 change and suggest complex responses to warming in the future, which could in turn, have escalating impacts on plant community dynamics.

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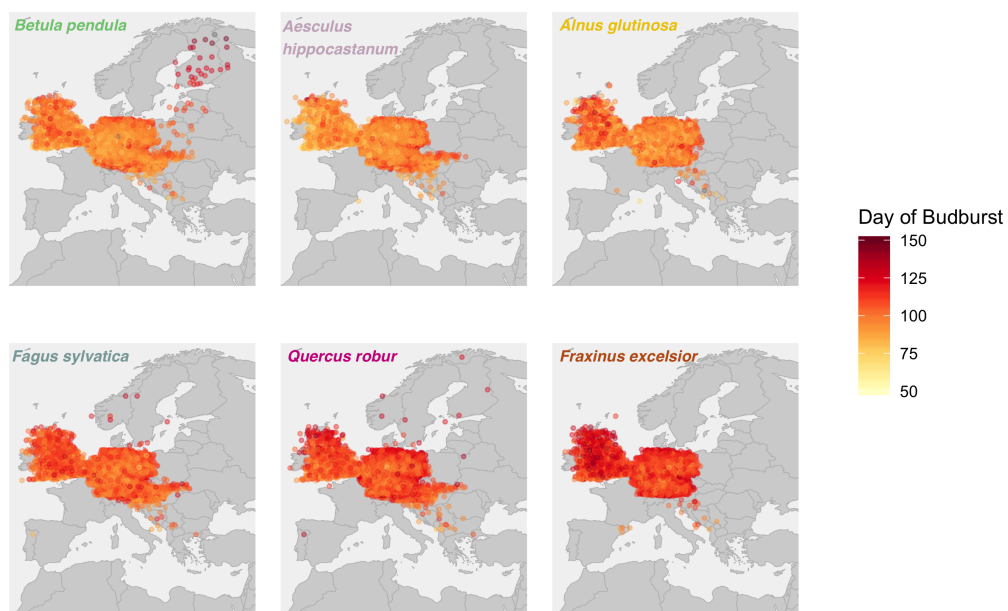


Figure 1: The average day of budburst is mapped by site for each species. Species are ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*. Earlier budburst dates are yellow and later budburst dates are in red.

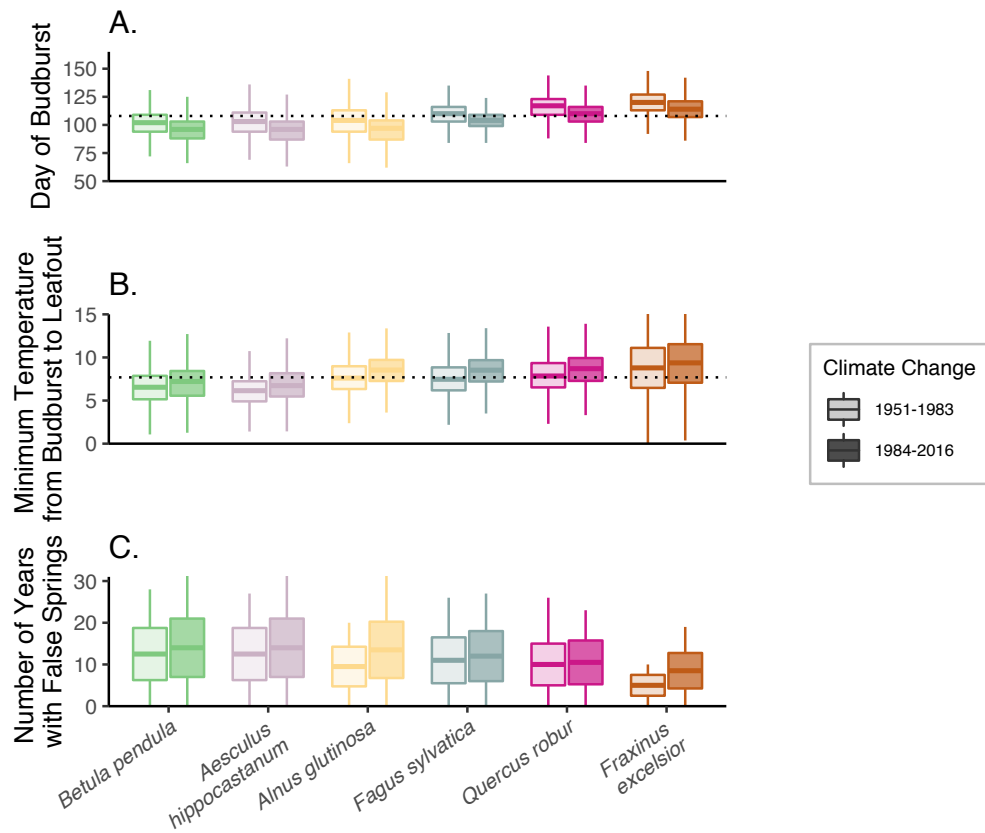


Figure 2: Budburst, minimum temperatures and false springs were compared before and after 1983 for each species. We plotted the day of budburst (A.) before and after 1983 for each species across all sites. We then compared the average minimum temperatures (B.) between budburst and leafout for all species 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.

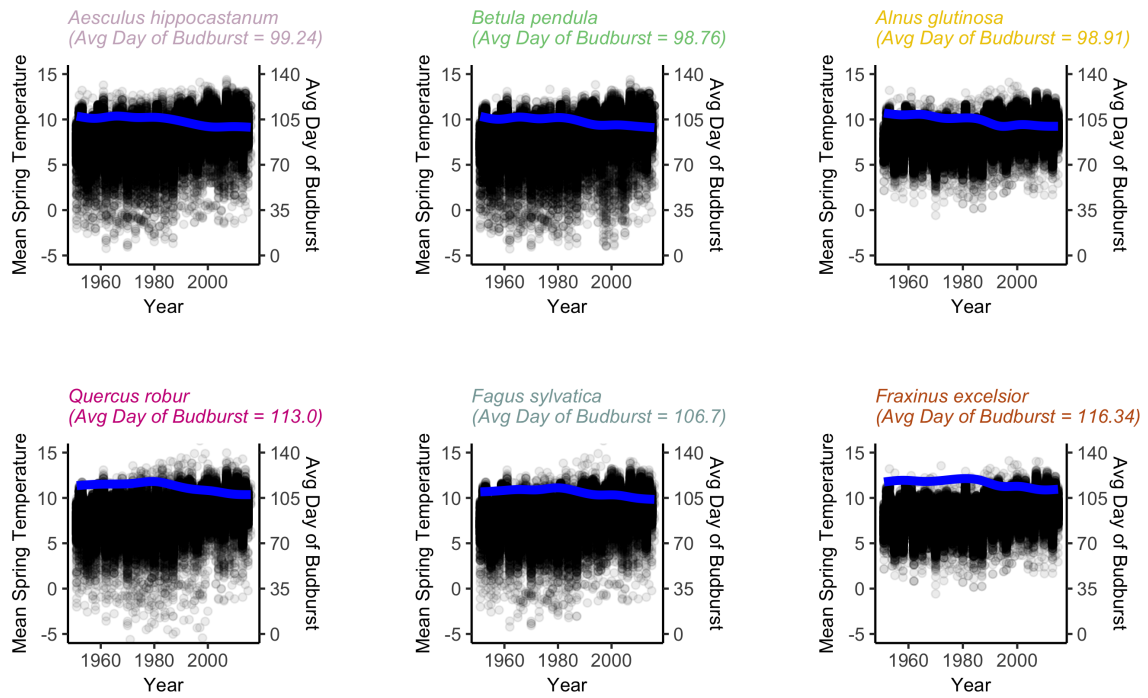


Figure 3: Mean spring temperatures are plotted for each site over time (from 1951-2016) for each species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula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

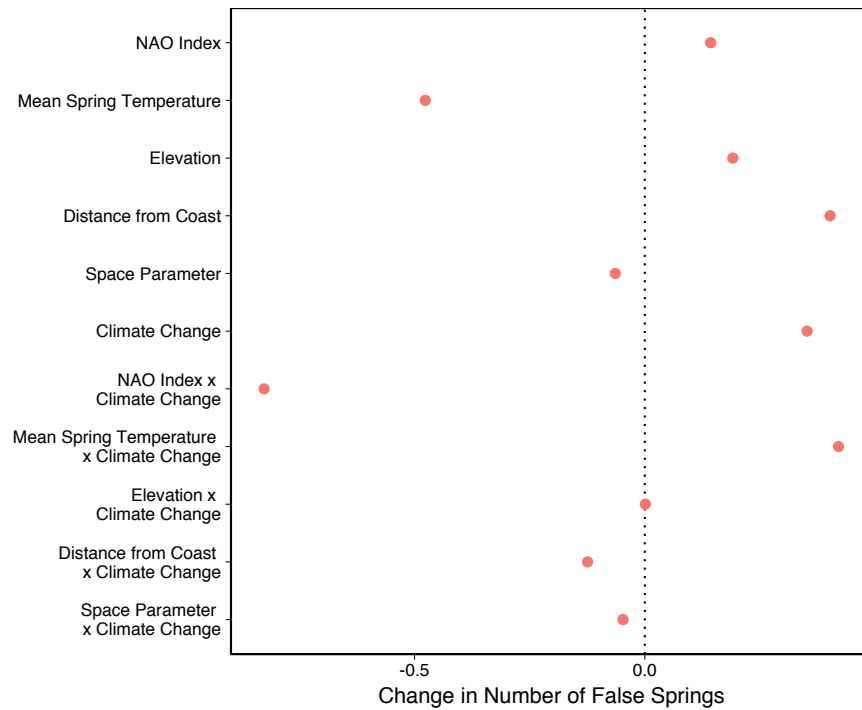


Figure 4: Model output with standardized durations of vegetative risk for each species. More positive parameter effects indicate an increased probability of a false spring whereas more negative effects suggest a lower probability of a false spring. Uncertainly intervals are at 50%. Parameter effects closer to zero have less of an effect on false springs. There were 582,211 zeros and 172,877 ones for false spring in the data.

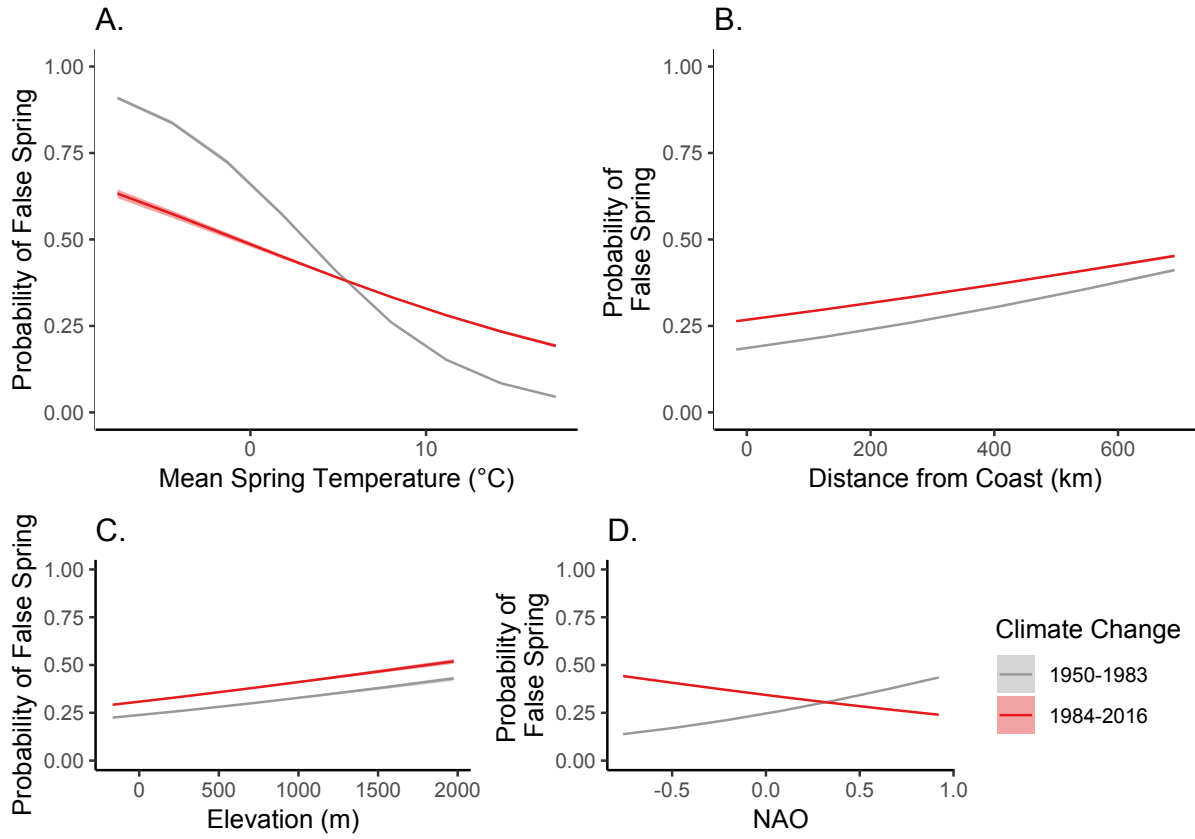


Figure 5: Plots showing the interaction effects on false spring risk for each predictor coupled with climate change. (A.) As mean spring temperature increases, there were fewer false springs but there were fewer false springs after 1983 at sites with lower mean spring temperatures. (B.) There were more 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.

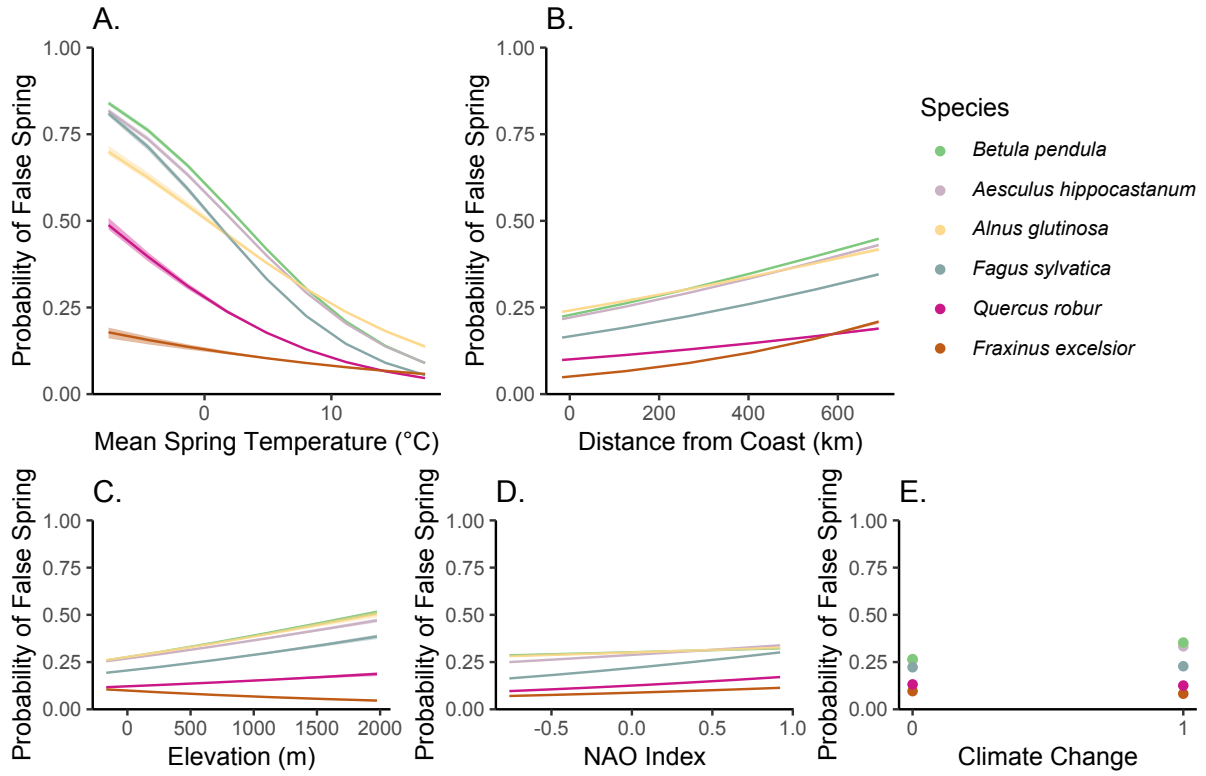


Figure 6: Plots showing the interaction effects of each predictor with species. (A.) As mean spring temperature increases, the probability of a false spring decreases for each species but *Fraxinus excelsior* always has the lowest risk of false spring. (B.) There's an increase in false spring risk for 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.