Regional and climatic effects on false spring risk in a changing world

Authors:

C. J. Chamberlain [1,2], B. I. Cook [3], I. Morales Castilla [1,4] & E. M. Wolkovich [1,2]

Author affiliations:

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

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

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

[4]Edificio Ciencias, Campus Universitario 28805 Alcalã de Henares, Madrid, Spain

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

Abstract 💬

~~Temperate and boreal forests have always been at risk of late spring freezing events — also known as false springs — but with climate change it is unclear whether these events will continue to pose a threat. There is growing interest in false springs, which has lead to diverging evidence: some studies have found false springs are increasing with climate change while others are finding the reverse or even no change in frequency. There are many regional factors that contribute to a plants risk of a false spring but, to date, no study has compared all of these 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 were the strongest predictors of false spring risk and how these predictors shifted with climate change. False spring risk varied across the six species but, overall, false spring risk is increasing with climate change in most 💬 regions. 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; Kukal & Irmak, 2018; Liu *et al.*, 2006), but late spring frosts are still occurring in many of these regions (Wypych *et al.*, 2016b). Temperate tree and shrub species are initiating leafout 4-6 days on average earlier per °C of warming (IPCC, 2015; Wolkovich *et al.*, 2012) but 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 refoliate (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).

Spring frosts are one of the largest limiting factors in species range limits and have greatly shaped plant life history strategies (Kollas *et al.*, 2014). ~~T~~Temperate plants are exposed to freezing temperatures numerous times throughout the year, ~~however,~~ individuals are most at risk to damage in the spring, when frost tolerance is lowest (Sakai & Larcher, 1987). Temperate plants have adapted to these early spring risks through various mechanisms with one common strategy being avoidance ~~(i.e., delayed leafout when temperatures are more consistent).~~ 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 leafout. 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 essential 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 are at risk currently and which regions will be 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 these predictors and their interactions 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. 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

₈₆ in temperature trends (Kharouba *et al.*, 2018; Stocker *et al.*, 2013). We predicted that: (1) Earlier budburst

₈₇ species would experience more false springs, especially after 1983, (2) there would be different regional effects

₈₈ (i.e. mean spring temperature, NAO index, elevation, distance from the coast) on false spring incidence and

₈₉ those trends would shift when coupled with the effects of climate change.

Methods

Phenological Data and Calculating Vegetative Risk

₉₂ We obtained phenological data from the Pan European Phenology network (PEP725, www.pep725.edu),

₉₃ which provides open access phenology records across Europe (Templ *et al.*, 2018). Since plants are most

₉₄ susceptible to damage from frost between budburst and full leafout, we selected leafout data (i.e., in Meier,

₉₅ 2001, BBCH 11, which is defined as the point of leaf unfolding and the first visible leaf stalk) from the

₉₆ PEP725 dataset. The species used in the study were *Aesculus hippocastanum* Poir., *Alnus glutinosa* (L.)

₉₇ Gaertn., *Betula pendula* Roth., *Fagus sylvatica* Ehrh., *Fraxinus excelsior* L., and *Quercus robur* L. Selection

₉₈ criteria for the species were as follows: (1) to be temperate, deciduous species that were not cultivars or

₉₉ used for crops, (2) there were at least 90,000 observations of BBCH 11 (leafout), (3) to represent over half

₁₀₀ of the total number of sites available (11,684), and (4) there were observations for at least 65 out of the 66

₁₀₁ years of the study (1951-2016) (Table S1). We then subtracted 12 days from the leafout date to establish a

₁₀₂ standardized estimate for day of budburst (Donnelly *et al.*, 2017) since the majority of the individuals were

₁₀₃ missing budburst observations.

Climate Data

₁₀₅ We collected daily gridded climate data from the European Climate Assessment & Dataset (ECA&D) and

₁₀₆ used the E-OBS 0.25 degree regular latitude-longitude grid from version 16. We used the daily minimum

₁₀₇ temperature dataset to determine if a false spring occurred. False springs in this study were defined as

₁₀₈ temperatures at or below -2.2°C (Schwartz, 1993) during the duration of vegetative risk. In order to capture

₁₀₉ regional climatic effects we calculated the mean spring temperature by using the daily mean temperature from

₁₁₀ March 1 through May 31. Mean spring temperature was calculated – likely after chilling was accumulated –

₁₁₁ in an attempt to incorporate the general effects of spring forcing temperatures in our Bayesian model and to

4

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) (see supplement 'Methods: Space parameter' for more details). We then took the calculated eigenvectors determined from the M approach and regressed these against the number of false springs for each data point 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, assessed chain convergence and posterior predictive checks (Figure SXX) and through leave-one-out cross-validation (Gelman & Hill, 2006).

Testing the duration of vegetative risk 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). 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.

Results

Species variation in budburst and false spring incidence

There was variation in day of budburst across the six species and across space (Figure 1). The top three species (*Betula pendula*, *Aesculus hippocastanum*), *Alnus glutinosa* generally initiated budburst earlier than the bottom three species (*Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*). Across all six species, higher latitude sites and sites closer to the coast tend to initiate budburst later in the season.

As seen in Figure 2, we look at all sites combined and determined the range of mean spring temperatures experienced for each species. Most species had mean spring temperatures that ranged from -5°C to 12°C, but for *Alnus glutinosa* and *Fraxinus excelsior* temperatures rarely dropped below 0°C, whereas *Quercus robur* experienced some of the lowest spring temperatures.

After 1983, all species initiated budburst earl⬚ (Figure 3A) and the minimum temperature between budburst and leafout was, on average, higher. The average minimum temperature between budburst and leafout, however, varied across the six species with *Betula pendula* and *Aesculus hippocastanum* experiencing the lowest minimum temperatures (Figure 3B) and with *Fraxinus excelsior* experiencing the greatest variation. There was wide variation across sites in false spring risk for each species and some species were more at risk of false springs after 1983 than others (Figure 3C).

The effects of climatic regional variation on false spring incidence

The effects of the predictors varied in both direction and magnitude (Figure 4A). Mean spring temperature had the biggest effect (-0.48) on the number of false springs, with warmer spring temperatures resulting is fewer false springs. More positive NAO indices slightly heightened the risk of false spring (+0.14) but sites further from the coast and at higher elevations increased the likelihood of false spring incidence: +0.40 and +0.19 respectively. Overall, there were more false springs after 1983 (+0.35).

Most of the interactions with increasing temperatures (i.e., the climate change predictor) exhibit a decreased risk in false springs, however, the probability of false spring incidence increased at sites with higher mean spring temperatures after 1983 (+0.42) (Figure 4B), which is evident for both *Betula pendula* and *Fraxinus excelsior*. There was little change in the risk of a false springs further from the coast before and after climate change and it varied across species (Figure 4C), however most sites had a slightly decreased risk in false springs further from the coast after climate change. The probability of a false spring remained the same before and after 1983 across elevations (Figure 4D) – which was consistent across species – but, after climate change, the rate of false spring incidence largely decreased (-0.83) with increasing NAO indices (Figure 4E).

The probability of a false spring occurring varied by species with each predictor (Figure 5). With increasing mean spring temperatures, there were fewer false springs for each species, however *Betula pendula* had the greatest risk of false springs and *Fraxinus excelsior* had the lowest risk (Figure 5A). There was an increased risk of false spring for all species at sites further from the coast (Figure 5B). With increasing elevation,

all species had a greater risk of a false spring occurring except for *Fraxinus excelsior*, which had a slightly decreased risk at higher elevations (Figure 5C). With increasing NAO indices, the risk of false spring remained consistent for most species except *Fagus sylvatica* experienced more with higher NAO indices (Figure 5D). *Betula pendula*, *Aesculus hippocastanum* and *Alnus glutinosa* all experienced more false springs after 1983 (Figure 5E).

Changing duration of vegetative risk

By having different durations of vegetative risk for each species, the magnitude and direction of the predictors remained consistent with the original model (Figure SXX). There were fewer false springs after 1983 and mean spring temperature and distance from the coast were the strongest predictors for false spring risk. Mean spring temperature had a slightly stronger positive interaction effect with climate change as compared to the original model and there was a slight increase in false spring risk after climate change at higher elevations.

Lower temperature threshold

With a lower temperature threshold for defining a false spring (i.e., -5°C), the magnitude and direction of the predictors again remained consistent with the original model (Figure SXX). There was slightly higher risk of false springs for individuals at higher elevations than those further from the coast and, after climate change, this risk decreased. Otherwise, mean spring temperature had the strongest effect and warmer sites after climate change were at a higher risk. There were a lot more zeros in this temperature threshold model, rendering the model less stable.

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. The six study species all exhibit strong differences, 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 still had a risk of damage after 1983 and some — i.e., *Betula pendula*, *Aesculus hippocastanum* and *Alnus glutinosa* — had an even higher risk than before. Mean spring temperature,

8

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 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. Additionally, our results indicate that higher NAO indices — which typically leads to earlier budburst — slightly increased the risk of false springs but that risk diminished significantly after climate change. The compounding effect of high NAO with climate-change induced warming could decrease the risk of freezing temperatures occurring in those years, however, this interplay should be investigated further.

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 incorporating all regional effects is more important that adjusting the duration of vegetative risk or the temperature threshold. 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 suggest there is a heightened risk of false springs with climate change and that there will be complex responses to warming in the future, which could in turn, have escalating impacts on plant community dynamics and, thus, further augment climatic shifts.

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.

286 Basler D, Körner C (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural*
287   *and Forest Meteorology*, **165**, 73–81. doi:10.1016/j.agrformet.2012.06.001.

288 Buerki S, Lowry II P, Alvarez N, Razafimandimbison S, Kupfer P, Callmander M (2010) Phylogeny and
289   circumscription of *Sapindaceae* revisited: Molecular sequence data, morphology and biogeography support
290   recognition of a new family, *Xanthoceraceae*. *Plant Ecology and Evolution*, **143**, 148–159. doi:10.5091/
291   plecevo.2010.437.

292 Bürkner PC (2017) brms: An R Package for Bayesia Multilevel Models. *Journal of Statistical Software*, **80**,
293   1–28.

294 Chen X, Hu B, Yu R (2005) Spatial and temporal variation of phenological growing season and climate
295   change impacts in temperate eastern China. *Global Change Biology*, **11**, 1118–1130. doi:10.1111/j.1365-
296   2486.2005.00974.x.

297 Chmielewski FM, Rötzer T (2001) Response of tree phenology to climate change across Europe. *Agricultural*
298   *and Forest Meteorology*, **108**, 101 – 112. doi:https://doi.org/10.1016/S0168-1923(01)00233-7.

299 Cleland E, Chiariello N, Loarie S, Mooney H, Field C (2006) Diverse responses of phenology to global changes
300   in a grassland ecosystem. *PNAS*, **103**, 13740–13744.

301 Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to
302   global change. *Trends in Ecology and Evolution*, **22**, 357–365. doi:10.1016/j.tree.2007.04.003.

303 David B, Thomas D, Stéphane D, Jason V (2017) Disentangling good from bad practices in the selection of
304   spatial or phylogenetic eigenvectors. *Ecography*, **0**. doi:10.1111/ecog.03380. URL https://onlinelibrary.
305   wiley.com/doi/abs/10.1111/ecog.03380.

306 Donnelly A, Yu R, Caffarra A, *et al.* (2017) Interspecific and interannual variation in the duration of spring
307   phenophases in a northern mixed forest. *Agricultural and Forest Meteorology*, **243**, 55–67.

308 Flynn DFB, Wolkovich EM (2018) Temperature and photoperiod drive spring phenology across all species in
309   a temperate forest community. *New Phytologist*. doi:10.1111/nph.15232. URL http://dx.doi.org/10.
310   1111/nph.15232.

311 Fu YH, Piao S, Vitasse Y, *et al.* (2015) Increased heat requirement for leaf flushing in temperate woody
312   species over 1980-2012: effects of chilling, precipitation and insolation. *Global Change Biology*, **21**, 2687–
313   2697. doi:10.1111/gcb.12863. URL http://dx.doi.org/10.1111/gcb.12863.

314 Gelman A, Hill J (2006) *Data analysis using regression and multilevel/hierarchical models*. Cambridge uni-
315   versity press.

316 Gu L, Hanson PJ, Post WM, *et al.* (2008) The 2007 Eastern US spring freeze: Increased cold damage in a
317   warming world. *BioScience*, **58**, 253. doi:10.1641/B580311.

318 Hänninen H (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell*
319   *& Environment*, **14**, 449–454. doi:10.1111/j.1365-3040.1991.tb01514.x. URL `https://onlinelibrary.`
320   `wiley.com/doi/abs/10.1111/j.1365-3040.1991.tb01514.x`.

321 Hipp A, S Manos P, González-Rodríguez A, *et al.* (2017) Sympatric parallel diversification of major oak clades
322   in the Americas and the origins of Mexican species diversity. *New Phytologist*, **217**. doi:10.1111/nph.14773.

323 Hufkens K, Friedl MA, Keenan TF, Sonnentag O, Bailey A, O'Keefe J, Richardson AD (2012) Ecological
324   impacts of a widespread frost event following early spring leaf-out. *Global Change Biology*, **18**, 2365–2377.
325   doi:10.1111/j.1365-2486.2012.02712.x.

326 Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane
327   wildflowers. *Ecology*, **89**, 353–362.

328 IPCC (2015) *Climate change 2014: mitigation of climate change*, vol. 3. Cambridge University Press.

329 Kharouba HM, Ehrlén J, Gelman A, Bolmgren K, Allen JM, Travers SE, Wolkovich EM (2018) Global shifts in
330   the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy*
331   *of Sciences*, **115**, 5211–5216. doi:10.1073/pnas.1714511115. URL `http://www.pnas.org/content/115/`
332   `20/5211`.

333 Klosterman S, Hufkens K, Richardson AD (2018) Later springs green-up faster: the relation between onset
334   and completion of green-up in deciduous forests of North America. *International Journal of Biometeorology*.
335   doi:10.1007/s00484-018-1564-9.

336 KNMI (2018) Daily CPC NAO data. URL `https://climexp.knmi.nl/getindices.cgi?WMO=NCEPData/`
337   `cpc_nao_daily&STATION=NAO&TYPE=i&id=someone@somewhere&NPERYEAR=366`.

338 Kollas C, Körner C, Randin CF (2014) Spring frost and growing season length co-control the cold range
339   limits of broad-leaved trees. *Journal of Biogeography*, **41**, 773–783. doi:10.1111/jbi.12238.

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 `http://dx.doi.org/10.1111/1365-2745.12574`.

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:10.1111/j.1365-3040.1994.tb00305.x. URL `https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1365-3040.1994.tb00305.x`.

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.

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.

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 —- Geochemical 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.

R Development Core Team (2017) R: A language and environment for statistical computing. *R Foundation for Statistical Computing, Vienna, Austria*.

Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest 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)**, 536–550.

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.

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, 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/s00484-018-1512-8. URL https://doi.org/10.1007/s00484-018-1512-8.

Vitasse Y, Lenz A, Kẫûrner 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://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 `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.

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.

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/nclimate3138.
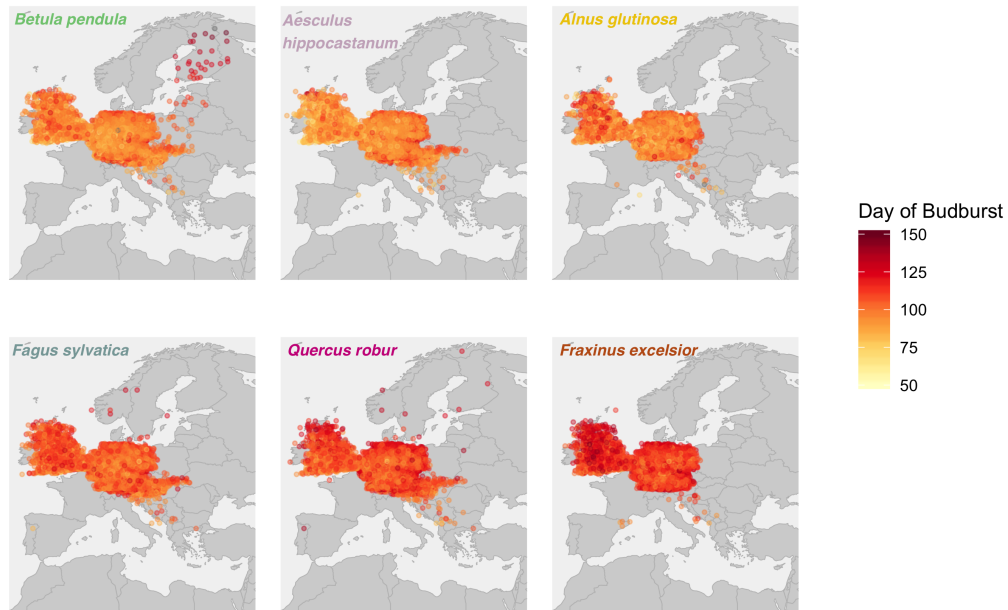
Tables and Figures

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.
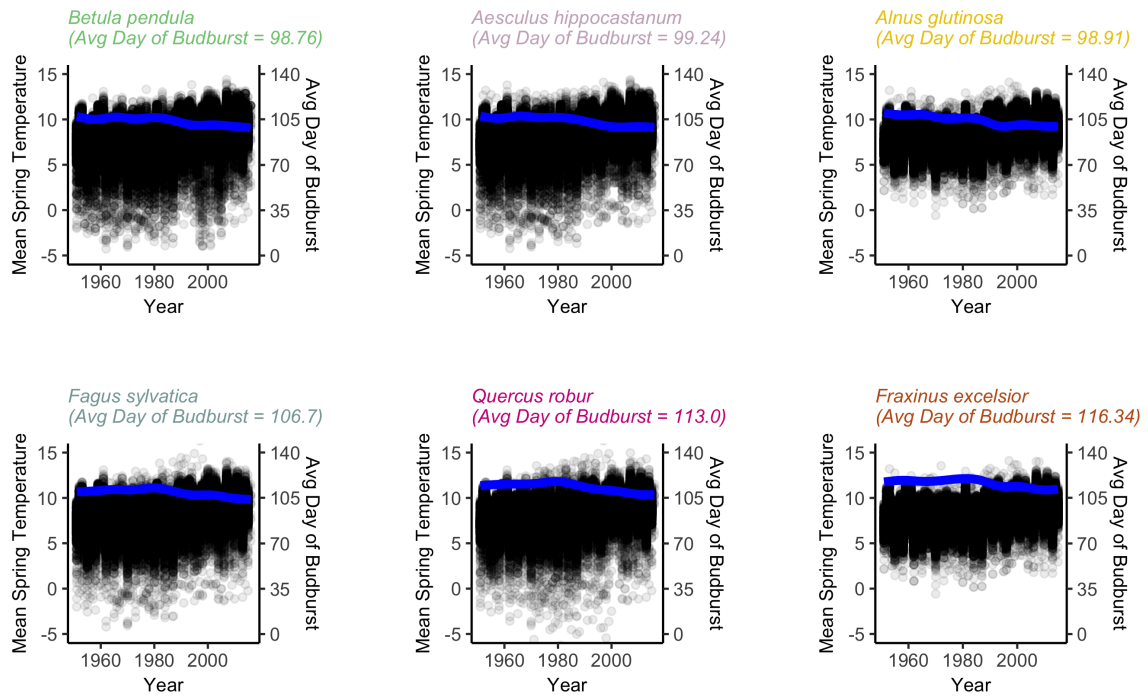
Figure 2: Mean spring temperatures are plotted for each site over time (from 1951-2016) for each species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula pendula* and the latest being *Fraxinus excelsior*.
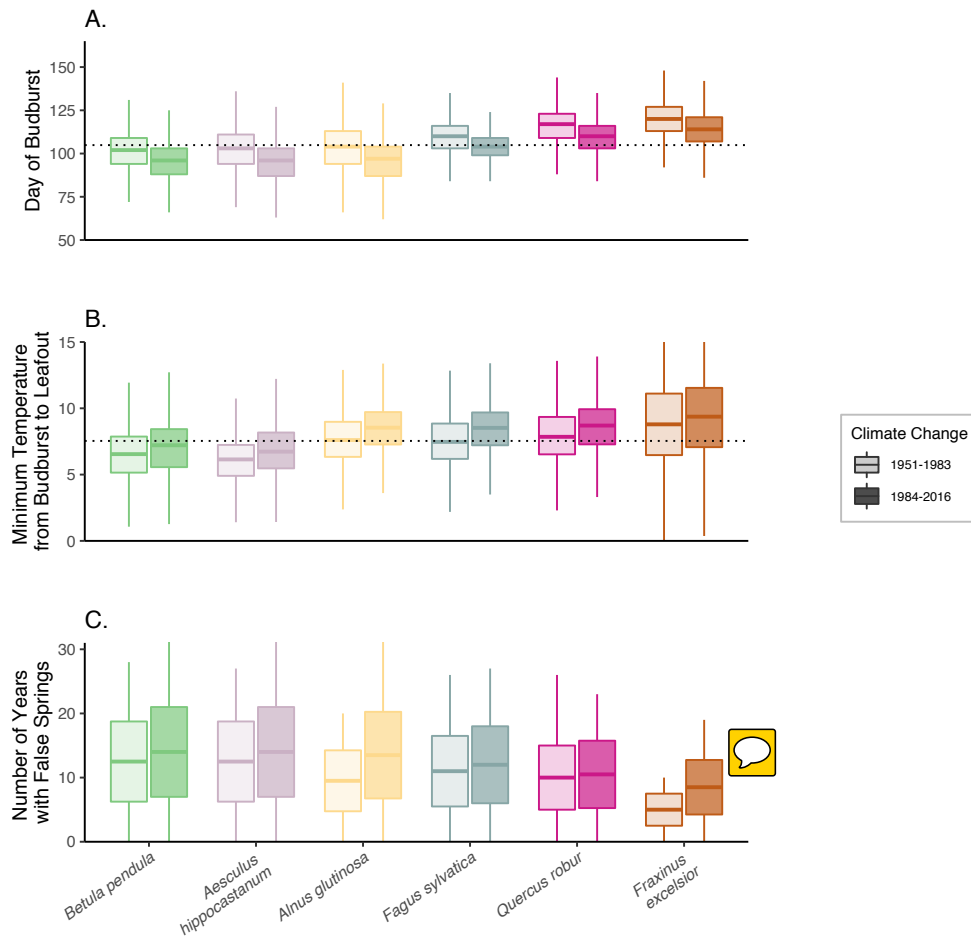
Figure 3: Budburst, minimum temperatures and false springs were compared before and after 1983 for each species. We plotted the day of budburst (A.) before and after 1983 for each species across all sites. We then compared the average minimum temperatures (B.) between budburst and leafout for all species 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.
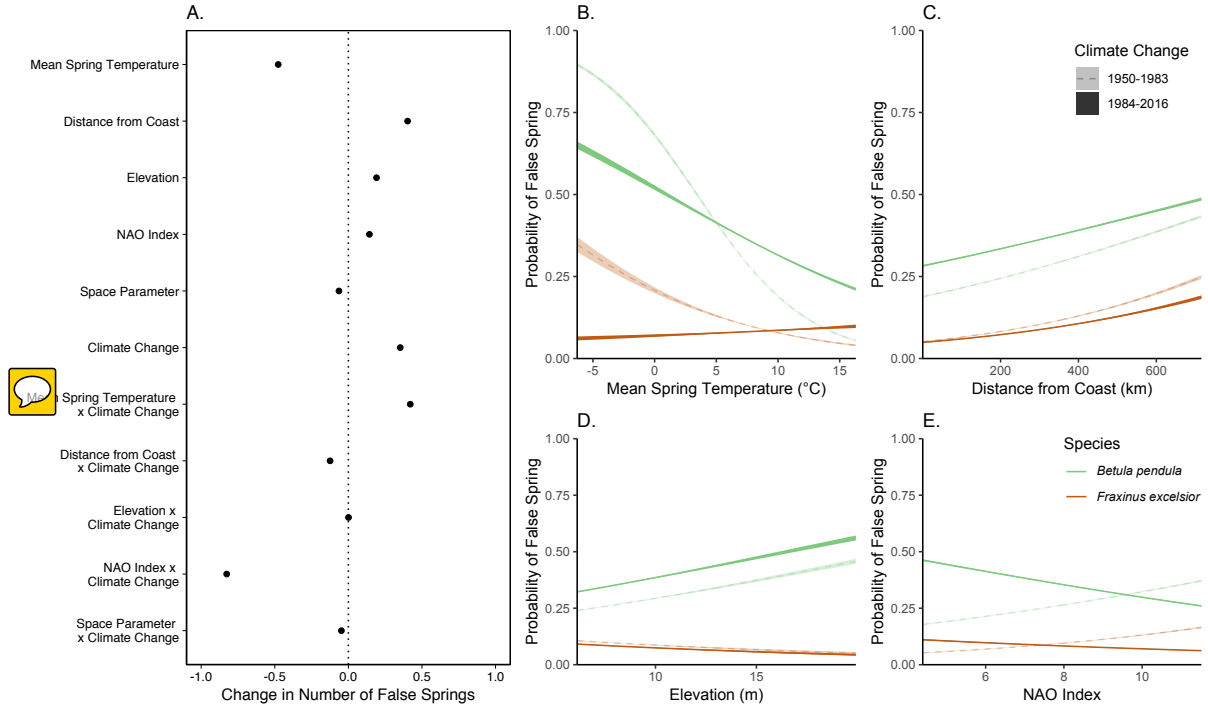
Figure 4: (A) Model output with standardized durations of vegetative risk for each species. More positive parameter effects indicate an increased probability of a false spring whereas more negative effects suggest a lower probability of a false spring. Uncertainly intervals are at 50%. Parameter effects 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. Average predictive comparisons (panels B-E) breakdown the interactions of each of the main effects with climate change (i.e., Mean spring temperature, distance from the coast, elevation, and NAO index). The two extreme species – *Betula pendula* and *Fraxinus excelsior* — were chosen to best represent the variation across all species. See the supplement (Figure SXX) for all species.
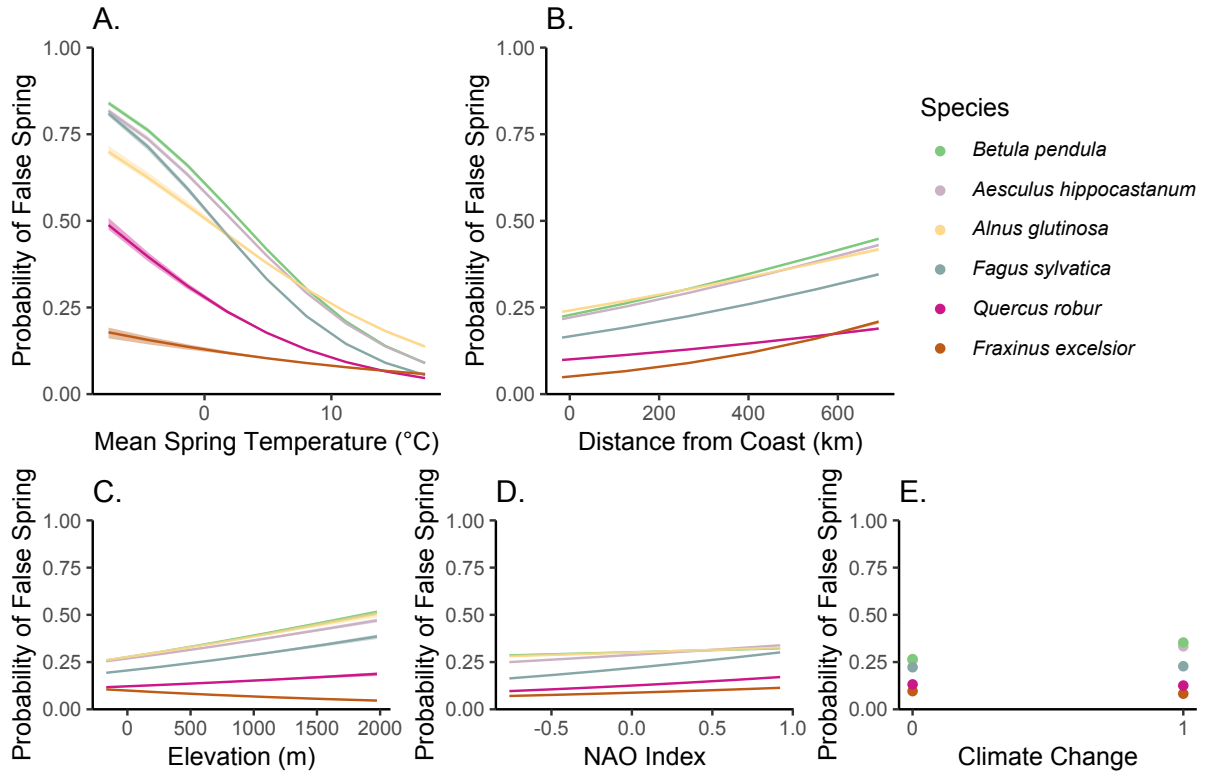
Figure 5: Plots showing the interaction effects of each predictor with species. (A.) As mean spring temperature increases, the probability of a false spring decreases for each species but *Fraxinus excelsior* always has the lowest risk of false spring. (B.) There's an increase in false spring risk for 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.