

Heightened risk false springs with climate change across six European tree species

OR

False spring risk increases across European trees in the face of climate change

OR

Climate change increases the risk of false springs in European trees

Authors:

C. J. Chamberlain^{1,2}, B. I. Cook³, I. Morales Castilla^{1,4} & E. M. Wolkovich^{1,2,5}

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

⁵ Forest & Conservation Sciences, Faculty of Forestry, University of British Columbia, 2424 Main Mall, Vancouver, BC V6T 1Z4

*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 are many spatial and environmental factors that contribute to a plants risk of a false spring but, to date, no study has compared all of these 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 across both early and late bud bursting 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 (-3.3% for every 2°C increase) and sites further from the coast experiencing more false springs (4.8% for every 150km from the coast), however elevation (1.8% for every 200m increase in altitude) and NAO index (1.5% for every 0.3 increase) also contributed to false spring risk. Our results suggest that considering multiple spatial 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 (???), but late spring frosts are still occurring in many of these regions (?). Temperate tree and shrub species are initiating leafout 4-6 days on average earlier per °C of warming (??) but last spring freeze dates are not predicted to advance at the same rate (????), 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 (?) but budburst has advanced around twice as fast. Major false spring events have been recorded in recent years and studies have found it can take 16-38 days for trees to refoliate after a freeze (????), which can detrimentally affect crucial processes such as carbon uptake and nutrient cycling (???).

Spring frosts are one of the largest limiting factors in species range limits and have greatly shaped plant life history strategies (?). 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 (?). Temperate plants have adapted to these early spring risks through various mechanisms with one common strategy being avoidance (?). Trees and shrubs in temperate regions minimize frost risk and optimize growth 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 and sites, making some species less – or more — vulnerable to false springs than before. Earlier-leafing species may be especially at risk with warming, as their budburst occurs during times of year when the occurrence of freeze events is relatively high.

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 (??). 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 (??). Thus, it is essential to consider the length of time between budburst and leafout — when individuals are most at risk to spring freeze damage (?) — in order to better predict false spring risk. We will refer to this timing between budburst and leafout as the duration of vegetative risk (?).

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. Spring freeze damage may increase (???), remain the same (?) or even decrease (??) with climate change. 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 (?). Furthermore, recent studies have demonstrated site effects may be more closely related to false spring risk: whether via altitudinal variation (???) or distance from the coast (??). 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. False spring risk is influenced by multiple climatic and geographic factors, thus all predictors must be assessed to best predict spatiotemporal and species-specific shifts in false springs. Our primary aim is to investigate the influence of known spatial and climatic factors on false spring risk and compare the effect of these predictors and their interactions with climate change. The key 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 (?), however it is unclear if more positive NAO phases also translates into 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 defined as when temperatures fell below

-2.2° (?) between estimated 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 in temperature trends (??). We predicted that: (1) Earlier budburst species would experience more false springs, especially after 1983 as compared to before, (2) the environmental predictors (i.e. mean spring temperature, NAO index, elevation, distance from the coast) will differ in how they influence false spring incidence and (3) climate change would impact the strength of the predictors on false springs by, for example, reducing the influence of mean spring temperature as the climate warms.

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 (?). Since plants are most susceptible to damage from frost between budburst and full leafout, we selected leafout data (i.e., in ?, 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., and *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 (???) since the majority of the individuals were missing budburst observations. We additionally considered a model that altered the durations of vegetative risk for each species. For this alternate duration of vegetative risk model, 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 (????).

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 (?) during the duration of vegetative risk. We additionally tested this model by changing the definition of a freezing temperature from -2.2°C (?) to -5°C (??) in an alternative model. In order to assess regional climatic effects we calculated the mean spring temperature by using the daily mean temperature from March 1 through May 31. We used this date range to best capture temperatures likely after chilling had accumulated to compare differences in spring forcing temperatures across sites (??). 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 (?). 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, ??) to represent climate change.

Data Analysis

To best compare across the effects of each climate variable, we scaled all of the predictors and used a z-score following the binary predictor approach (?). To control for spatial autocorrelation and to account for spatially structured processes independent from our regional predictors of false springs, we generate an additional spatial predictor for the model. To generate our spatial predictor we first extracted spatial eigenvectors corresponding to our analyses' units and selected the subset that minimizes spatial autocorrelation of the residuals of a model including all predictors except for the spatial predictor (??) (see supplement 'Methods: Spatial parameter' for more details). We then took the eigenvector subset determined from the minimisation of Moran's I in the residuals (MIR approach) and regressed them against the above residuals—i.e. number of false springs *vs.* regional factors. Finally we used the fitted values of that regression as our spatial predictor, which, by definition, represents the portion of the variation in false springs that is both spatially structured and independent from all other predictors in the model (e.g. average spring temperature, altitude, etc. ??). To best estimate the number of false springs across-species levels we used a Bayesian modeling approach . 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 (Equation 1), using the brms package (??), version 2.3.1, in R (??), version 3.3.1, and was written as follows:

$$\begin{aligned}
y_i = & \text{Bernoulli}(\alpha_{[i]} + \beta_{NAO_{[i]}} + \beta_{MST_{[i]}} + \beta_{Elevation_{[i]}} + \beta_{DistanceCoast_{[i]}} + \beta_{Space_{[i]}} \\
& + \beta_{ClimateChange_{[i]}} + \beta_{NAO \times Species_{[i]}} + \beta_{MST \times Species_{[i]}} + \beta_{Elevation \times Species_{[i]}} + \beta_{DistanceCoast \times Species_{[i]}} \\
& + \beta_{Space \times Species_{[i]}} + \beta_{ClimateChange \times Species_{[i]}} + \beta_{NAO \times ClimateChange_{[i]}} + \beta_{MST \times ClimateChange_{[i]}} \\
& + \beta_{Elevation \times ClimateChange_{[i]}} + \beta_{DistanceCoast \times ClimateChange_{[i]}} + \beta_{Space \times ClimateChange_{[i]}} + \epsilon_{[i]}), \\
\epsilon_i \sim & \text{Bernoulli}(0, \sigma_y^2)
\end{aligned} \tag{1}$$

We ran four 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.

Results

Species variation in budburst and false spring incidence

There was variation in day of budburst across the six species and across geographical gradients (Figure ??). 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 tended to initiate budburst later in the season.

As seen in Figure ??, we looked 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 around six days earlier on average (Figure ??A and Table SXX) and the minimum temperature between budburst and leafout was 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 ??B) 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 ??C). Although the increased risk seen for some species — namely *Fraxinus excelsior* — could be due to environmental effects and where the sites were before and after climate change for *Fraxinus excelsior*. Thus, species alone is not a sufficient predictor for false spring risk. Spatial and climatic effects must be included to understand what drives false spring risk.

The effects of climatic and spatial variation on false spring incidence

The effects of the predictors varied in both direction and magnitude (Figure ?? and Figure SXX) for the overall model testing climatic and spatial variation in false spring risk. Distance from the coast had the biggest effect on false spring incidence. Individuals at sites further from the coast tend to have earlier budburst dates, which corresponded to an increased risk in false springs. For every 150kms away from the coast there was a 4.83% increase in risk in false springs. Mean spring temperature had the second strongest effect on false springs, with warmer spring temperatures resulting in fewer false springs. For every 2°C increase in mean spring temperature there was a 3.33% decreased risk in the number of false springs. More positive NAO indices, which generally advance budburst, slightly heightened the risk of false spring, with every 0.3 unit increase in NAO index there was a 1.54% increased risk in false spring. Sites at higher elevations also had higher risks of false spring incidence — likely due to more frequent colder temperatures — with a 1.89% increase in risk for every 200m increase in elevation. Overall, there were more false springs after 1983 (7.23% increased risk).

Most of the interactions with increasing temperatures (i.e., the climate change predictor) exhibit a reduced effect of the predictor after climate change on false spring risk (Figure ??). Warmer sites tend to have lower risks of false springs but with climate change, warmer sites are at a higher risk of false springs than before as seen by the positive interaction term with climate change. This is likely due to advancing budburst with warming a climate but late spring freezes are not advancing at the same rate. There was a slightly reduced risk in false springs further from the coast after climate change, potentially due to warming temperatures, rendering higher risk sites further from the coast to be less at risk after climate change than they were before. The level of risk remained consistent before and after 1983 across elevations, with false spring risk being

higher at higher elevation before and after climate change. After climate change, the rate of false spring incidence largely decreased with increasing NAO indices – likely due to a large advancement in budburst and warmer temperatures overall for those years.

The probability of a false spring occurring varied across species along environmental gradients (Figure ??). Species generally follow similar positive or negative trends along each predictor but variation in effect is evident from the differing slopes of the lines. 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 ??A). There was an increased risk of false spring for all species at sites further from the coast (Figure ??B), with a sharp increase in risk for *Fraxinus excelsior* at sites further from the coast. 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 ??C) — demonstrating inconsistent effects of elevation on a species' risk. With increasing NAO indices, the risk of false spring remained consistent for most species except *Fagus sylvatica* experienced more with higher NAO indices (Figure ??D). *Betula pendula*, *Aesculus hippocastanum* and *Alnus glutinosa* all experienced more false springs after 1983 (Figure ??E).

Sensitivity analyses

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.

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 7.225% across the European distribution of our species. But this average hides many important complexities as the ability of our models to predict false springs is contingent on species *and* climate gradients. While all six study species are at risk of false springs, they show marked differences in their climate-false springs clines. *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, 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. The strength of 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 (???) and some studies indicate earlier budburst species are more at risk of false spring damage (?). After 1983, all of our species initiated budburst earlier in the spring and there was an overall increase 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. Simply looking at number of false springs for species suggests that *Fraxinus excelsior* had the biggest increase in false spring risk after climate change (Figure ??C.), however this conflicts with the overall model output (Figure ??E). The distribution of *Fraxinus excelsior* data is likely influencing the results seen in Figure ??C, thus, simply looking at budburst time is not a sufficient proxy to forecast false spring risk. Additional climatic and regional factors —e.g., altitude, continentality— must be evaluated to more thoroughly assess false spring risk across species.

Climatic and regional effects

Past studies using single predictors for false spring events (?????) lead to contradicting predictions in future false spring risk. Through our multivariate 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. Further,

incorporating a *spatial predictor* let us simultaneously control for autocorrelation issues and account for spatially structured latent processes that were not represented by other predictors. Approaches such as ours may provide more robust forecasts of false spring risk and more clearly elucidate species level differences in risk — which were minimal — versus stronger predictors (i.e., mean spring temperature and continentality).

Our study supports findings from previous studies: higher elevations tend to experience more false springs (??), sites that are generally warmer have lower risks of false springs (?), and risk increases with climate change (?). However, we also discovered that effects of elevation and distance from the coast cannot be assumed to be the same, which contradicts previous studies (?). 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. Sites further from the coast are potentially slightly less at risk to false springs after climate change due to the overall increase in warming temperatures, rendering higher risk sites further from the coast to be slightly less at risk after climate change than they were before.

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 (?). 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 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.

Forecasting future false springs

Our study does not assess the intensity or severity of the false spring events nor does it record the amount of damage to individuals. It is possible that with increasing false spring risk, the events after 1983 could be lasting longer or could reach even harsher temperatures. Additionally, there is sufficient evidence that species

vary in their tolerance to minimum temperature extremes (????). 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 (?). 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 of damage 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 (??). 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 multiple environmental 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 than 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 events consistently increased with climate change across species, thus we need a better understanding of the major drivers of false spring risk, how these events are changing in duration and intensity and if there are shifts in the level of damage to individuals. False spring risk is influenced by multiple climatic and geographic factors, all of which must be incorporated into models to best predict spatiotemporal, species-specific 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 and also increase the prediction accuracy of the overall model. Individuals that initiate budburst earlier in the season are not necessarily exposed to more false springs, thus, investigating site effects is a more consistent proxy for false spring risk than budburst time. 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 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.
- 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.
- Bennett JM, Calosi P, Clusella-Trullas S, *et al.* (2018) Globtherm, a global database on thermal tolerances for aquatic and terrestrial organisms. *Scientific data*, **5**, 180022.
- Buerki S, Lowry II P, Alvarez N, Razafimandimbison S, Kupfer P, Callmender 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 PC (2017) brms: An R Package for Bayesia Multilevel Models. *Journal of Statistical Software*, **80**, 1–28.
- Chamberlain CJ, Cook BI, de Cortazar Aauri IG, Wolkovich EM (2019) Rethinking false spring risk. *Global Change Biology*, **25**, 2209–2220. doi:10.1111/gcb.14642. URL <https://onlinelibrary.wiley.com/doi/abs/10.1111/gcb.14642>.

- 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.
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD (2007) Shifting plant phenology in response to 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>.
- Diniz-Filho JAF, Bini LM, Rangel TF, Morales-Castilla I, Olalla-Tárraga MÁ, Rodríguez MÁ, Hawkins BA (2012) On the selection of phylogenetic eigenvectors for ecological analyses. *Ecography*, **35**, 239–249.
- 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>.
- Gelman A, Hill J (2006) *Data analysis using regression and multilevel/hierarchical models*. Cambridge university press.
- Griffith DA, Peres-Neto PR (2006) Spatial modeling in ecology: the flexibility of eigenfunction spatial analyses. *Ecology*, **87**, 2603–2613.
- 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.
- Inouye DW (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology*, **89**, 353–362.
- 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>.
- 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.
- KNMI (2018) Daily CPC NAO data. URL https://climexp.knmi.nl/getindices.cgi?WMO=NCEPData/cpc_ao_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.
- 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.
- Morales-Castilla I, Olalla-Tarraga MA, Purvis A, Hawkins BA, Rodriguez MA (2012) The imprint of cenozoic migrations and evolutionary history on the biogeographic gradient of body size in new world mammals. *The American Naturalist*, **180**, 246–256.

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

408 Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M (2013) Climate change, phe-
409 nology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest*
410 *Meteorology*, **169**, 156 – 173. doi:<https://doi.org/10.1016/j.agrformet.2012.09.012>.

411 Sakai A, Larcher W (1987) *Frost Survival of Plants*. Springer-Verlag.

412 Scheifinger H, Menzel A, Koch E, Peter C (2003) Trends of spring time frost events and phenological dates
413 in Central Europe. *Theoretical and Applied Climatology*, **74**, 41–51. doi:10.1007/s00704-002-0704-6. URL
414 <http://dx.doi.org/10.1007/s00704-002-0704-6>.

415 Schwartz MD (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography*, **14**(6),
416 536–550.

417 Sgubin G, Swingedouw D, Dayon G, de Cortázar-Atauri IG, Ollat N, Pagé C, van Leeuwen C (2018) The risk
418 of tardive frost damage in French vineyards in a changing climate. *Agricultural and Forest Meteorology*,
419 **250-251**, 226 – 242. doi:<https://doi.org/10.1016/j.agrformet.2017.12.253>.

420 Stocker TF, Qin D, Plattner GK, *et al.* (2013) Climate Change 2013: The Physical Science Basis. Contribution
421 of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change,
422 1535 pp.

423 Templ B, Koch E, Bolmgren K, *et al.* (2018) Pan European Phenological database (PEP725): a single point
424 of access for European data. *International Journal of Biometeorology*, **62**, 1109–1113. doi:10.1007/s00484-
425 018-1512-8. URL <https://doi.org/10.1007/s00484-018-1512-8>.

426 USA-NPN (2019) Plant and animal phenology data. *USA National Phenology Network*. doi:10.5066/
427 F78S4N1V. URL <http://doi.org/10.5066/F78S4N1V>.

428 Vitasse Y, Lenz A, Körner C (2014) The interaction between freezing tolerance and phenology in temperate
429 deciduous trees. *Frontiers in Plant Science*, **5**. doi:10.3389/fpls.2014.00541. URL [http://dx.doi.org/](http://dx.doi.org/10.3389/fpls.2014.00541)
430 [10.3389/fpls.2014.00541](http://dx.doi.org/10.3389/fpls.2014.00541).

431 Vitasse Y, Schneider L, Rixen C, Christen D, Rebetez M (2018) Increase in the risk of exposure of forest
432 and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. *Agricultural*

433 *and Forest Meteorology*, **248**, 60 – 69. doi:<https://doi.org/10.1016/j.agrformet.2017.09.005>. URL <http://www.sciencedirect.com/science/article/pii/S0168192317303003>.

435 Vitra A, Lenz A, Vitasse Y (2017) Frost hardening and dehardening potential in temperate trees from winter
436 to budburst. *New Phytologist*, **216**, 113–123. doi:10.1111/nph.14698. URL [http://dx.doi.org/10.1111/](http://dx.doi.org/10.1111/nph.14698)
437 [nph.14698](http://dx.doi.org/10.1111/nph.14698).

438 Wang N, McAllister HA, Bartlett PR, Buggs RJA (2016) Molecular phylogeny and genome size evolution
439 of the genus *Betula* (Betulaceae). *Annals of Botany*, **117**, 1023–1035. doi:10.1093/aob/mcw048. URL
440 <http://dx.doi.org/10.1093/aob/mcw048>.

441 Wolkovich EM, Cook BI, Allen JM, *et al.* (2012) Warming experiments underpredict plant phenological
442 responses to climate change. *Nature*, **485**, 18–21. doi:10.1038/nature11014.

443 Wypych A, Sulikowska A, Ustrnul Z, Czekierda D (2016a) Variability of growing degree days in Poland
444 in response to ongoing climate changes in Europe. *International Journal of Biometeorology*, **61**, 49–59.
445 doi:10.1007/s00484-016-1190-3. URL <http://dx.doi.org/10.1007/s00484-016-1190-3>.

446 Wypych A, Ustrnul Z, Sulikowska A, Chmielewski FM, Bochenek B (2016b) Spatial and temporal variability of
447 the frost-free season in Central Europe and its circulation background. *International Journal of Climatology*,
448 **37**, 3340–3352. doi:10.1002/joc.4920.

449 Zhuo X, Zheng T, Zhang Z, *et al.* (2018) Genome-wide analysis of the NAC transcription factor gene family
450 reveals differential expression patterns and cold-stress responses in the woody plant *Prunus mume*. *Genes*,
451 **9**. doi:10.3390/genes9100494. URL <http://www.mdpi.com/2073-4425/9/10/494>.

452 Zohner CM, Benito BM, Svenning JC, Renner SS (2016) Day length unlikely to constrain climate-driven
453 shifts in leaf-out times of northern woody plants. *Nature Climate Change*, **6**, 1120–1123. doi:10.1038/
454 [nclimate3138](https://doi.org/10.1038/nclimate3138).

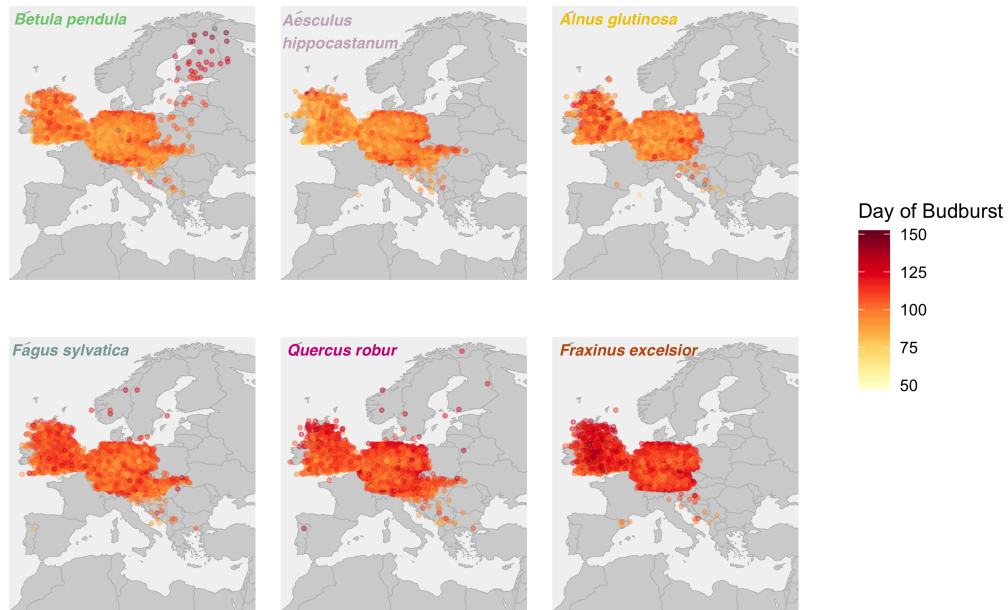


Figure 1: The average day of budburst is mapped by site for each species. Species are ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*. Earlier budburst dates are yellow and later budburst dates are in red.

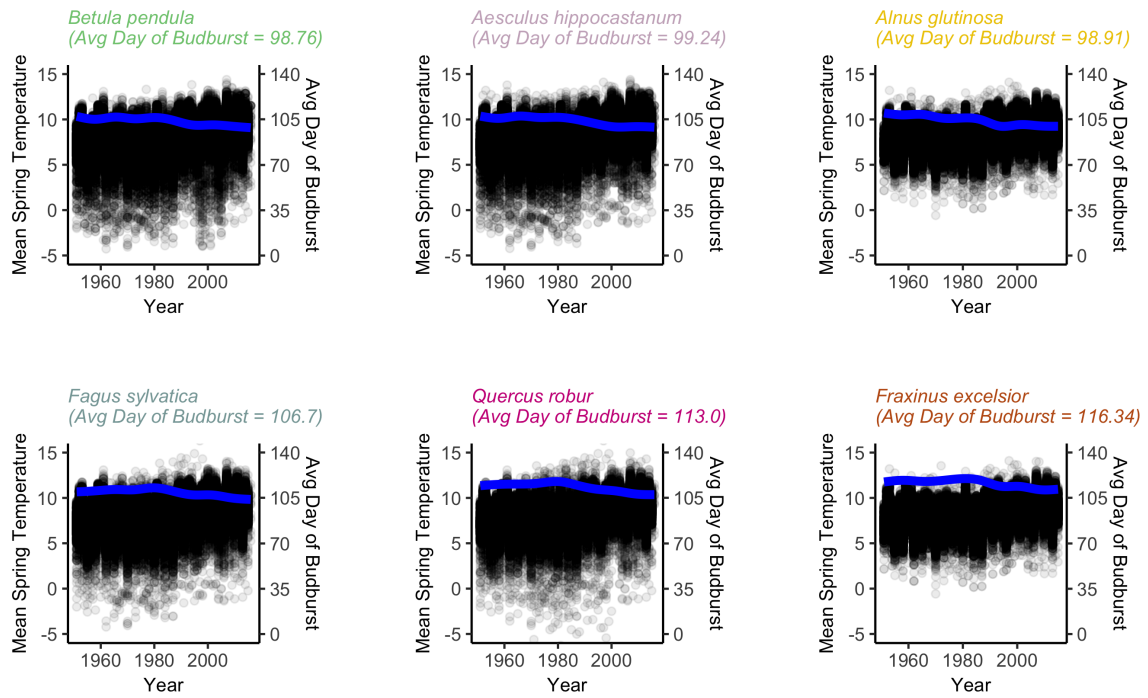


Figure 2: Mean spring temperatures are plotted for each site over time (from 1951-2016) for each species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula pendula* and the latest being *Fraxinus excelsior*.

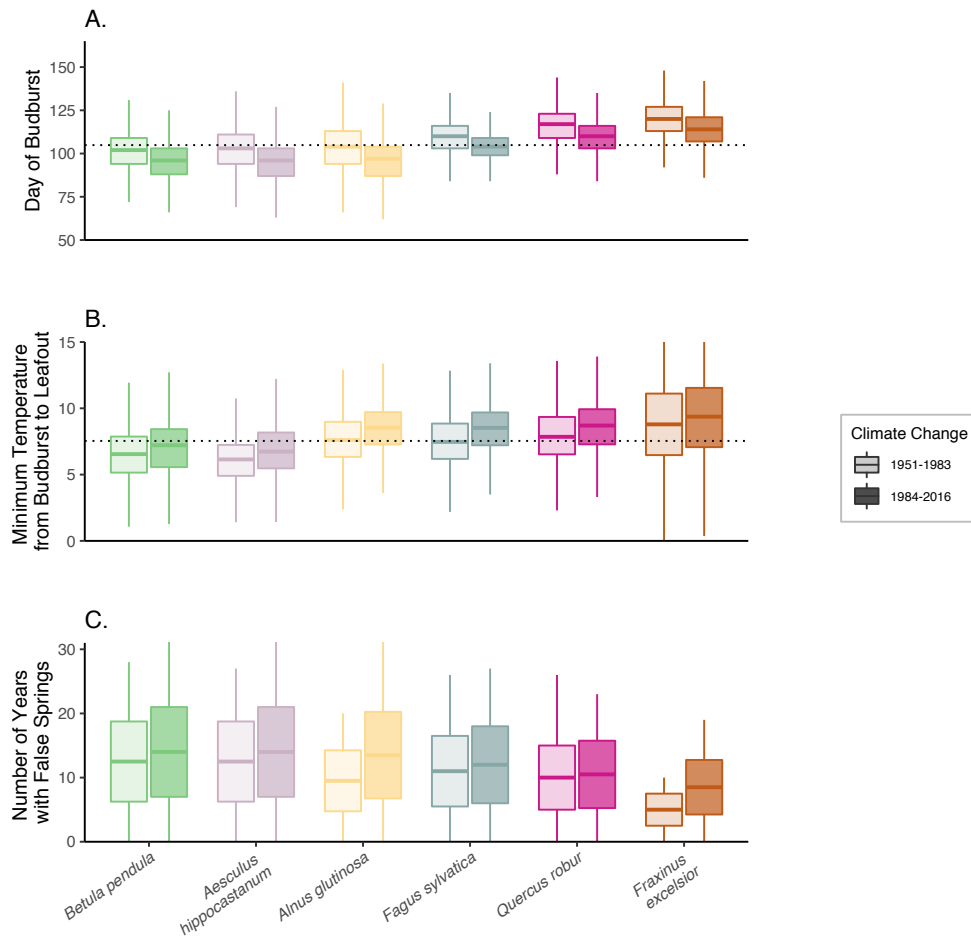


Figure 3: Budburst, minimum temperatures and false springs were compared before and after 1983 for each species. We plotted the day of budburst (A.) before and after 1983 for each species across all sites. We then compared the average minimum temperatures (B.) between budburst and leafout for all species 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.

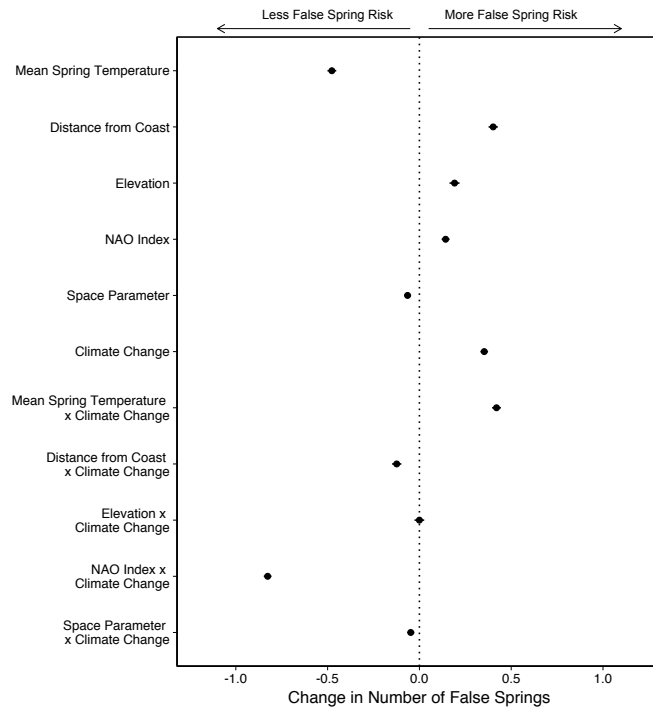


Figure 4: Model output with standardized durations of vegetative risk for each species. More positive parameter effects indicate an increased probability of a false spring whereas more negative effects suggest a lower probability of a false spring. Uncertainly intervals are at 90%. Parameter effects 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.

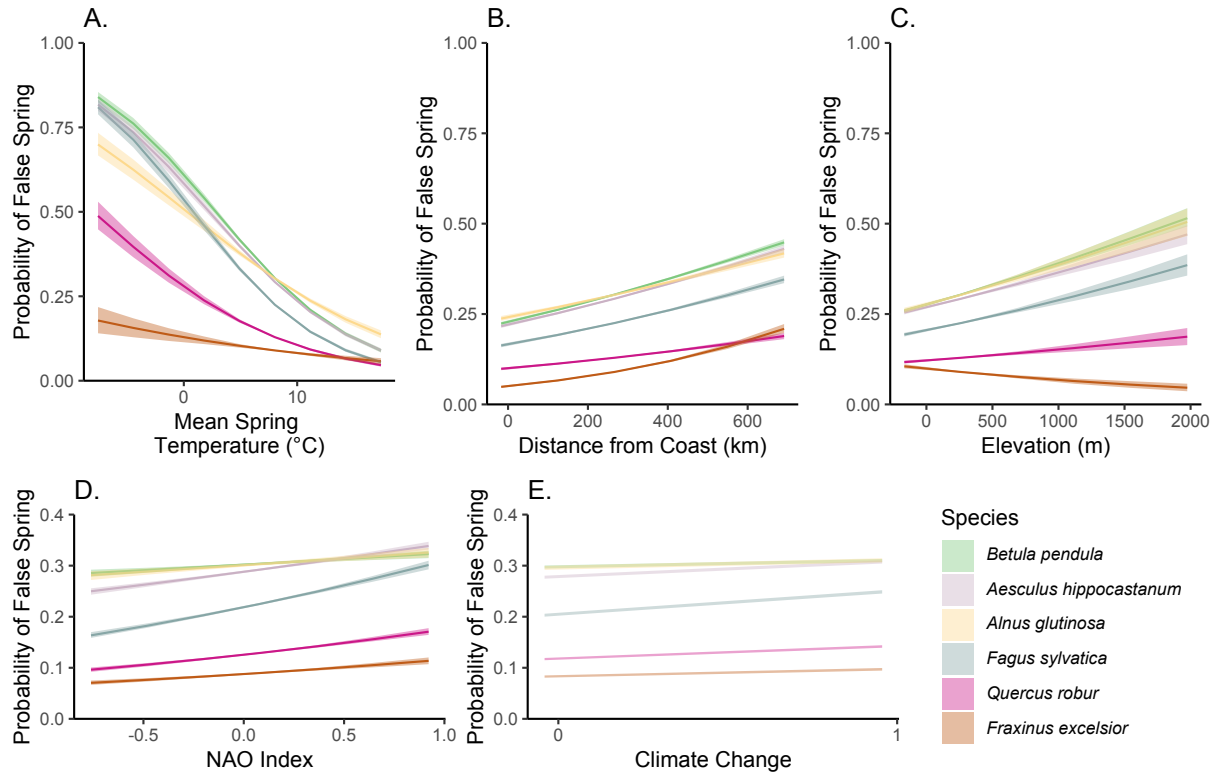


Figure 5: Plots showing the interaction effects of each predictor with species. (A.) As mean spring temperature increases, the probability of a false spring decreases for each species but *Fraxinus excelsior* always has the lowest risk of false spring. (B.) There's an increase in false spring risk for 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.