

# Climate change reshapes the drivers of false spring risk across European trees

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## Abstract

Temperate and boreal forests are at risk of late spring freezing events after budburst—also known as false springs. Research to date has generated conflicting results of whether climate change will decrease false springs, and thus reshape a fundamental factor that influences species' ranges. Conflicting results may be due to the myriad climatic and geographic factors that contribute to a plant's risk of a false spring, which—to date—no study has compared at once. Here, we assessed the effects of mean spring temperature, distance from the coast, elevation and the North Atlantic Oscillation (NAO) using PEP725 leafout data for six tree species across 11,648 sites in Europe, to determine which were the strongest predictors of false spring risk and how these predictors shifted with climate change. Across species, mean spring temperature and distance from the coast were the strongest predictors, with higher mean spring temperatures having a decreased risk in false springs (−7.64% for every 2°C increase) and sites further from the coast experiencing an increased risk in false springs (5.32% for every 150km from the coast). Elevation (2.23% for every 200m increase in elevation) and

NAO index (1.91% for every 0.3 increase) also increased false spring risk. The effects of these major drivers have been reshaped by climate change and are influencing false spring risk in new ways, with the climatic factors shifting considerably compared to the geographic factors. Though false spring risk is decreasing across species, the residual, unexplained effects of climate change have magnified the variation in risk across species, with a split among early- versus late-leafout species. Our results suggest that considering multiple spatial and climatic factors is essential for predicting false spring risk and having a better understanding of the unexplained complexities of climate change is critical.

## Introduction

Temperate tree and shrub species are at risk of damage from late spring freezing events after budburst, also known as false springs, and this risk may shift with climate change. With earlier springs due to warming (IPCC, 2015; Wolkovich *et al.*, 2012), the growing season is lengthening across many regions in the northern hemisphere (Chen *et al.*, 2005; Kukul & Irmak, 2018; Liu *et al.*, 2006). Longer growing seasons could translate to increased plant growth, assuming such increases are not offset by tissue losses due to false springs. Last spring freeze dates are not predicted to advance at the same rate as warming (Inouye, 2008; Labe *et al.*, 2016; Martin *et al.*, 2010; Wypych *et al.*, 2016b; Sgubin *et al.*, 2018), potentially amplifying the effects of false spring events in some 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 has advanced roughly twice as fast. Major false spring events have been recorded in recent years but studies have variously found that spring freeze damage may 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. Regardless, studies have found it can take 16-38 days for trees to refoliate after a freeze (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 freezes are one of the largest limiting factors to species ranges and have greatly shaped plant life history strategies (Kollas *et al.*, 2014). Temperate plants are exposed to freezing temperatures numerous times throughout the year, however, individuals are most at risk to damage in the spring, when freeze tolerance is lowest (Sakai & Larcher, 1987). Plants have adapted to these early spring risks through various mechanisms with one common strategy being avoidance (Vitasse *et al.*, 2014). Many temperate species

minimize freeze risk and optimize growth by using a complex mix of cues to initiate budburst: low winter temperatures (i.e., chilling), warm spring temperatures (i.e., forcing), and increasing spring daylengths (i.e., photoperiod). With climate change advancing, the interaction of these cues may shift spring phenologies both across and within species and sites, making some species less—or more—vulnerable to false springs than before. Species that leafout first each spring are especially at risk of false springs, as their budburst occurs during times of year when the risk of freeze events is relatively high. To date these species also appear to advance the most with warming (Wolkovich *et al.*, 2012), thus, if climate change increases the prevalence of late spring freezes, we would expect these species to see major increases in false spring risk. If climate change has restructured the timing and prevalence of false springs to later in the spring, then later-leafout species may experience major increases in false spring risk 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 (Liu *et al.*, 2018). Furthermore, recent studies have demonstrated site-specific effects may be more closely related to false spring risk: whether via elevation, where higher elevations appear at higher risk (Ma *et al.*, 2018; Vitasse *et al.*, 2018; Vitra *et al.*, 2017), or distance from the coast, where inland areas appear at higher risk (Ma *et al.*, 2018; Wypych *et al.*, 2016b). Improved understanding of which regional climatic factors impact false spring risk, including 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, thus failing to compare how multiple factors may together shape risk. False spring risk is influenced by multiple climatic and geographic factors, which may vary across species and time. Further, because predictors can co-vary—for example, higher elevation sites are often more distant from the coast—the best predictions of false springs should examine all predictors at once.

Here we investigate the influence of known spatial and climatic factors on false spring risk (defined here as when fell temperatures below  $-2.2^{\circ}$  between estimated budburst and leafout Schwartz, 1993). We assessed the number of false springs that occurred across 11,648 sites across Europe 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. We focus on the major factors shown or hypothesized to influence false spring risk: mean spring temperature, elevation, distance from the coast, and a major climatic oscillation that structures European climate—the North Atlantic Oscillation (NAO). The NAO is tied to

winter and spring circulation across Europe, with more positive NAO phases tending to result in higher than average winter and spring temperatures. With climate-change induced shifts, years with higher NAO indices have correlated to even earlier budburst dates since the late 1980s in some regions (Chmielewski & Rötzer, 2001), however little research has tested if more positive NAO phases also translates into more false springs. We aimed to understand which factors are the strongest predictors of false spring risk, and how the major predictors have shifted with climate change.

## Methods

### Phenological Data and Calculating Vegetative Risk

We obtained phenological data from the Pan European Phenology network (PEP725, [www.pep725.edu](http://www.pep725.edu)), which provides open access phenology records across Europe (Templ *et al.*, 2018). Since plants are most susceptible to damage from freezing temperatures between budburst and full leafout, we selected leafout data (i.e., in Meier, 2001, BBCH 11, which is defined as the point of leaf unfolding and the first visible leaf stalk) from the PEP725 dataset. The species used in the study were *Aesculus hippocastanum* Poir., *Alnus glutinosa* (L.) Gaertn., *Betula pendula* Roth., *Fagus sylvatica* Ehrh., *Fraxinus excelsior* L., and *Quercus robur* L. Selection criteria for the species were as follows: (1) to be temperate, deciduous species that were not cultivars or used as 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).

Plants are generally the most freeze tolerant in the winter but this freeze 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). Thus, for most 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). To capture this ‘high-risk’ timeframe, we subtracted 12 days from the leafout date to establish a standardized estimate for day of budburst (Donnelly *et al.*, 2017; Flynn & Wolkovich, 2018; USA-NPN, 2019) since the majority of the individuals were missing budburst observations. We additionally considered a model that altered the timing between budburst and leafout for each species. For this alternate 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 (Buerki *et al.*, 2010; Wang *et al.*, 2016; Hipp *et al.*, 2017; Flynn & Wolkovich, 2018).

## 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  $-2.2^{\circ}\text{C}$  (Schwartz, 1993) between budburst to leafout. We additionally tested this model by changing the definition of a freezing temperature from  $-2.2^{\circ}\text{C}$  (Schwartz, 1993) to  $-5^{\circ}\text{C}$  (Lenz *et al.*, 2013; Sakai & Larcher, 1987) in an additional 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 (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 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 and which will be referred to as the ‘climate change’ parameter henceforth.

## Data Analysis

### Simple regression models

We initially ran three simple regression models—following the same equation (below) but with varying responses—to assess the effects of climate change on budburst, minimum temperatures between budburst and leafout and the number of false springs across species (Equation 2).

$$\epsilon_i \sim \text{Normal}(y_i, \sigma^2) y_i = \alpha_{[i]} + \beta_{\text{ClimateChange}_{[i]}} + \beta_{\text{Species}_{[i]}} + \beta_{\text{ClimateChange} \times \text{Species}_{[i]}} + \epsilon_{[i]} \quad (2)$$

## 138 Main Model

139 To best compare across the effects of each climatic and geographic variable, we scaled all of the predictors  
 140 and used a z-score following the binary predictor approach (Gelman & Hill, 2006). To control for spatial  
 141 autocorrelation and to account for spatially structured processes independent from our regional predictors of  
 142 false springs, we generate an additional ‘space’ parameter for the model. To generate our space parameter  
 143 we first extracted spatial eigenvectors corresponding to our analyses’ units and selected the subset that  
 144 minimizes spatial autocorrelation of the residuals of a model including all predictors except for the space  
 145 parameter (Diniz-Filho *et al.*, 2012; Bauman *et al.*, 2017) (see supplement ‘Methods: Spatial parameter’ for  
 146 more details). We then took the eigenvector subset determined from the minimization of Moran’s I in the  
 147 residuals (MIR approach) and regressed them against the above residuals—i.e. number of false springs *vs.*  
 148 climatic and geographical factors. Finally we used the fitted values of that regression as our space parameter,  
 149 which, by definition, represents the portion of the variation in false springs that is both spatially structured  
 150 and independent from all other predictors in the model (e.g. average spring temperature, elevation, etc.  
 151 Griffith & Peres-Neto, 2006; Morales-Castilla *et al.*, 2012).

152 To estimate the probability of false spring risk across species and our predictors we used a Bayesian modeling  
 153 approach. By including all parameters in the model, as well as species, we were able to distinguish the  
 154 strongest contributing factors to false spring risk. We fit a Bernoulli distribution model (also know as a logistic  
 155 regression) using mean spring temperature (written as MST in the model equation), NAO, elevation, distance  
 156 from the coast, space, and climate change as predictors and all two-way interactions and species as two-way  
 157 interactions (Equation 1), using the brms package (Bürkner, 2017), version 2.3.1, in R (R Development Core  
 158 Team, 2017), version 3.3.1, and was written as follows:

$$y_i \sim \text{Binomial}(1, p) \quad (1)$$

$$\begin{aligned} \text{logit}(p) = & \alpha_{[i]} + \beta_{MST_{[i]}} + \beta_{DistanceCoast_{[i]}} + \beta_{Elevation_{[i]}} + \beta_{NAO_{[i]}} + \beta_{Space_{[i]}} + \beta_{ClimateChange_{[i]}} + \beta_{Species_{[i]}} \\ & + \beta_{MST \times Species_{[i]}} + \beta_{DistanceCoast \times Species_{[i]}} + \beta_{Elevation \times Species_{[i]}} + \beta_{NAO \times Species_{[i]}} \\ & + \beta_{Space \times Species_{[i]}} + \beta_{ClimateChange \times Species_{[i]}} + \beta_{MST \times ClimateChange_{[i]}} \\ & + \beta_{DistanceCoast \times ClimateChange_{[i]}} + \beta_{Elevation \times ClimateChange_{[i]}} \\ & + \beta_{NAO \times ClimateChange_{[i]}} + \beta_{Space \times ClimateChange_{[i]}} \end{aligned}$$

We ran four chains, each with 2,500 warm-up iterations and 4,000 sampling iterations for a total of 6,000 posterior samples for each predictor. We evaluated our model performance based on  $\hat{R}$  values that were close to one. We also evaluated effective sample size estimates, which were 1,994 or above. We additionally assessed chain convergence visually and posterior predictive checks. Due to the large number of observations in the data we used the FASRC Cannon cluster supported by the FAS Division of Science Research Computing Group at Harvard University to run the model.

Model estimates were on the logit scale (shown in all tables) and were converted to probability percentages in all figures for easier interpretation by using the ‘divide by 4’ rule (Gelman & Hill, 2006) and then back converted to the original scale by multiplying by two standard deviations. We calculated overall estimates (i.e., across species) of main effects in Figure 3, Figure S3 and Figure S4 from the average of the posteriors of each effect by species. We report all estimated values in-text as mean  $\pm$  98% uncertainty intervals, unless otherwise noted. The combined effects of climate change with all of the climatic and geographic factors across species were determined by adding all effects in the model plus species for after climate change and subtracting this from the combined effects in the model for each species after climate change. This difference was reported as the combined change in false spring risk for each species.

## Results

### Basic shifts in budburst and number of false springs

Day of budburst varied across the six species and across geographical gradients (Figure 1). *Betula pendula*, *Aesculus hippocastanum*, *Alnus glutinosa* (Figure 1A-C) generally initiated budburst earlier than *Fagus sylvatica*, *Quercus robur*, and *Fraxinus excelsior* (Figure 1D-F). Across all six species, higher latitude sites and sites closer to the coast tended to initiate budburst later in the season (Figure 1).

Across species, budburst dates advanced  $-5.22 \pm 0.15$  days after 1983 (Table S3) and minimum temperatures between budburst and leafout increased by  $0.62 \pm 0.3^\circ\text{C}$  after climate change (Table S4). This trend in advancing day of budburst for each species corresponds closely with increasing mean spring temperatures (Figure S1). While all species initiated budburst approximately seven days earlier (Figure 2A, Table S2 and Table S3), the average minimum temperature between budburst and leafout varied across the six species with *Betula pendula* and *Aesculus hippocastanum* experiencing the lowest minimum temperatures (Figure 2B), *Quercus robur* and *Fraxinus excelsior* experiencing the highest minimum temperatures, and *Fraxinus excelsior* experiencing the greatest variation (Figure 2B).

A simplistic view of changes in false springs—one that does not consider changes in climatic and geographic factors or effects of spatial autocorrelation—suggests that the number of false springs increased across species by 0.03% ( $\pm 0.05\%$ ) after climate change (i.e., after 1983), but with important variation by species (Figure 2C). Early-leafout species (*Aesculus hippocastanum*, *Alnus glutinosa* and *Betula pendula*) showed an increased risk whereas later bursting species (*Fagus sylvatica*, *Quercus robur* and *Fraxinus excelsior*) showed a decrease in risk (Table S5).

### The effects of climatic and geographic variation coupled with climate change on false spring risk

Climatic and geographic factors underlie variation across years and space in false springs (Figure 3 and Table S6) before recent climate change (1983). Mean spring temperature had the strongest effect on false springs, with warmer spring temperatures resulting in fewer false springs (Figure 3 and Table S6; comparable estimates come from using standardized variables, see Methods for more details). For every  $2^\circ\text{C}$  increase in mean spring temperature there was a -7.64% decrease in the probability of a false spring ( $-0.48 \pm 0.03$



probability of false spring/standard unit). Distance from the coast had the second biggest effect on false spring incidence. Individuals at sites further from the coast tended to have earlier leafout dates, which corresponded to an increased risk in false springs (Figure 3 and Table S6). For every 150km away from the coast there was a 5.32% increase in risk in false springs ( $0.4 \pm 0.03$  probability of false spring/standard unit). Sites at higher elevations also had higher risks of false spring incidence—likely due to more frequent colder temperatures—with a 2.23% increase in risk for every 200m increase in elevation ( $0.19 \pm 0.04$  probability of false spring/standard unit, Figure 3 and Table S6). More positive NAO indices, which generally advance leafout, slightly heightened the risk of false spring, with every 0.3 unit increase in NAO index there was a 1.91% increased risk in false spring or  $0.14 \pm 0.03$  probability of false spring/standard unit (Figure 3 and Table S6).

These effects varied across species (Figure 4). While there were fewer false springs for each species with increasing mean spring temperatures, *Betula pendula* had the greatest risk of false springs and *Fraxinus excelsior* had the lowest risk (Figure 4A). There was an increased risk of false spring for all species at sites further from the coast (Figure 4B), 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, except for *Fraxinus excelsior*, which had a slightly decreased risk at higher elevations (Figure 4C). With increasing NAO indices, the risk of false spring remained consistent for most species, except *Fagus sylvatica* experienced more with higher NAO indices (Figure 4D).

After climate change, the effects of these climatic and geographic factors on false spring risk shifted (Figure 3). Warmer sites still tended to have lower risks of false springs, but with climate change, increasing mean spring temperatures had much less of an effect on false spring risk with -2.84% decrease in risk per  $2^{\circ}\text{C}$  (or  $-0.06 \pm 0.06$  probability of false spring/standard unit versus -7.64% decrease per  $2^{\circ}\text{C}$  or -0.48 before climate change; Figure 3 and Figure S2A). There was a slightly reduced risk in false springs further from the coast after climate change (Figure 3 and Figure S2B) with 3.68% increase in risk per 150km (or  $0.28 \pm 0.07$  probability of risk/standard unit versus 5.32% increase 150km or  $0.4 \pm 0.04$  before climate change). The level of risk remained consistent before and after 1983 across elevations (Figure 3 and Figure S2C), with false spring risk being higher at higher elevations. After climate change, the rate of false spring incidence largely decreased with increasing NAO indices (Figure 3 and Figure S2D), now with a -9.15% decrease in risk per 0.3 unit increase in the NAO index (or  $-0.69 \pm 0.06$  probability of false spring/standard unit or versus 1.91% 0.3 unit increase in the NAO index or  $0.14 \pm 0.03$  before climate change). After climate change, NAO had the

strongest effect on false spring risk, with higher NAO indices rendering fewer false springs. Together there was a -14.55% decrease in risk of false springs (or a 0.58 decrease in probability or risk/standard unit) due to the combined effects of all the climatic and geographic factors after 1983 across species.

In addition to these combined changes in climatic and geographic factors, which we estimated across all species, there is still an unexplained shift in false spring risk due to climate change for most species. This unexplained effect of climate change varied strongly by species, with an 8.86% increased risk in false springs after climate change for *Aesculus hippocastanum* (or  $0.35 \pm 0.03$  probability of false spring/standard unit; Figure 3, Figure 4E and Table S6), a 10.54% increase for *Alnus glutinosa*, a 10.29% increase for *Betula pendula*, and a 0.75% for *Fagus sylvatica* (or a  $0.4 \pm 0.08$ ,  $0.41 \pm 0.08$  and  $0.032 \pm 0.08$  probability of false spring/standard unit respectively; Figure 3, Figure 4E and Table S6). Climate change decreased risk for *Fraxinus excelsior* by -4.27% and *Quercus robur* by -1.76% (or a  $-1.08 \pm 0.1$  and  $-0.67 \pm 0.08$  probability of false spring/standard unit respectively; Figure 3, Figure 4E and Table S6).

Considering the total effect of climate change on species—by combining the unexplained shifts in false spring risk with climate change for each species with the effects of the climatic and geographic factors after climate change—yields an overall mean decrease in risk of false springs after climate change for all species, but effects vary between early and later-leafout species. Earlier leafout species tended to see smaller declines in risk after climate change with a -5.77% decrease in risk for *Aesculus hippocastanum* (or  $-0.23 \pm 0.06$  probability of risk/standard unit), and a -4.27% decrease in risk for *Alnus glutinosa* and *Betula pendula* (or  $-0.17 \pm 0.09$  probability of risk/standard unit). Whereas the later leafout species had larger declines in risk, with a -13.8% decrease in risk for *Fagus sylvatica* (or  $-0.55 \pm 0.08$  probability of risk/standard unit), -18.82% decrease in risk for *Fraxinus excelsior* (or  $-0.75 \pm 0.11$  probability of risk/standard unit), and -16.06% decrease in risk for *Quercus robur* (or  $-0.64 \pm 0.09$  probability of risk/standard unit).

## Sensitivity of results to duration of risk and temperature thresholds

Our results remained consistent (in direction and magnitude) when we applied different rates of leafout for each species (i.e., varied the length of time between estimated budburst and leafout). Mean spring temperature (-8.08% decrease for every 2°C or  $-0.5 \pm 0.04$  probability of risk/standard unit) and distance from the coast (5.36% increase for every 150km or  $0.4 \pm 0.03$  probability of risk/standard unit) were the strongest predictors for false spring risk (Figure S3 and Table S7). After climate change, there was a slight increase in false spring risk at higher elevations (Figure S3 and Table S7) compared to our main findings.

Results remained generally consistent also when we applied a lower temperature threshold for defining a false spring (i.e.,  $-5^{\circ}\text{C}$ ), though there were more shifts in the magnitude of some effects, especially those of climate change. Mean spring temperature ( $-11.56\%$  decrease for every  $2^{\circ}$  or  $-0.72 \pm 0.07$  probability of risk/standard unit) and elevation ( $7.35\%$  increase in risk for every 200m or  $0.63 \pm 0.08$  probability of risk/standard unit) were the strongest predictors, with a weaker effect of distance from the coast ( $2.75\%$  for every 150km or  $0.21 \pm 0.08$  probability of risk/standard unit; Figure S4 and Table S8). There was much higher risk of false springs by climate change unexplained by climatic and geographic factors included in the model ( $14.55\%$  increase or  $0.58 \pm 0.07$  probability of risk/standard unit; Figure S4 and Table S8) and this was consistent across all six species, averaging a  $10.0\%$  increase ( $0.4$  probability of risk/standard unit).

## Discussion

Integrating over 66 years of data and 11648 sites across Central Europe and major climatic and geographic factors known to influence false spring risk, our results suggest climate change has decreased false spring risk for all six studied species. In line with previous work, our results support that higher elevations tend to experience more false springs (Vitasse *et al.*, 2018; Vitra *et al.*, 2017) and sites that are generally warmer have lower risks of false springs (Wypych *et al.*, 2016a). Individuals further from the coast typically initiated leafout earlier in the season, which subsequently lead to an increase in risk and, similarly, years with higher NAO indices experienced a slight increase in risk. But many of these factors have been re-shaped by climate change, in particular the effect of climatic factors have shifted dramatically compare to shifts in geographical factors. Across species, we find that NAO and mean spring temperature have shifted the most after 1983, while the effect of distance from the coast has only shifted slightly and the effect of elevation has not shifted (Figure S2.)

These shifts in the influence of climatic and geographic factors in turn result in different effects of climate change on species. Though there has been a consistent decrease in false spring risk for all species we studied—given the combined effects of all factors that contribute to false spring risk—some species (e.g. *Fraxinus excelsior* and *Quercus robur*) have experienced total decreases while others have experienced smaller shifts in risk (e.g., *Aesculus hippocastanum*, *Alnus glutinosa* and *Betula pendula*.) These species-specific effects integrate over shifts in the influence of climatic and geographic factors on false spring risk, as well as residual variation not explained by these factors, suggesting for which species we have a robust understanding of what

drivers underlie shifts in false spring risk with climate change, versus those species where more understanding is most critically needed.

## Climatic and geographic effects on false spring risk

Past studies using single parameters for false spring events (Liu *et al.*, 2018; Vitasse *et al.*, 2018; Ma *et al.*, 2018; Wypych *et al.*, 2016b) have led to contradicting predictions in future false spring risk. Some studies are finding an increased risk at higher elevations after climate change (Vitasse *et al.*, 2018), others are finding an increase in risk only in Europe but not in other regions (Liu *et al.*, 2018), while still others found a decrease in false spring risk across Central Europe (Wypych *et al.*, 2016b). Research to date has also found variation in false spring risk after climate change across species (Ma *et al.*, 2018). By integrating both climate gradients and geographical factors, we were able to disentangle the major predictors of false spring risk and merge these with species differences to determine which factors have the strongest effects on false spring risk. Mean spring temperature, distance from the coast and climate change were the strongest predictors for false spring risk, however, NAO and elevation also affected risk, emphasizing the need to incorporate multiple predictors. Further, climatic and geographic factors varied in how consistent, or not, they were across species. Mean spring temperature, distance from the coast and NAO effects were fairly consistent across species in direction, though *Fraxinus excelsior* experienced a much greater increase in risk at sites further from the coast and *Fagus sylvatica* had a heightened risk to higher NAO indices compared to the other species. Elevation was the only factor that varied in direction among the species with most species having an increased risk at higher elevations except for *Fraxinus excelsior*, which had a decreased risk. These inconsistencies may capture range differences among species, with contrasting effects of factors on individuals closer to range edges (Chaine & Beaubien, 2001).

Since the onset of recent major climate change, the strength of these climatic and geographic effects have changed, highlighting the need to better understand and model shifting drivers of false spring. After climate change, our results show a large decrease in risk of false spring with higher NAO indices. This could be because high NAO conditions no longer lead to temperatures low enough to trigger a false spring—that is, with climate-change induced warming high NAO conditions may no longer produce the freezing temperatures needed for false springs (Screen, 2017). Conversely, we found an increased risk with warmer mean spring temperatures after climate change, which may be driven by our studied plant species responding very strongly to increased spring warming with climate change (i.e., large advances in spring phenology, Figure S1), resulting in an

increased risk of exposure to false springs at these locations. Improved mechanistic models of how warming temperatures affect budburst (Gauzere *et al.*, 2017; Chuine *et al.*, 2016) could improve our understanding of how NAO and mean spring temperatures contribute to false spring risk.

## Variation in risk across species

By integrating climatic and regional factors—e.g., elevation, distance from the coast—we can unravel phenological effects on the probability risk from the climatic and geographic factors that contribute to an individual’s level of false spring risk. Due to the prominent shifts in the geographic and climatic factors (i.e., mean spring temperature, elevation, distance from the coast and NAO indices) with climate-change induced warming, we estimated a combined decrease in risk of false springs across all species after 1983, though residual (unexplained by climatic and geographic) effects of climate change resulted in marked differences in risk between early- and late-leafout species. Before 1983, false spring risk was slightly higher for species initiating leafout earlier in the spring but overall the risk was more consistent across species (Figure 4E). After climate change, however, species differences in risk amplified: the early-leafout species (i.e., *Aesculus hippocastanum*, *Alnus glutinosa* and *Betula pendula*) had an increased risk, the middle-leafout species—i.e. *Fagus sylvatica*—had a similar level of risk as before and the later-leafout species (i.e., *Fraxinus excelsior* and *Quercus robur*) had a decreased risk (Figure 4E).

Our combined estimates suggest all species have experienced a decline in false spring risk, in contrast with simple estimates of absolute changes in number of false springs across species (2C). These simple estimates, which suggested an increase in risk for early-leafout species and a decline or no change for later-leafout species, correlated more closely with estimated effects of climate change on species unexplained by climatic or geographic factors. The three early species (*Betula pendula*, *Aesculus hippocastanum*, *Alnus glutinosa*) had much higher unexplained shifts in false spring with climate change than the later species (*Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*), suggesting the climatic and geographic factors we examined are better capturing variation in false spring risk for later species—and that we still fundamentally lack information on what drives false spring risk for the early-species, which are also fundamentally the species with highest risk. While our model examines the major factors expected to influence false spring risk (Liu *et al.*, 2018; Ma *et al.*, 2018; Vitasse *et al.*, 2018; Wypych *et al.*, 2016b), these results highlight the need to explore other climatic factors to improve forecasting. We expect factors that affect budburst timing, such as shifts in over-winter chilling temperature, may help explain these discrepancies, but progress will require improved models of

chilling beyond the current models, which have been mainly developed for crops (Luedeling & Brown, 2011; Dennis, 2003).

Habitat preference and range differences among the species could also explain some of the species-specific variation in the results, but would require data on more species—and species that vary strongly in their climatic and geographic ranges—for robust analyses. The overall ranges of the predictors are similar across species, but *Betula pendula* extends to the highest elevation and latitude and spans the greatest range of distances from the coast, while *Quercus robur* experiences the greatest range of mean spring temperatures. Within our species, *Betula pendula* has the largest global distribution, extending the furthest north and east into Asia. The distribution of *Fraxinus excelsior* extends the furthest south (into the northern region of Iran). These range differences could potentially underlie the unexplained effect of climate change seen in our results and why the shifts in climatic and geographic factors did not explain much of the variation in false spring risk across species. *Fagus sylvatica*) was better explained by the model and this species has a smaller range, more confined to Central Europe. Future research that captures these spatial, temporal and climatic differences across myriad of species could greatly enhance predictions and help us understand these residual effects of climate change.

## Forecasting false springs

Our study shows how robust forecasting must integrate across major climatic and geographic factors that underlie false spring, and allow for variation in these factors across species and over time as warming continues. Of the four climatic and geographic factors we examined, only the effect of elevation remained constant before and after climate change. This is perhaps not surprising as climate change is shifting critical spring temperatures and reshaping the temporal and spatial dynamics of how climate effects budburst, leafout and freezing temperatures, yet it highlights the complexity that robust forecasting will require. Further, the differences we found across species suggest we can forecast some species better than others—such as *Fagus sylvatica*—which experienced almost zero unexplained climate change effects, thus, risk was likely determined by the climatic and geographic factors already included in the model.

Moving forward, more data on more species will be critical for estimates at community or ecosystem scales (at least in species-rich ecosystems). Related to this, more research on the effects of climate change on both budburst and leafout, the timing when individuals are most at risk to spring freeze damage (Chamberlain *et al.*, 2019; Lenz *et al.*, 2016) and on what temperatures cause leaf damage will help better understand

differences across species. Though we found that differing rates of leafout across species had minimal effects on predicting risk, we did find that the lower temperature threshold can have an impact on model estimates (and thus forecasts), with lower temperature thresholds (i.e.,  $-5^{\circ}\text{C}$  versus  $-2.2^{\circ}\text{C}$ ) predicting increased risk across all six study species. Our study uses an index of false spring risk, to estimate when damage may have occurred; it does not assess the intensity or severity of the false spring events observed, nor does it record the amount of damage to individuals. Other research has shown that this temperature threshold may vary importantly by species (Körner *et al.*, 2016; Lenz *et al.*, 2013; Zhuo *et al.*, 2018; Bennett *et al.*, 2018). Some species or individuals may be less freeze tolerant (i.e., are damaged from higher temperatures than  $-2.2^{\circ}\text{C}$ ), whereas other species or individuals may be able to tolerate temperatures as low as  $-8.5^{\circ}\text{C}$  (Lenz *et al.*, 2016). Further, cold tolerance can be highly influenced by fall and winter climatic dynamics that influence tissue hardiness (Hofmann & Bruelheide, 2015; Vitasse *et al.*, 2014; Charrier *et al.*, 2011) and can also influence budburst timing (Morin *et al.*, 2007). Thus, we expect these effects are likely integrated and that useful forecasting will require far better species-specific models of budburst, leafout and hardiness—including whether budburst and hardiness may be inter-related.

Our results highlight how climate change complicates forecasting through multiple levels. It has shifted the influence of climatic and geographic factors, fundamentally reshaping relationships with major climatic factors such that relationships before climate change no longer hold. It has also magnified species-level variation in false spring risk. Layered onto this complexity is unexplained variation that suggests we are missing key factors that drive interspecific variation in false spring risk. Our study focuses on one region (i.e., Central Europe) with high-quality and abundant data and we hope that our results can be applied to other systems as more and more data becomes available. Integrating these findings into future models will provide more robust forecasts and help us begin to unravel the complexities of climate change effects across species.

False spring events increased with climate change, though it was more pronounced in species that initiated budburst earlier in the season. 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. Our integrated approach may help direct future modelling advancements in false spring research. We show here the importance of using multiple geographic and climatic 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 for inter-specific risk. Additionally, we demonstrate that incorporating all regional effects is more important than simply assessing budburst

timing across species. Individuals that initiate budburst earlier in the season are not necessarily exposed to more false springs, thus, investigating site effects is essential for false spring risk in addition to day of budburst. Our results suggest there is a heightened risk of false springs with climate change for some species 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.
- Bauman D, Drouet T, Dray S, Vleminckx J (2017) Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography*, **0**. doi:10.1111/ecog.03380.
- 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 Atauri IG, Wolkovich EM (2019) Rethinking false spring risk. *Global Change Biology*, **25**, 2209–2220. doi:10.1111/gcb.14642.
- Charrier G, Bonhomme M, Lacoïnte A, Améglio T (2011) Are budburst dates, dormancy and cold acclimation in walnut trees (*Juglans regia* L.) under mainly genotypic or environmental control? *International Journal of*



*Biometeorology*, **55**, 763–774. doi:10.1007/s00484-011-0470-1. URL <https://doi.org/10.1007/s00484-011-0470-1>.

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](https://doi.org/10.1016/S0168-1923(01)00233-7).

Chuine I, Beaubien EG (2001) Phenology is a major determinant of tree species range. *Ecology Letters*, **4**, 500–510. doi:10.1046/j.1461-0248.2001.00261.x. URL <https://onlinelibrary.wiley.com/doi/abs/10.1046/j.1461-0248.2001.00261.x>.

Chuine I, Bonhomme M, Legave JM, García de Cortázar-Atauri I, Charrier G, Lacointe A, Améglio T (2016) Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global Change Biology*, **22**, 3444–3460. doi:10.1111/gcb.13383. URL <http://dx.doi.org/10.1111/gcb.13383>.

Dennis F (2003) Problems in standardizing methods for evaluating the chilling requirements for the breaking of dormancy in buds of woody plants. *HortScience*, **38**, 347–350.

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.

Gauzere J, Delzon S, Davi H, Bonhomme M, Garcia de Cortazar-Atauri I, Chuine I (2017) Integrating interactive effects of chilling and photoperiod in phenological process-based models. A case study with two European tree species: *Fagus sylvatica* and *Quercus petraea*. *Agricultural and Forest Meteorology*, pp. 9–20.

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.
- 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.
- Hofmann M, Bruelheide H (2015) Frost hardiness of tree species is independent of phenology and macroclimatic niche. *Journal of Biosciences*, **40**, 147–157. doi:10.1007/s12038-015-9505-9.
- 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.
- 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](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.
- Kukal MS, Irmak S (2018) U.S. Agro-Climat 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.
- 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.
- Luedeling E, Brown PH (2011) A global analysis of the comparability of winter chill models for fruit and nut trees. *International Journal of Biometeorology*, **55**, 411–421.
- 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.
- 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<sub>2</sub>. *Global Change Biology*, **16**, 1057–1070. doi:10.1111/j.1365-2486.2009.01987.x.

- Meier U (2001) Growth stages of mono-and dicotyledonous plants BBCH Monograph Edited by Uwe Meier  
Federal Biological Research Centre for Agriculture and Forestry. *Agriculture*, **12**, 141—147 ST — Geo-  
chemical study of the organic mat. doi:10.5073/bbch0515.
- 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.
- Morin X, Améglio T, Ahas R, *et al.* (2007) Variation in cold hardiness and carbohydrate concentration from  
dormancy induction to bud burst among provenances of three European oak species. *Tree Physiology*, **27**,  
817–825. doi:10.1093/treephys/27.6.817. URL <https://doi.org/10.1093/treephys/27.6.817>.
- 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, phe-  
nology, 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.
- Schwartz MD (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography*, **14(6)**,  
536–550.
- Screen JA (2017) The missing northern european winter cooling response to arctic sea ice loss. *Nature*  
*Communications*, **8**, 14603. doi:10.1038/ncomms14603. URL <https://doi.org/10.1038/ncomms14603>.
- 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>.
- USA-NPN (2019) Plant and animal phenology data. *USA National Phenology Network*. doi:10.5066/F78S4N1V. URL <http://doi.org/10.5066/F78S4N1V>.
- Vitasse Y, Lenz A, Körner C (2014) The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science*, **5**. doi:10.3389/fpls.2014.00541.
- Vitasse Y, Schneider L, Rixen C, Christen D, Rebetez M (2018) Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades. *Agricultural and Forest Meteorology*, **248**, 60 – 69. doi:<https://doi.org/10.1016/j.agrformet.2017.09.005>.
- 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.
- 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.
- 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.
- 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.

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

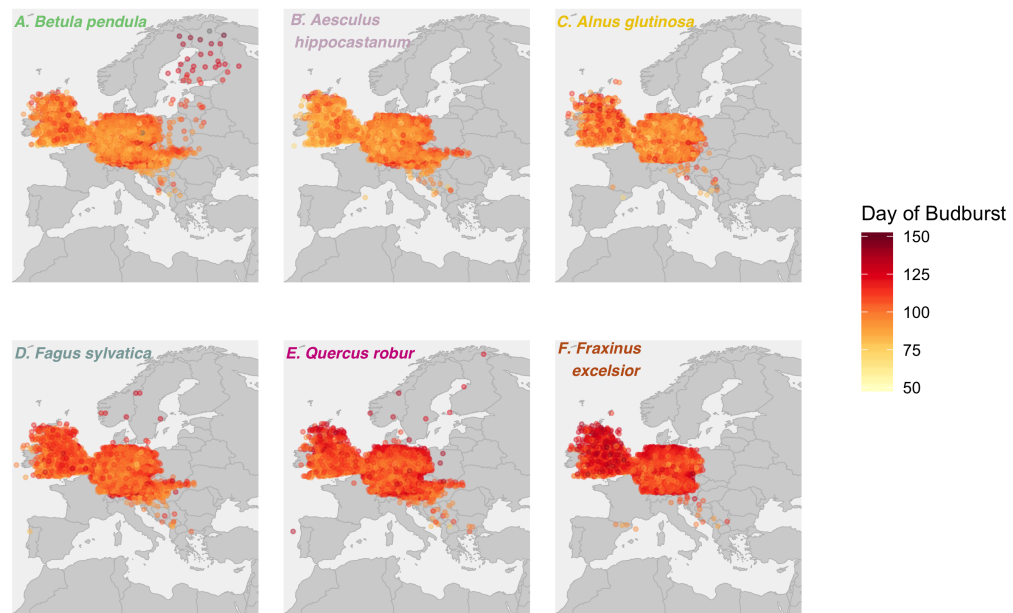


Figure 1: The average day of budburst mapped by site for each species (ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*). Species names are color-coded to match figures throughout the text.

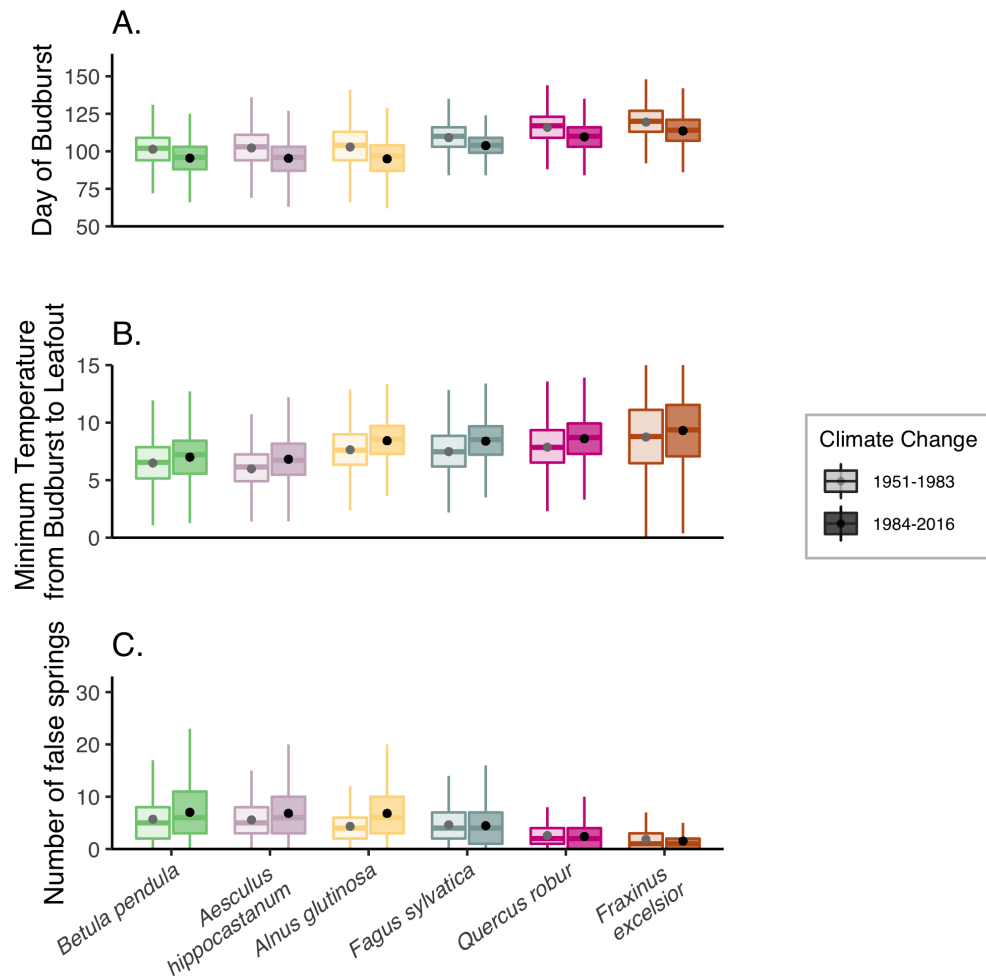


Figure 2: Day of budburst (A.), minimum temperatures between budburst and leafout (B.) and number of false springs (C.) before and after 1983 across species for all sites. Box and whisker plots show the 25th and 75th percentiles (i.e., the interquartile range) with notches indicating 95% uncertainty intervals. Dots and error bars overlaid on the box and whisker plots represent the model regression outputs (Tables S3-S5). Error bars from the model regressions indicate 98% uncertainty intervals but, given the number of sites, are quite small and thus not easily visible (see Tables S3-S5). Species are ordered by day of budburst and are color-coded to match the other figures.

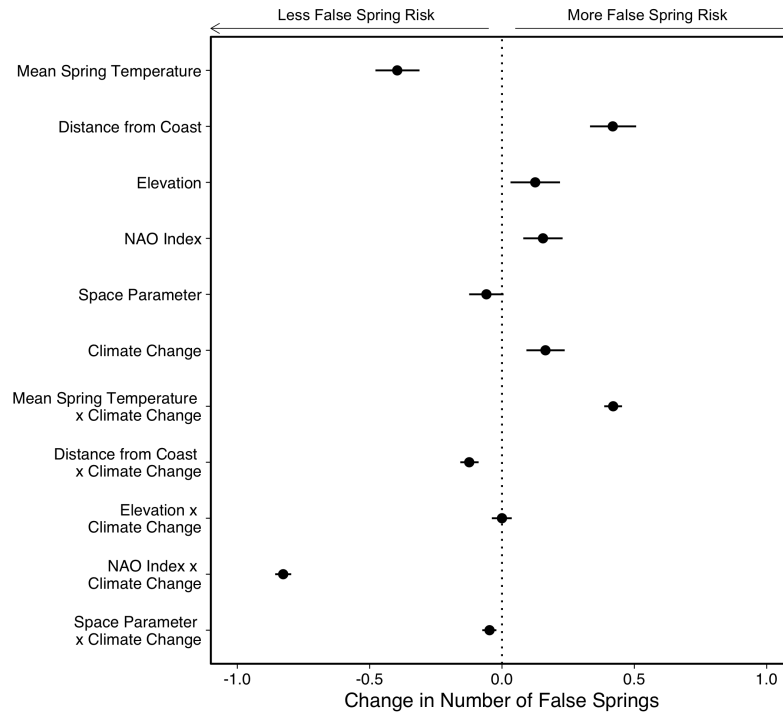


Figure 3: Effects of species, climatic and geographical predictors on false spring risk. More positive values indicate an increased probability of a false spring whereas more negative values suggest a lower probability of a false spring. Dots and lines show means and 98% uncertainty intervals. Values closer to zero have less of an effect on false springs. There were 582,211 zeros and 172,877 ones for false springs in the data. See Table S6 for full model output.



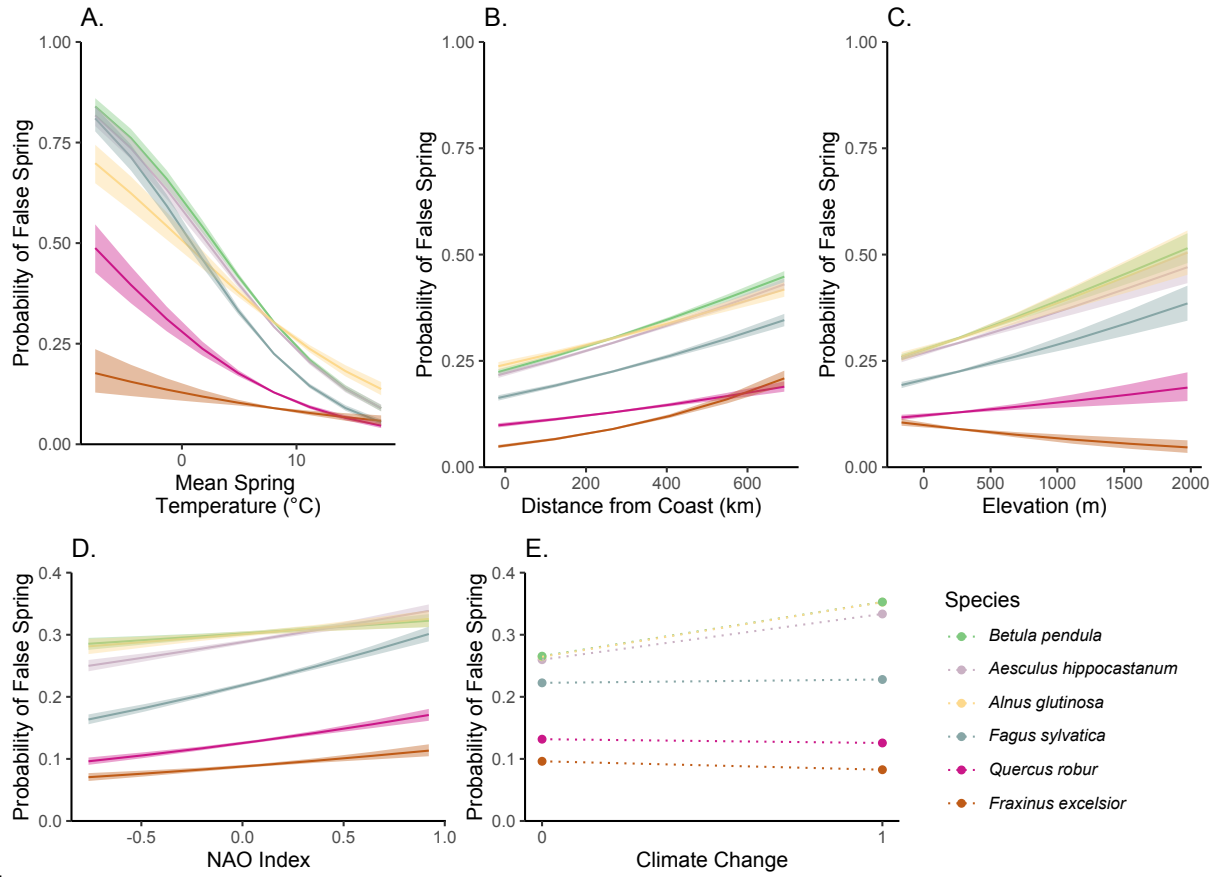


Figure 4: Species-level variation across geographic and spatial predictors (i.e., mean spring temperature (A.), distance from the coast (B.), elevation (C.), and NAO index (D.)). Lines and shading are the mean and 98% uncertainty intervals for each species. To reflect the raw data, we converted the model output back to the original scale for the x-axis in each panel. See Table S6 for full model output.