Climate change increases the risk of false springs in European trees

OR

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

OR

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

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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,

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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 (Chen *et al.*, 2005; Kukal & Irmak, 2018; Liu *et al.*, 2006), but late spring frosts are still occurring in many of these regions (Wypych *et al.*, 2016b). Temperate tree and shrub species are initiating leafout 4-6 days on average earlier per °C of warming (IPCC, 2015; Wolkovich *et al.*, 2012) but last spring freeze dates are not predicted to advance at the same rate (Inouye, 2008; Labe *et al.*, 2016; Martin *et al.*, 2010; Sgubin *et al.*, 2018), potentially amplifying the effects of false spring events in these regions. In Germany, for example, the last freeze date has advanced by 2.6 days per decade since 1955 (Zohner *et al.*, 2016) but budburst 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 (Augspurger, 2009, 2013; Gu *et al.*, 2008; Menzel *et al.*, 2015), which can detrimentally affect crucial processes such as carbon uptake and nutrient cycling (Hufkens *et al.*, 2012; Klosterman *et al.*, 2018; Richardson *et al.*, 2013).

Spring frosts are one of the largest limiting factors in species range limits and have greatly shaped plant life history strategies (Kollas *et al.*, 2014). Temperate plants are exposed to freezing temperatures numerous times throughout the year, however, individuals are most at risk to damage in the spring, when frost tolerance is lowest (Sakai & Larcher, 1987). Temperate plants have adapted to these early spring risks through various mechanisms with one common strategy being avoidance (Vitasse *et al.*, 2014). 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 (Lenz *et al.*, 2016; Vitasse *et al.*, 2014). Individuals that initiate budburst and have not fully leafed out before the last spring freeze are at risk of leaf tissue loss, damage to the xylem, and slowed canopy development (Gu *et al.*, 2008; Hufkens *et al.*, 2012). Thus, it is essential to consider the length of time between budburst and leafout — when individuals are most at risk to spring freeze damage (Lenz *et al.*, 2016) — in order to better predict false spring risk. We will refer to this timing between budburst and leafout as the duration of vegetative risk (Chamberlain *et al.*, 2019).

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 (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.Some research suggests false spring incidence has already begun to decline in many regions (i.e. across parts of North America and Asia), however the prevalence of spring frosts has consistently increased across Europe since 1982 (Liu *et al.*, 2018). Furthermore, recent studies have demonstrated site effects may be more closely related to false spring risk: whether via altitudinal variation (Ma *et al.*, 2018; Vitasse *et al.*, 2018; Vitra *et al.*, 2017) or distance from the coast (Ma *et al.*, 2018; Wypych *et al.*, 2016b). By better understanding these regional climatic implications and which factors are most crucial for predicting risk, we may be able to determine which regions are at risk currently and which regions will be more at risk in the future.

The majority of false spring studies assess the effects of one predictor (e.g. temperature, elevation or distance from the coast) on false spring prevalence but most fail to incorporate multiple effects. 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 (Chmielewski & Rötzer, 2001), 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° (Schwartz, 1993) 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 (Kharouba *et al.*, 2018; Stocker *et al.*, 2013). 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 (Templ *et al.*, 2018). Since plants are most susceptible to damage from frost 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 for crops, (2) there were at least 90,000 observations of BBCH 11 (leafout), (3) to represent over half

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of the total number of sites available (11,684), and (4) there were observations for at least 65 out of the 66 years of the study (1951-2016) (Table S1). We then subtracted 12 days from the leafout date to establish a standardized estimate for day of budburst (Donnelly *et al.*, 2017; Flynn & Wolkovich, 2018; USA-NPN, 2019) 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 (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°C (Schwartz, 1993) during the duration of vegetative risk. We additionally tested this model by changing the definition of a freezing temperature from -2.2°C (Schwartz, 1993) to -5°C (Lenz *et al.*, 2013; Sakai & Larcher, 1987) 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 (Basler & Körner, 2012; Körner *et al.*, 2016). We collected NAO-index data from the KNMI Climate Explorer CPC daily NAO time series and selected the NAO indices from November until April to best capture the effects of NAO on budburst for each region and then took the mean NAO index during these months (KNMI, 2018). Since the primary aim of the study is to predict false spring incidence in a changing climate, we split the data: before temperature trends increased (1951-1983) and after trends increased (1984-2016, Kharouba *et al.*, 2018; Stocker *et al.*, 2013) to represent climate change.

Data Analysis

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 (Gelman & Hill, 2006). 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 (Diniz-Filho *et al.*, 2012; David *et al.*, 2017) (see supplement 'Methods: Spatial parameter' for more details). We then took the eigenvector subset determined from the minimization 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. Griffith & Peres-Neto, 2006; Morales-Castilla *et al.*, 2012).

To best estimate the number of false springs across-species levels we used a Bayesian modeling approach. By including all parameters in the model, as well as species levels groups, we were able to distinguish the strongest contributing factors to false spring risk while eliminating artifacts due to data availability or data distribution for specific species. 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 (Bürkner, 2017), version 2.3.1, in R (R Development Core Team, 2017), version 3.3.1, and was written as follows:

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

162 We ran four chains, each with 2,500 warm-up iterations and 4,000 sampling iterations for a total of 6,00
163 posterior samples for each predictor. We evaluated our model performance on $\hat{R}$ values that were close to
164 one and low ratios of effective sample size estimates to total sample size (most parameters were below 1.05,
165 with two parameters above 1.1). We additionally assessed chain convergence and posterior predictive checks.

Results

Species variation in budburst and false spring incidence

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

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

176 After 1983, all species initiated budburst s̃ix days earlier (Figure 3A and Table SXX) and the minimum
177 temperature between budburst and leafout was higher. The average minimum temperature between bud-
178 burst and leafout, however, varied across the six species with *Betula pendula* and *Aesculus hippocastanum*
179 experiencing the lowest minimum temperatures (Figure 3B) and with *Fraxinus excelsior* experiencing the
180 greatest variation (Figure 3B). There was wide variation across sites in false spring risk for each species but
181 all species were more at risk of false springs after 1983 (Figure 3C). False spring risk for *Fraxinus excelsior*
182 increased the most (Figure 3C), likely due to data availability and data distribution for *Fraxinus excelsior*
183 over time. Thus, species alone is not a sufficient predictor for false spring risk. Spatial and climatic effects
184 must additionally be included to understand what drives false spring risk and to eliminate influence from
185 data availability.

The effects of climatic and spatial variation on false spring incidence

The effects of the spatial and climatic predictors varied in both direction and magnitude (Figure 4 and Table SXX) for the main model testing climatic and spatial variation in false spring risk. Mean spring temperature had the strongest effect on false springs, with warmer spring temperatures resulting is fewer false springs (Figure 4 and Table SXX). For every 2°C increase in mean spring temperature there was a 7.6% decreased risk in the number of false springs. Distance from the coast had the second 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 (Figure 4 and Table SXX). For every 150km away from the coast there was a 5.3% increase in risk in false springs. Sites at higher elevations also had higher risks of false spring incidence — likely due to more frequent colder temperatures — with a 2.2% increase in risk for every 200m increase in elevation (Figure 4 and Table SXX). 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 1.9% increased risk in false spring (Figure 4 and Table SXX). Overall, there were more false springs after 1983 (8.8% increased risk, Figure 4 and Table SXX).

After climate change, the effects of these spatial and climatic factors on false spring risk shifted (Figure 4). 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 (Figure 4 and Figure S1A). This is likely due to advancing budburst with a warming 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 (Figure 4 and Figure S1B). The level of risk remained consistent before and after 1983 across elevations (Figure 4 and Figure S1C), 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 4 and Figure S1D) – likely due to a large advancement in budburst and warmer temperatures overall for those years.

The rate of false spring incidence varied across species and site location (Figure 5). Species respond similarly in direction (i.e., positive or negative trends along each predictor) – except for *Fraxinus excelsior* with elevation (Figure 5C) – but the magnitude of the effects varied (i.e., as is evident from the differing slopes of the lines, Figure 5). With increasing mean spring temperatures, there were fewer false springs for each species, however *Betula pendula* had the greatest risk of false springs and *Fraxinus excelsior* had the lowest risk (Figure 5A). There was an increased risk of false spring for all species at sites further from the coast (Figure 5B), with a sharp increase in risk for *Fraxinus excelsior* at sites further from the coast. With increasing elevation, all

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species had a greater risk of a false spring occurring except for *Fraxinus excelsior* — which had a slightly decreased risk at higher elevations (Figure 5C) — 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 5D). *Betula pendula*, *Aesculus hippocastanum* and *Alnus glutinosa* all experienced more false springs after 1983 (Figure 5E).

Sensitivity analyses

1. <u>Model with varying durations of vegetative risk</u>: By having different durations of vegetative risk for each species, the magnitude and direction of the predictors remained consistent with the main model (Figure SXX). There were more false springs after 1983 (8.6% increase, Figure SXX) and mean spring temperature (-8.1% for every 2 °C) and distance from the coast (5.4% increase for every 150km) were the strongest predictors for false spring risk (Figure SXX). 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 (Figure SXX and Figure SXX). Thus, the results did not largely vary from the main model.

2. <u>Model with lower temperature threshold for false spring definition</u>: 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), though less consistent than the model with varying durations of vegetative risk. There was much higher risk of false springs after 1983 (14.6% increase). Mean spring temperature (-11.6% for every 2°) and elevation (7.4% increase in risk for every 200m) were the strongest predictors, with a weaker effect of distance from the coast (2.8% for every 150km). Overall, the results remained consistent with the main model, with some differences.

Discussion

Climate change has increased false spring risk by 8.8% across the European distribution of our species. But this average hides many important complexities as we found that 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 probability of risk. *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.

Past studies using single predictors for false spring events (Liu *et al.*, 2018; Ma *et al.*, 2018; Vitasse *et al.*, 2018; Vitra *et al.*, 2017; Wypych *et al.*, 2016b) lead to contradicting predictions in future false spring risk. By integrating climate gradients and spatial factors, we are able to disentangle the major predictors of false spring risk and integrate these with species differences. 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, further emphasizing the need to incorporate all predictors. 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, thus studying these predictors over time is also essential to forecast false spring risk.

Species differences

There is robust evidence for advancing budburst with climate change (Cleland *et al.*, 2007; IPCC, 2015; Wolkovich *et al.*, 2012) and some studies indicate earlier budburst species are more at risk of false spring damage (Ma *et al.*, 2018). After 1983, all of our species initiated budburst earlier in the spring and there was an overall increase in false spring risk. Additionally, some of the early bursting species were more susceptible to false springs (i.e. *Betula pendula* and *Aesuculus hippocastanum*) but all species were still susceptible to risk. 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 3C), however this conflicts with the overall model output (Figure 5E). The distribution of *Fraxinus excelsior* data is likely influencing the results seen in Figure 3C, 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.

Habitat preference and range differences among the species could explain some of the species-specific variation in the results. Within our species, *Betula pendula* has the largest distribution, extending the furthest north and east into Asia. The distribution of *Fraxinus excelsior* extends the furthest south into the northern region of Iran. Looking at our data distribution alone, the overall ranges of the predictors are similar across species but *Betula pendula* extends to the highest altitude and latitude and spans the greatest range of distances from the coast, while *Quercus robur* experiences the greatest range of temperatures. However, we would need

more species to investigate inter-specific differences in traits in order to explain the variation in results.

Climatic and regional effects

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 these 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 (Griffith & Peres-Neto, 2006; Diniz-Filho *et al.*, 2012; Morales-Castilla *et al.*, 2012; David *et al.*, 2017). Approaches such as ours may provide more robust forecasts of false spring risk and more clearly elucidate species level differences in risk 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 (Vitasse *et al.*, 2018; Vitra *et al.*, 2017), sites that are generally warmer have lower risks of false springs (Wypych *et al.*, 2016a), and risk increases with climate change (Liu *et al.*, 2018). However, we also discovered that effects of elevation and distance from the coast cannot be assumed to be the same (i.e., sites close to the coast does not necessarily correspond to sites at low elevations), which contradicts previous studies (Ma *et al.*, 2018). This is evident given our results, which show that sites further from the coast had a stronger effect on false spring risk than sites at higher elevations. And the relationship of these predictors shifted after 1983. With shifts in climate, sites further from the coast experienced fewer false springs, whereas there was little change for sites at higher elevations.

In summary, false spring risk is increasing across our study species, even with increasing minimum temperatures during the duration of vegetative risk (Figure 3B). Recent studies have also found that sites experiencing warming with climate change are experiencing more false springs, especially in Europe (Liu *et al.*, 2018). This may suggest a shifting relationship among spring warming, budburst and false spring risk. Plants at certain regions could be responding more strongly to increased spring warming with climate change but 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.

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Forecasting future false springs

Our study does not assess the intensity or severity of the false spring events observed nor does it record the amount of damage to individuals. It is possible that with increasing false spring risk, these events coupled with climate change could be lasting longer or could reach lower temperatures. Additionally, there is sufficient evidence that species vary in their tolerance to minimum temperature extremes (Körner *et al.*, 2016; Lenz *et al.*, 2013; Zhuo *et al.*, 2018; Bennett *et al.*, 2018). Some species or individuals may be less frost tolerant (i.e., are damaged from higher temperatures than -2.2°C), whereas other species or individuals may be able to tolerate temperatures as low as -8.5°C (Lenz *et al.*, 2016). For this reason, future models should ideally incorporate species-specific temperature thresholds to best capture the shifts in false spring risk of damage over time and space.

Similarly, shifts in phenological cues with climate change may impact individuals and species differently. 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 (Chamberlain *et al.*, 2019; Lenz *et al.*, 2016). 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.

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. 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 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 a more consistent proxy for false spring risk than budburst time. 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.

Conclusion

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. 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.

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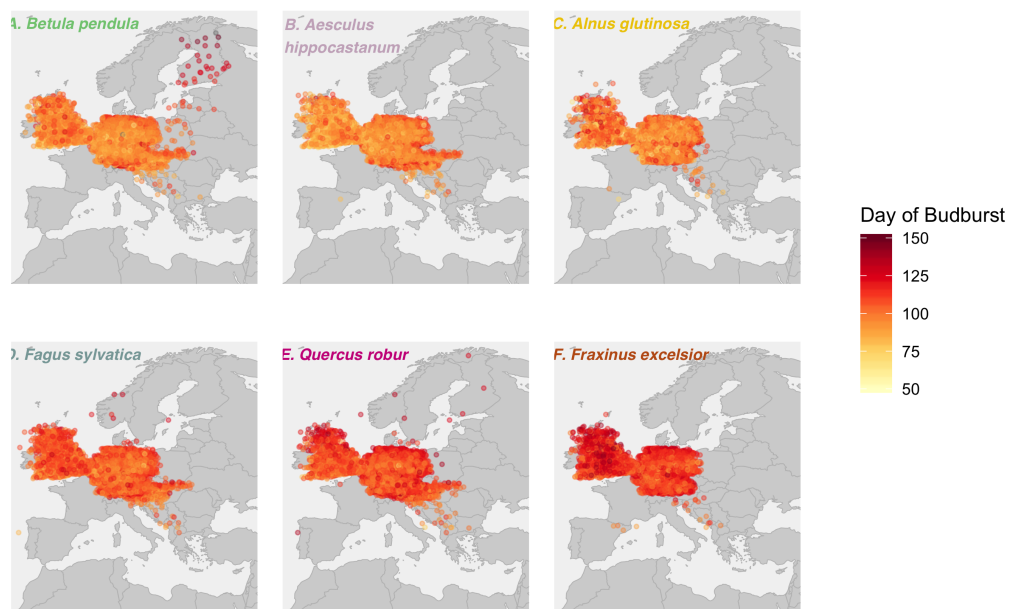
Tables and Figures

Figure 1: The average day of budburst is mapped by site for each species. Species are ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*. Earlier budburst dates are yellow and later budburst dates are in red. Species are color-coded to match figures throughout the text.
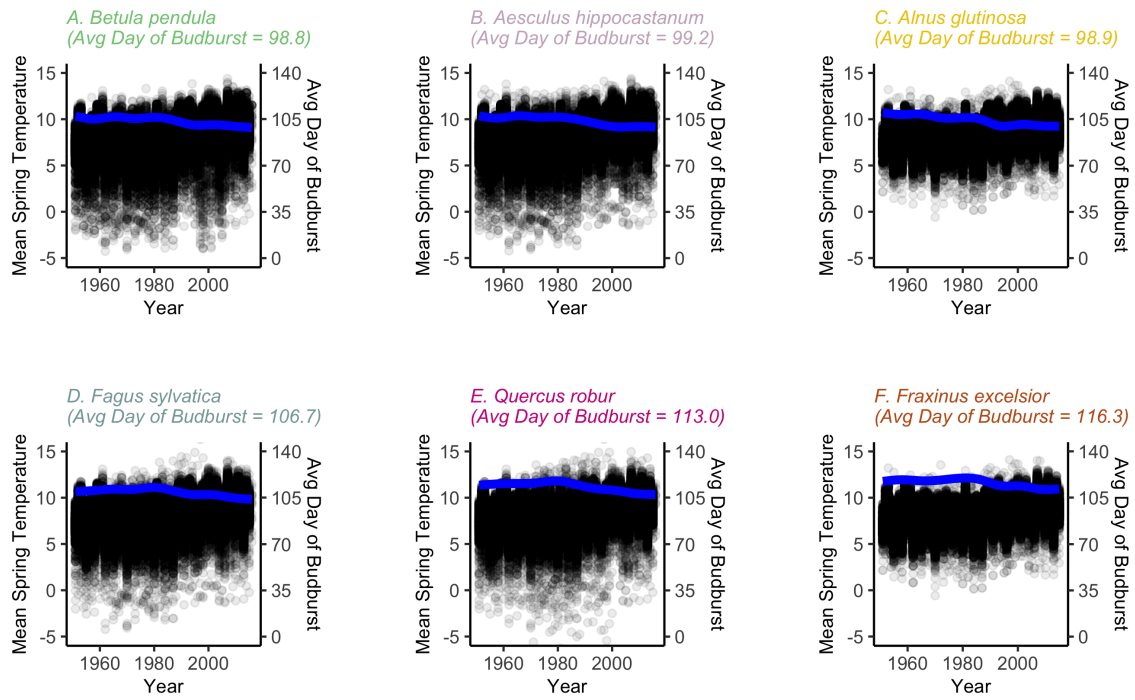
Figure 2: Mean spring temperatures are plotted for each site and year (from 1951-2016) for each species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula pendula* and the latest being *Fraxinus excelsior* and are color-coded to match the other figures.
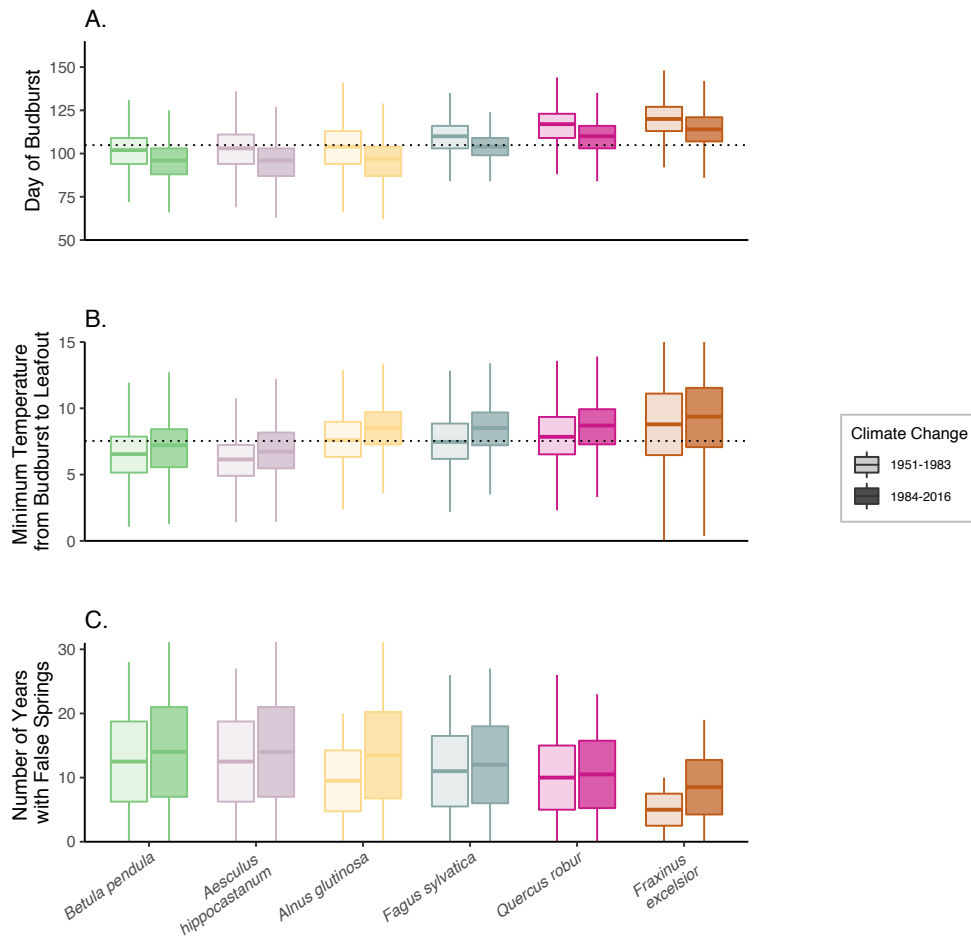
Figure 3: Budburst, minimum temperatures and false springs were compared before and after 1983 for each species. We plotted the day of budburst (A.) before and after 1983 for each species across all sites. We then compared the average minimum temperatures (B.) between budburst and leafout for all species 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 and are color-coded to match the other figures.
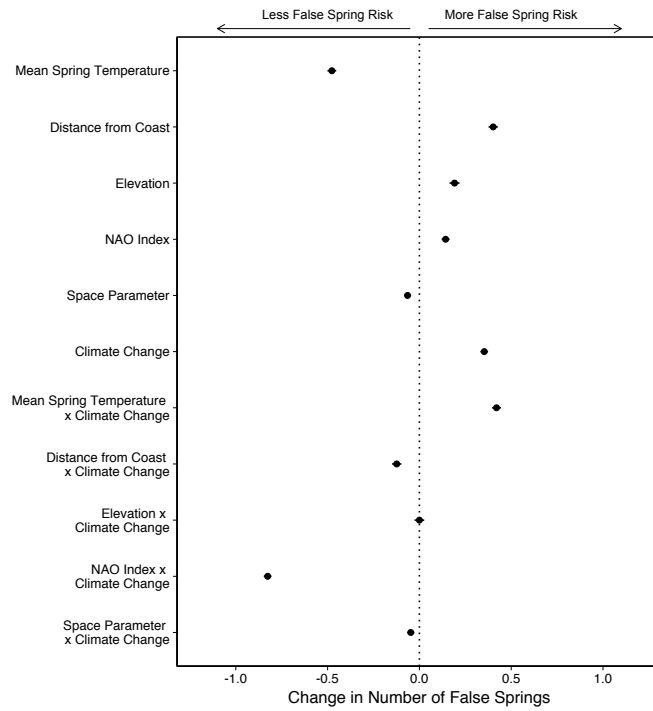
Figure 4: Model output with standardized durations of vegetative risk for each species. More positive values indicate an increased probability of a false spring whereas more negative values suggest a lower probability of a false spring. Dots and lines show means and 10% uncertainty intervals. Values closer to zero have less of an effect on false springs. There were 582,211 zeros and 172,877 ones for false spring in the data.
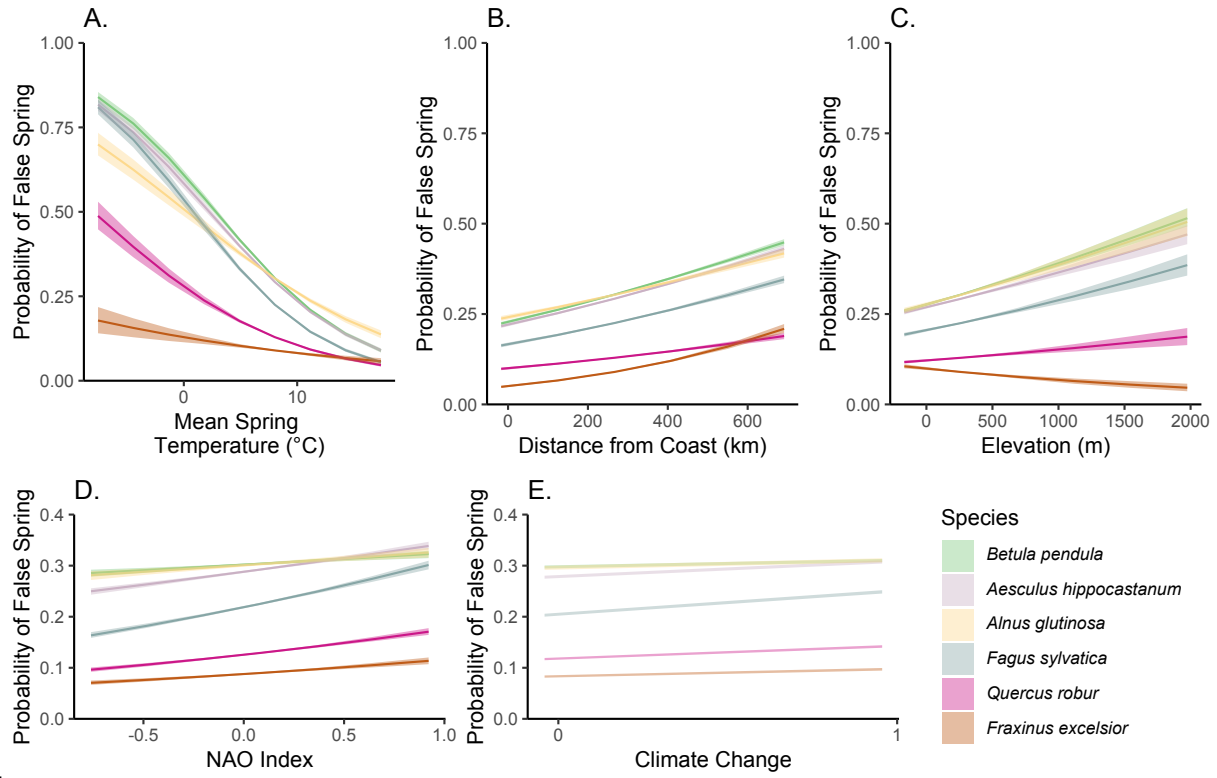
Figure 5: Interactions of the main effects with species (i.e., mean spring temperature (A.), distance from the coast (B.), elevation (C.), and NAO index (D.)). Lines and shading are the mean and 10% uncertainty intervals for each species. To reflect the raw data, we converted the model output back to the original scale for the x-axis in each panel.