Regional Risk Outline

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Abstract

Late spring freezing events, also known as false springs, can be ecologically damaging to many plants. A number of studies have found evidence that these events have become more frequent with climate change, but some studies have found the reverse. These diverging results across studies may occur because of the location of studies and because most investigate differing regional and climatic effects linked to false spring risk, which have shifted with climate change. However none have compared multiple factors at once. Using PEP725 leafout data for six tree species across 11,648 sites in Europe, we assessed the effects of NAO, mean spring temperature, elevation and distance from the coast to determine which factors were the strongest predictors of false spring risk and how these predictors shifted with climate change.

- 1. Overall, false spring risk decreased with climate change for all species.
- 2. Species varied highly in their risk of false springs, however species that initiated budburst early did not always have an increased risk of false spring.
- 3. Mean spring temperature and elevation were the strongest predictors of false spring risk, with higher mean spring temperatures having fewer false springs and higher elevations experiencing more false springs.
- 4. Our results suggest that considering multiple regional and climatic factors is essential for predicting false spring risk.

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. The growing season is lengthening (mainly due to earlier springs) across many regions in the northern hemisphere (Chen et al., 2005; Liu et al., 2006; Kukal & Irmak, 2018), but last spring frosts still pose a threat in many of these regions (Wypych et al., 2016b). Spring onset is advancing, with temperate tree and shrub species initiating leafout 4-6 days on average earlier per °C of warming (Wolkovich et al., 2012; IPCC, 2015). Last spring freeze dates are not predicted to advance at the same rate (Inouye, 2008; Martin et al., 2010; Labe et al., 2016; Sgubin et al., 2018), potentially amplifying the effects of false spring events in these regions. In Germany, for example, the last freeze date has advanced by 2.6 days per decade since 1955 (Zohner et al., 2016) but budburst is advancing around twice as fast. Major false spring events have been recorded in recent years and have found it can take 16-38 days for trees to refoliate (Gu et al., 2008; Augspurger, 2009, 2013; Menzel et al., 2015), which can detrimentally affect crucial processes such as carbon updake and nutrient cycling (Hufkens et al., 2012; Richardson et al., 2013; Klosterman et al., 2018).

Episodic frosts are one of the largest limiting factors in species range limits and have shaped plant life history strategies (Kollas et al., 2014). Temperate plants are exposed to freezing temperatures numerous times throughout the year, however, individuals are most at risk to damage from spring frosts, when frost tolerance is lowest (Sakai & Larcher, 1987). Plants can avoid damage by carefully timing budburst each year. Indeed, trees and shrubs in temperate regions optimize growth and minimize frost risk by using a complex mix of cues to initiate budburst: low winter temperatures, warm spring temperatures, and increasing spring daylengths. With climate change advancing, this interaction of cues may shift spring phenologies both across and within species, making some species less – or more — vulnerable to false springs than before. Early-leafout species may be especially at risk.

Plants are least frost resistant during certain phenophases. Frost tolerance greatly diminishes once individuals exit the dormancy phase (i.e. processes leading to budburst) through full leaf expansion (Vitasse et al., 2014; Lenz et al., 2016). Individuals that initiate budburst and have not fully leafed out before the last spring freeze are at risk of leaf tissue loss, damage to the xylem, and slowed canopy development (Gu et al., 2008; Hufkens et al., 2012). Thus, It is important to consider the length of time between budburst and leafout — when individuals are most at risk to spring freeze damage (Lenz et al., 2016) — in order to better predict false spring risk. We will refer to this timing between budburst and leafout as the duration of vegetative risk (Rethinking).

Given its importance to plant performance and survival, understanding how false spring is shifting with

climate change has been a major topic in the literature. There is large debate over whether or not spring freeze damage will increase (Hänninen, 1991; Augspurger, 2013; Labe et al., 2016), remain the same (Scheifinger et al., 2003) or even decrease (Kramer, 1994; Vitra et al., 2017) with climate change and there is also great variation within studies. Some research suggests false spring incidence has already begun to decline in many regions (i.e. across parts of North America and Asia), however the prevalence of spring frosts has consistently increased across Europe since 1982 (Liu et al., 2018). Furthermore, recent studies have demonstrated site effects may be more closely related to false spring risk: whether via altitudinal variation (Vitra et al., 2017; Ma et al., 2018) or distance from the coast (Wypych et al., 2016b; Ma et al., 2018). By better understanding these regional climatic implications and which factors are most crucial for predicting risk, we may be able to determine which regions may be at risk currently and which regions may become more at risk in the future.

The majority of false spring studies assess the effects of one predictor (e.g. temperature, elevation or distance from the coast) on false spring prevalence but most fail to incorporate multiple effects. Our primary aim is to investigate the known regional factors on false spring risk and compare the effect of them and their interaction with climate change. The key regional factors we identify for this study are: mean spring temperature, elevation and distance from the coast. Given our focus on Europe, we additionally examine the North Atlantic Oscillation (NAO) index, which is tied to winter and spring circulation across Europe. More positive NAO phases tend to result in higher than average winter and spring temperatures. With climate-change induced shifts, higher NAO phases has correlated to even earlier budburst dates since the late 1980s in some regions (Chmielewski & Rötzer, 2001), however it is unclear if more positive NAO phases also translates to more false springs.

By refining and identifying budburst and climate trends in recent years, we could improve future projections in false springs. For this purpose, we assessed the number of false springs that occured across 11,648 sites around Europe, spanning altitudinal and coastal gradients, using observed phenological data (754,786 observations) for six temperate, deciduous trees and combined that with daily gridded climate data for each site that extended from 1951-2016. In this study, a false spring was tallied when temperatures fell below -2.2° (Schwartz, 1993) between budburst and leafout (CITE Rethinking here?). Since the primary aim of the study is to predict false spring incidence in a changing climate, we split our data to before and after 1983 to capture reported temporal shifts in temperature trends (Stocker et al., 2013; Kharouba et al., 2018). We predicted that: (1) Earlier budburst species would experience more false springs, especially after 1983, (2) there would be different regional effects (i.e. mean spring temperature, NAO index, elevation, distance from the coast) on false spring incidence and those trends would shift when coupled with the effects of climate change

Methods

Phenological Data and Calculating Vegetative Risk

We obtained phenological data from the Pan European Phenology network (PEP725, www.pep725.edu), which provides open access phenology records across Europe (Templ et al., 2018). Since plants are most susceptible to damage from frost between budburst and full leafout, we selected only leafout data (i.e., in Meier, 2001, BBCH 11, which is defined as the point of leaf unfolding and the first visible leaf stalk) from the PEP725 dataset. The species used in the study were Aesculus hippocastanum Poir., Alnus glutinosa (L.) Gaertn., Betula pendula Roth., Fagus sylvatica Ehrh., Fraxinus excelsior L., Quercus robur L. Selection criteria for the species were as follows: (1) to be temperate, deciduous species that were not cultivars or used for crops, (2) there were at least 90,000 observations of BBCH 11 (leafout), (3) to represent over half of the total number of sites available (11,684), and (4) there were observations for at least 65 out of the 66 years of the study (1951-2016) (Table S1). We then subtracted 12 days from the leafout date to establish a standardized estimate for day of budburst (Donnelly et al., 2017).

Climate Data

We collected daily gridded climate data from the European Climate Assessment & Dataset (ECA&D) and used the E-OBS 0.25 degree regular latitude-longitude grid from version 16. We used the daily minimum temperature dataset to determine if a false spring occurred. False springs in this study were defined as temperatures at or below -2.2°C (Schwartz, 1993) during the duration of vegetative risk. In order to capture regional climatic effects we calculated the mean spring temperature by using the daily mean temperature from March 1 through May 31. Mean spring temperature was calculated – likely after chilling was accummulated – in an attempt to incorporate the general effects of spring forcing temperatures in our Bayesian hierarchichal model and to compare differences in spring across sites (Basler & Körner, 2012; Körner et al., 2016). We collected NAO-index data from the KNMI Climate Explorer CPC daily NAO time series and selected the NAO indices from November until April to best capture the effects of NAO on budburst for each region and then took the mean NAO indice 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, Stocker et al., 2013; Kharouba et al., 2018) to represent climate change.

Data Analysis

A false spring was determined if temperatures fell below -2.2° C at least once between budburst and leafout. We scaled all of the predictors and used a z-score following the binary predictor approach in order to best compare the effects of each climate variable to each other (Gelman & Hill, 2006). We used a space parameter, rather than a more traditional latitude parameter, to adjust for spatial autocorrelation issues using a minimization of Moran's I of the residuals (David et al., 2017) (Figure S1). We then took the calculated eigenvectors determined from the MIR approach and regressed these against the number of false springs for each datapoint to establish a spatial parameter (space).

We used a Bayesian hierarchical model approach to analyze our data to best estimate the number of false springs across-species levels. We fit a bernoulli distribution model using mean spring temperature, NAO, elevation, distance from the coast, space, and climate change as predictors and all two-way interactions (fixed effects) and species as two-way interactions to simulate modeled groups on the main effects. The Bayesian hierarchical model was fit using the brms package (Bürkner, Paul-Christian, 2017), version 2.3.1, in R (R Development Core Team, 2017), version 3.3.1, and was written as follows:

$$y_{i} \sim N(\alpha(i)) + \beta_{NAO_{(i)}} + \beta_{MeanSpringTemp_{(i)}} + \beta_{Elevation_{(i)}} + \beta_{DistanceCoast_{(i)}} + \beta_{Space_{(i)}}$$

$$+ \beta_{ClimateChange_{(i)}} + \beta_{NAO \times Species_{(i)}} + \beta_{MeanSpringTemp \times Species_{(i)}} + \beta_{Elevation \times Species_{(i)}}$$

$$+ \beta_{DistanceCoast \times Species_{(i)}} + \beta_{Space \times Species_{(i)}} + \beta_{ClimateChange \times Species_{(i)}}$$

$$+ \beta_{NAO \times ClimateChange_{(i)}} + \beta_{MeanSpringTemp \times ClimateChange_{(i)}} + \beta_{Elevation \times ClimateChange_{(i)}}$$

$$+ \beta_{DistanceCoast \times ClimateChange_{(i)}} + \beta_{Space \times ClimateChange_{(i)}} + \sigma_{sp_{(i)}}$$

We ran two chains, each with 2,500 warm-up iterations and 4,000 sampling iterations for a total of 8,000 posterior samples for each predictor. We evaluated our model performance on \hat{R} values that were close to one and assessed chain convergence and posterior predictive checks (Gelman & Hill, 2006).

Testing the rate of budburst on false spring incidence

The definition of a false spring has been established to be freezing temperatures of -2.2°C (Schwartz, 1993) after budburst but plants are most susceptible to damage during the duration of vegetative risk (Augspurger, 2013; Lenz et al., 2016). Different species have different durations of vegetative risk, which is also shifting with climate change (Cleland et al., 2006; Fu et al., 2015; Xin, 2016). We tested our original model by making a different more biologically relevant model with different durations of vegetative risk for each species. Due to insufficient budburst data from PEP725, we calculated budburst by subtracting 11 days from leafout for Aesculus hippocastanum and Betula pendula, 12 days for Alnus glutinosa, 5 days for Fagus sulvatica, and 7 days

for 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).

Results

Species variation in budburst and false spring incidence

There was variation in day of budburst across the six species and across space (Figure 1). The top three species (*Betula pendula*, *Aesculus hippocastanum*), *Alnus glutinosa* generally initiated budburst earlier than the bottom three species (*Fagus sylvatica*, *Quercus robur*, *Fraxinus excelsior*).

After 1983, all species initiated budburst earlier (Figure 2A) and the minimum temperature between budburst and leafout was, on average, higher. As seen in Figure 3, mean spring temperature for most species ranged from -5°C to 12°C, but for *Alnus glutinosa* and *Fraxinus excelsior* the mean spring temperature rarely dropped below 0°C, whereas *Quercus robur* experienced some of the lowest spring temperatures. The average minimum temperature between budburst and leafout, however, varied across the six species with *Betula pendula* and *Aesculus hippocastanum* experiencing the lowest minimum temperatures (Figure 2B) and with *Fraxinus excelsior* experiencing the greatest variation.

The effects of climatic regional variation on false spring incidence

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

Most of the interactions with increasing temperatures (i.e., the Climate Change predictor) exhibit a decreased risk in false springs, especially with NAO (-0.83) however, the probability of false spring incidence increased at sites with higher mean spring temperatures after 1983 (+0.42) (Figure 4). After climate change, the rate of false spring incidence largely decreased with increasing NAO indices (Figure 5A). The probability of a false spring remained the same after 1983 and before 1983 (Figure 5B). After climate change, the probability of a false spring is higher at sites with warmer mean spring temperatures (Figure 5C). There was a slightly decreased risk of a false springs further from the coast before climate change (Figure 5D).

The probability of a false spring occurring varied by species with each predictor (Figure 6). 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. With increasing elevation, all species had a greater risk of a false spring occurring except for Fraxinus excelsior, which had a slightly decreased risk at higher elevations. There was an increased risk of false spring for all species at sites further from the coast. With increasing NAO indices, the risk of false spring remained consistent for most species except Fagus sylvatica experienced more with highter NAOs. Betula pendula, Aesculus hippocastenum and Alnus glutinosa all experienced more false springs after 1983.

Standardized rate of budburst

- 1. By having different durations of vegetative risk for each species the magnitude and direction of the predictors remained consistent with the original model (Figure S2).
 - (a) There were fewer false springs after 1983 and mean spring temperature and elevation were the strongest predictors for false spring risk.
 - (b) And, again, distance was the only, albeit weakly, positive interaction effect with climate change.

Discussion

- 1. Start with paragraph...
 - (a) Climate change has increased false spring risk by 0.35 across our data. But this average hides many important complexities as our models show that species and climate combine to predict false spring.
 - (b) Species are really different, however all species are at risk of false springs. Frazinus excelsior had the lowest number of false springs across our data and generally had the latest budburst dates.
 - (c) Mean spring temperature and distance from the coast were the strongest predictors for false springs, however, NAO, elevation and cliamte change all affected the risk of false spring incidence.
 - (d) These effects have changed with significantly fewer false springs with higher NAO indices and more false springs with warmer mean spring temperature sites — since the major onset of climate change.

Species differences

There is robust evidence for advancing budburst with climate change (Cleland et al., 2007; Wolkovich et al., 2012; IPCC, 2015) and some studies indicate earlier budburst species are more at risk of false spring damage (Ma et al., 2018). After 1983, all of our species initiated budburst earlier in the spring and there was a increase overall in false spring risk. Additionally, some of the early bursting species were more susceptible to false spring risk (i.e. Betula pendula and Aesuculus hippocastanum) but all species were susceptible to false spring risk. Thus, simply looking at budburst time is not a sufficient proxy to forecast false spring risk and other climatic and regional factors must be evaluated.

Climatic and regional effects

Past studies using single predictors for false spring events has lead to contradicting predictions in future false spring risk. Through our holistic approach, we were able to assess the myriad of climatic and regional effects on false spring risk – and how the magnitude of those effects compare to one another – by incorporating the space parameter, thus erasing the collinearity issues of certain effects (i.e., elevation and distance from the coast). This was an essential step in forecasting false spring risk.

Our study supports findings from previous studies: higher elevations tend to experience more false springs (Vitra et al., 2017) and sites that are generally warmer have lower risks of false springs (Wypych et al., 2016a) and that risk is increasing with climate change (Liu et al., 2018). However, we also discovered that effects of elevation and distance from the coast cannot be assumed to be the same, which contradicts previous studies (Ma et al., 2018). Our results suggest that sites further from the coast had a higher risk of false springs than sites at higher elevations and, with shifts in climate, sites further from the coast experienced fewer false springs whereas there was little change for sites at higher elevations.

Overall, mean spring temperature and distance from the coast are the best predictors for false spring risk: sites that are warmer generally have fewer false springs and sites that are at further from the coast generally have more false springs. Across our study sites, budburst initiated earlier after 1983 due to warming temperatures but the minimum temperatures also increased, however, false spring risk is increasing. Our results also indicate that higher NAO indices — which typically leads to earlier budburst — slightly increased the risk of false springs but that risk diminished significantly over time.

Forecasting future false springs

Our study fails to assess the intensity or severity of the false spring events. It is possible that with increasing false spring risk, the events after 1983 could be lasting longer or could at be at even harsher temperatures. Additionally, there is sufficient evidence that different species are able to tolerate different minimum temperature extremes (Lenz et al., 2013; Körner et al., 2016; Zhuo et al., 2018). Some species or individuals may be less tolerant of low temperatures (i.e., are damaged from higher temperatures than -2.2°C), whereas other species or individuals may be able to tolerate temperatures as low as -8.5°C (Lenz et al., 2016). Thus, species that are typically found in low risk sites but have early budburst (i.e. Alnus glutinosa) may be less tolerant of low temperatures and they may be at sites that are further from the coast, which are experiencing a slightly increased risk with climate change. For this reason, models should ideally incorporate species-specific temperature thresholds to best capture the shifts in false spring risk over time and space.

Biological spring is advancing with climate change-induced shifts but few studies have assessed the effects of climate change on the duration of vegetative risk: is leafout advancing at the same rate or is the duration of vegetative risk lengthening? For false spring studies, it is important to consider the effects of climate change on both budburst and leafout, the timing when individuals are most at risk to spring freeze damage (Lenz et al., 2016). 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 risk is influenced by numerous climatic and regional factors and all of these factors must be incorporated into models to best predict spatiotemporal shifts in false springs. Some factors are better at predicting risk than others (i.e., mean spring temperature and distance from the coast), however it is essential to additionally assess the effects of NAO and elevation, which contribute to an individual's risk of false spring. Individuals that initiate budburst earlier in the season aren't necessarily exposed to more false springs, thus, investigating site effects is a more consistent proxy for false spring risk than budburst time. Overall, the frequency of false spring events is increasing with climate change so it is essential to additionally understand how the intensity and duration of these events are shifting. Furthermore, incorporating both budburst and leafout data as well as species-specific temperature thresholds will advance our knowledge of false spring risk in a changing climate.

References

- Augspurger, C.K. (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. Functional Ecology 23, 1031–1039.
- Augspurger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: Spring damage risk is increasing. *Ecology* **94**, 41–50.
- Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species.

 Agricultural and Forest Meteorology 165, 73–81.
- Buerki, S., Lowry II, P., Alvarez, N., Razafimandimbison, S., Kupfer, P. & Callmander, 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.
- Bürkner, Paul-Christian (2017) brms: An R Package for Bayesia Multilevel Models. *Journal of Statistical Software* 80, 1–28.
- 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.
- Chmielewski, F.M. & Rötzer, T. (2001) Response of tree phenology to climate change across Europe. Agricultural and Forest Meteorology 108, 101 112.
- Cleland, E., Chiariello, N., Loarie, S., Mooney, H. & Field, C. (2006) Diverse responses of phenology to global changes in a grassland ecosystem. *PNAS* **103**, 13740–13744.
- Cleland, E.E., Chuine, I., Menzel, A., Mooney, H.A. & Schwartz, M.D. (2007) Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* **22**, 357–365.
- David, B., Thomas, D., Stéphane, D. & Jason, V. (2017) Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography* **0**.
- Donnelly, A., Yu, R., Caffarra, A., Hanes, J.M., Liang, L., Desai, A.R., Liu, L. & Schwartz, M.D. (2017) Interspecific and interannual variation in the duration of spring phenophases in a northern mixed forest. *Agricultural and Forest Meteorology* **243**, 55–67.
- Flynn, D.F.B. & Wolkovich, E.M. (2018) Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*.
- Fu, Y.H., Piao, S., Vitasse, Y., Zhao, H., De Boeck, H.J., Liu, Q., Yang, H., Weber, U., Hänninen, H. & Janssens, I.A. (2015) Increased heat requirement for leaf flushing in temperate woody species over 1980-2012: effects of chilling, precipitation and insolation. Global Change Biology 21, 2687–2697.

- Gelman, A. & Hill, J. (2006) Data analysis using regression and multilevel/hierarchical models. Cambridge university press.
- Gu, L., Hanson, P.J., Post, W.M., Kaiser, D.P., Yang, B., Nemani, R., Pallardy, S.G. & Meyers, T. (2008) The 2007 Eastern US spring freeze: Increased cold damage in a warming world. *BioScience* 58, 253.
- Hänninen, H. (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell & Environment* 14, 449–454.
- Hipp, A., S. Manos, P., González-Rodríguez, A., Hahn, M., Kaproth, M., McVay, J., Avalos, S. & Cavender-Bares, J. (2017) Sympatric parallel diversification of major oak clades in the Americas and the origins of Mexican species diversity. New Phytologist 217.
- Hufkens, K., Friedl, M.A., Keenan, T.F., Sonnentag, O., Bailey, A., O'Keefe, J. & Richardson, A.D. (2012)
 Ecological impacts of a widespread frost event following early spring leaf-out. Global Change Biology 18, 2365–2377.
- Inouye, D.W. (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, H.M., Ehrlén, J., Gelman, A., Bolmgren, K., Allen, J.M., Travers, S.E. & Wolkovich, E.M. (2018) Global shifts in the phenological synchrony of species interactions over recent decades. *Proceedings of the National Academy of Sciences* 115, 5211–5216.
- Klosterman, S., Hufkens, K. & Richardson, A.D. (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*.
- KNMI (2018) Daily cpc nao data.
- Kollas, C., Körner, C. & Randin, C.F. (2014) Spring frost and growing season length co-control the cold range limits of broad-leaved trees. *Journal of Biogeography* 41, 773–783.
- Körner, C., Basler, D., Hoch, G., Kollas, C., Lenz, A., Randin, C.F., Vitasse, Y. & Zimmermann, N.E. (2016) Where, why and how? Explaining the low-temperature range limits of temperate tree species. *Journal of Ecology* **104**, 1076–1088.
- 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.

- Kukal, M.S. & Irmak, S. (2018) U.S. Agro-Climate in 20th century: growing degree days, first and last frost, growing season length, and impacts on crop yields. *Scientific Reports* 8.
- Labe, Z., Ault, T. & Zurita-Milla, R. (2016) Identifying anomalously early spring onsets in the CESM large ensemble project. *Climate Dynamics* **48**, 3949–3966.
- 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.
- 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.
- Liu, Q., Piao, S., Janssens, I.A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R.B., Peñuelas, J. & Wang, T. (2018) Extension of the growing season increases vegetation exposure to frost. *Nature Communications* 9.
- 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.
- Ma, Q., Huang, J.G., 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**.
- Martin, M., Gavazov, K., Körner, C., Hattenschwiler, S. & Rixen, C. (2010) Reduced early growing season freezing resistance in alpine treeline plants under elevated atmospheric CO_2 . Global Change Biology 16, 1057–1070.
- Meier, U. (2001) Growth stages of mono-and dicotyledonous plants BBCH Monograph Edited by Uwe Meier Federal Biological Research Centre for Agriculture and Forestry. *Agriculture* 12, 141—147 ST Geochemical study of the organic mat.
- 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.
- R Development Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013) Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* **169**, 156 173.
- 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.
- Schwartz, M.D. (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography* **14(6)**, 536–550.
- Sgubin, G., Swingedouw, D., Dayon, G., de Cortázar-Atauri, I.G., 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.
- Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. & Midgley, P.M. (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., Ungersböck, M., Paul, A., Scheifinger, H., Rutishauser, T., Busto, M., Chmielewski, F.M., Hájková, L., Hodzić, S., Kaspar, F., Pietragalla, B., Romero-Fresneda, R., Tolvanen, A., Vučetič, V., Zimmermann, K. & Zust, A. (2018) Pan European Phenological database (PEP725): a single point of access for European data. *International Journal of Biometeorology* **62**, 1109–1113.
- Vitasse, Y., Lenz, A. & KÃÂűrner, C. (2014) The interaction between freezing tolerance and phenology in temperate deciduous trees. Frontiers in Plant Science 5.
- Vitra, A., Lenz, A. & Vitasse, Y. (2017) Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytologist* **216**, 113–123.
- Wang, N., McAllister, H.A., Bartlett, P.R. & Buggs, R.J.A. (2016) Molecular phylogeny and genome size evolution of the genus *Betula* (Betulaceae). *Annals of Botany* 117, 1023–1035.
- Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., Pau, S., Regetz, J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J., McCabe, G.J., McGill, B.J., Parmesan, C., Salamin, N., Schwartz, M.D. & Cleland, E.E. (2012) Warming experiments underpredict plant phenological responses to climate change. *Nature* 485, 18–21.
- 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.
- Wypych, A., Ustrnul, Z., Sulikowska, A., Chmielewski, F.M. & 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.

Xin, Q. (2016) A risk-benefit model to simulate vegetation spring onset in response to multi-decadal climate variability: Theoretical basis and applications from the field to the Northern Hemisphere. *Agriculture and Forest Meteorology* **228-229**, 139–163.

Zhuo, X., Zheng, T., Zhang, Z., Zhang, Y., Jiang, L., Ahmad, S., Sun, L., Wang, J., Cheng, T. & Zhang, Q. (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.

Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123.

Tables and Figures

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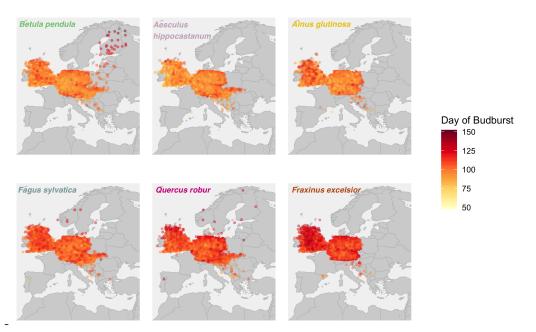


Figure 1: The average day of budburst is mapped by site for each species. Species are ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*. Earlier budburst dates are yellow and later budburst dates are in red.

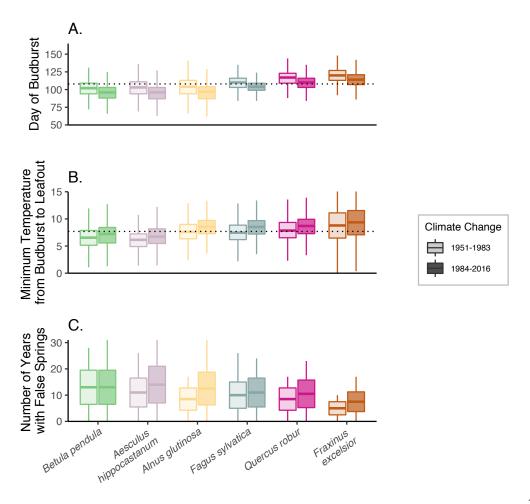


Figure 2: Budburst, minimum temperatures and false springs were compared before and after 1983 for each species. We plotted the day of budburst (A.) before and after 1983 for each species across all sites. We then compared the average minimum temperatures (B.) between budburst and leafout for all species across all sites. The bottom panel (C.), shows the total number of years there was a false spring before and after 1983 at each site across all species. Species are ordered by day of budburst.

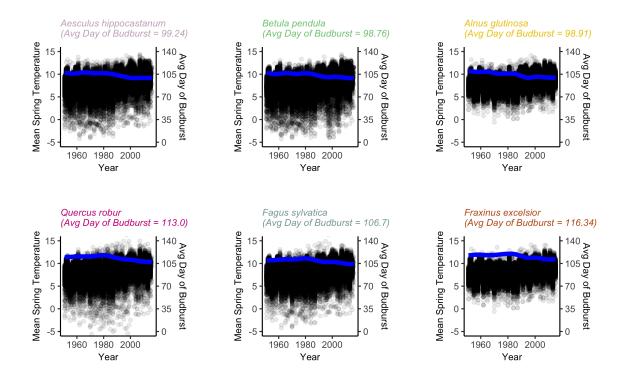


Figure 3: Mean spring temperatures are plotted for each site over time (from 1951-2016) for each species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula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

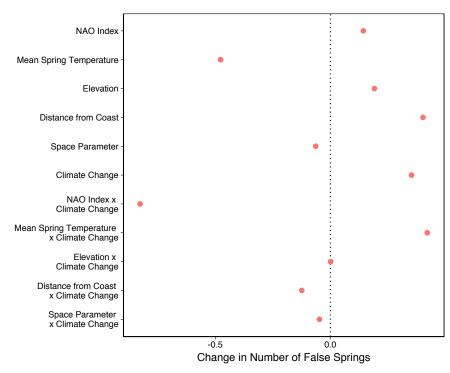


Figure 4: Model output with standardized durations of vegetative risk for each species. More positive parameter effects indicate an increased probability of a false spring whereas more negative effects suggest a lower probability of a false spring. Uncertainly intervals are at 50%. Parameter effects closer to zero have less of an effect on false springs. There were 743,086 zeros and 11,700 ones for false spring in the data.

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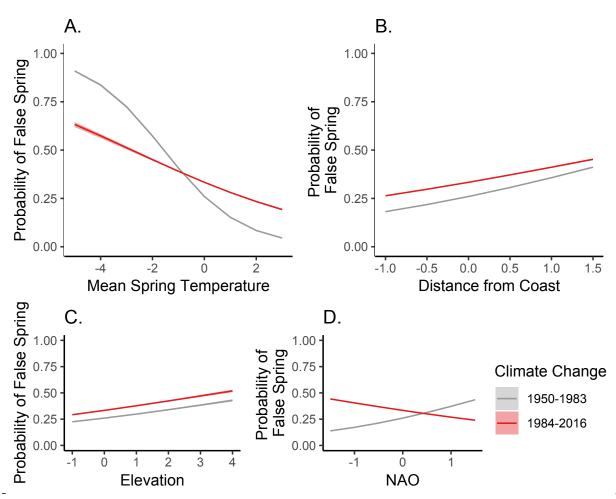


Figure 5: Plots showing the interaction effects on false spring risk for each predictor coupled with climate change. (A.) As mean spring temperature increases, there were fewer false springs but there were fewer false springs after 1983 at sites with lower mean spring temperatures. (B.) As elevation increased, false spring risk increased but there were fewer false springs at higher altitudes after 1983. (C.) As NAO indices increased, there were more false springs before 1983 but fewer after 1983. (D.) There were more false springs further from the coast and the rate of increase was consistent, however, there were fewer false springs in total after 1983. Note, the y-axis for panels A and B are from 0.00 to 1.00 but the y-axis is only from 0.00 to 0.20 for panels C and D to better see the relationships. Since we found the z-score for each predictor, the x-axis for each panel does not reflect the raw data.

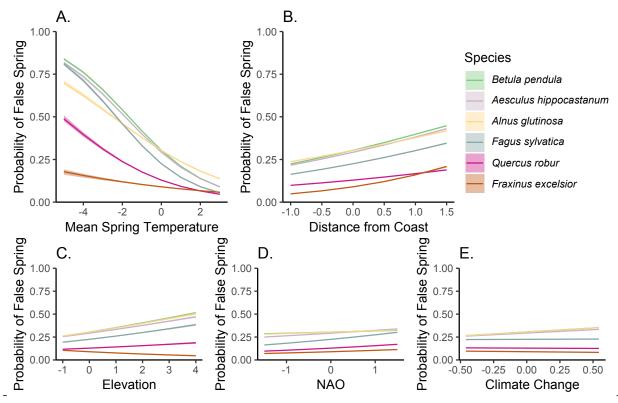


Figure 6: Plots showing the interaction effects of each predictor with species. (A.) As mean spring temperature increases, the probability of a false spring decreases for each species but *Fraxinus excelsior* always has the lowest risk of false spring. (B.) The risk of a false spring increases with increasing altitude but the relationship is strongest for *Aesculus hippocastanum* and *Betula pendula*. (C.) There are slightly fewer false springs for *Aesculus hippocastanum* and *Betula pendula* in years with higher NAO indices. (D.) There's an increase in false spring risk for individuals further from the coast, especially for *Fraxinus excelsior*. (E.) There are fewer false springs after 1983, especially for *Aesculus hippocastanum* and *Betula pendula*. Note, the y-axis for panels A and B are from 0.00 to 1.00 but the y-axis is only from 0.00 to 0.10 for panels C, D and E to better see the relationships. Since we found the z-score for each predictor, the x-axis for each panel does not reflect the raw data.