

¹ **Regional Risk Outline**

² Authors:

³ C. J. Chamberlain ^{1,2}, B. I. Cook ³, I. Morales Castilla ^{1,4} & E. M. Wolkovich ^{1,2}

⁴ *Author affiliations:*

⁵ ¹Arnold Arboretum of Harvard University, 1300 Centre Street, Boston, Massachusetts, USA;

⁶ ²Organismic & Evolutionary Biology, Harvard University, 26 Oxford Street, Cambridge, Massachusetts, USA;

⁷ ³NASA Goddard Institute for Space Studies, New York, New York, USA;

⁸ ⁴Edificio Ciencias, Campus Universitario 28805 AlcalÁ de Henares, Madrid, Spain

⁹ *Corresponding author: 248.953.0189; cchamberlain@g.harvard.edu

¹⁰

¹¹ **Introduction**

¹² 1. Temperate tree and shrub species are at risk of damage from late spring freezing events, also known as
¹³ false springs.

¹⁴ (a) The growing season is lengthening across many regions in the northern hemisphere (Chen *et al.*,
¹⁵ 2005; Liu *et al.*, 2006; Kukal & Irmak, 2018), but last spring frosts still pose a threat in many of
¹⁶ these regions (Wypych *et al.*, 2016).

¹⁷ (b) Due to the changing climate, spring onset is advancing and many temperate tree and shrub species
¹⁸ are initiating leafout 4-6 days earlier per °C of warming (Wolkovich *et al.*, 2012; IPCC, 2015).

¹⁹ (c) However, last spring freeze dates are not predicted to advance at the same rate as spring onset
²⁰ in some regions of the world (Inouye, 2008; Martin *et al.*, 2010; Labe *et al.*, 2016; Sgubin *et al.*,
²¹ 2018), potentially amplifying the effects of false spring events in these regions.

²² (d) In Germany, for example, the last freeze date has advanced by 2.6 days per decade since 1955
²³ (Zohner *et al.*, 2016).

²⁴ (e) Major false spring events have been recorded in recent years and have found it can take 16-38
²⁵ days for trees to refoliate (Gu *et al.*, 2008; Augspurger, 2009, 2013; Menzel *et al.*, 2015), which can
²⁶ detrimentally affect crucial processes such as carbon uptake and nutrient cycling (Hufkens *et al.*,
²⁷ 2012; Richardson *et al.*, 2013; Klosterman *et al.*, 2018).

²⁸ 2. Plant phenology, which is defined as the timing of recurring life-history events such as budburst, strongly
²⁹ tracks shifts in climate (Cleland *et al.*, 2007; Wolkovich *et al.*, 2012).

- 30 (a) Episodic frosts are one of the largest limiting factors in species range limits (Kollas *et al.*, 2014).
- 31 (b) Temperate plants are exposed to freezing temperatures numerous times throughout the year,
32 however, individuals are most at risk to damage from stochastic spring frosts, when frost tolerance
33 is lowest (Sakai & Larcher, 1987).
- 34 (c) Individuals that initiate budburst and have not fully leafed out before the last spring freeze are
35 at risk of leaf tissue loss, damage to the xylem, and slowed canopy development (Gu *et al.*, 2008;
36 Hufkens *et al.*, 2012).
- 37 (d) False spring events can result in photosynthetic tissue loss, which could potentially impact multiple
38 years of growth and, with the growing season extending, individuals could be exposed to more frosts
39 in the future (Liu *et al.*, 2018).
- 40 (e) Frost tolerance greatly diminishes once individuals exit the dormancy phase (i.e. processes leading
41 to budburst) through full leaf expansion (Vitasse *et al.*, 2014; Lenz *et al.*, 2016).
- 42 (f) Individuals that initiate budburst earlier in the season are more frost resistant (Körner *et al.*,
43 2016), however, as climate change advances, less frost resistant individuals may start initiating
44 budburst before the last freeze date.
- 45 (g) Despite the importance of false spring events, the extent of damage and the frequency and intensity
46 of false spring events is still largely unknown.
- 47 3. There is large debate over whether or not spring freeze damage will increase (Hänninen, 1991; Augspurger,
48 2013; Labe *et al.*, 2016), remain the same (Scheifinger *et al.*, 2003) or even decrease (Kramer, 1994)
49 with climate change.
- 50 (a) Some research suggests false spring incidence has declined in many regions (i.e. across parts of
51 North America and Asia), however the prevalence of spring frosts has consistently increased across
52 Europe since 1982 (Liu *et al.*, 2018).
- 53 (b) However, recent studies have demonstrated regional effects may be more closely related to false
54 spring risk: whether via altitudinal variation (Vitra *et al.*, 2017) or distance from the coast
55 (Wypych *et al.*, 2016).
- 56 (c) By better understanding these regional climatic implications, we may be able to determine which
57 regions may be at risk currently and which regions may become more at risk in the future.
- 58 4. The North Atlantic Oscillation (NAO) index is often used to describe winter and spring circulation
59 across Europe.
- 60 (a) More positive NAO phases tend to result in higher than average winter and early spring tempera-
61 tures, and with climate change, higher NAO phases has correlated to even earlier budburst dates

62 in some regions (Chmielewski & Rötzer, 2001), however it is unclear if more positive NAO phases
63 also translates to more false springs.

64 5. By improving and identifying budburst and climate trends in recent years, we could potentially amplify
65 our predictability of future projections in false springs.

66 (a) For this purpose, we assessed the number of false springs that occurred across 11,684 sites around
67 Europe, spanning altitudinal and coastal gradients, using observed phenological data (1,082,740
68 observations) for six temperate, deciduous trees and combined that with daily gridded climate
69 data for each site that extended from 1951-2016.

70 (b) In this study, a false spring was tallied when temperatures fell below -2.2° (Schwartz, 1993) between
71 budburst and leafout (CITE Rethinking here?)

72 (c) We predicted that: (1) Earlier budburst species would experience more false springs, especially
73 after 1983 and (2) there would be different regional effects on false spring incidence and those
74 trends would shift when coupled with the effects of climate change.

75 Methods

76 Phenological Data and Calculating Vegetative Risk

77 1. We obtained phenological data from the Pan European Phenology network (PEP725, www.pep725.edu),
78 which provides open access phenology records across Europe (Templ *et al.*, 2018).

79 2. Since plants are most susceptible to damage from frost between budburst and full leafout, we selected
80 only leafout data (i.e., in Meier, 2001, BBCH 11, which is defined as the point of leaf unfolding and the
81 first visible leaf stalk) from the PEP725 dataset.

82 3. We then subtracted 12 days from the leafout date to establish a rough estimate for day of budburst
83 (Donnelly *et al.*, 2017).

84 4. The species used in the study were *Aesculus hippocastanum* L., *Alnus glutinosa* (L.) Gaertn., *Betula*
85 *pendula* Roth., *Fagus sylvatica* Ehrh., *Fraxinus excelsior* L., *Quercus robur* L.

86 5. Selection criteria for the species were as follows: (1) to be temperate, deciduous species that were not
87 cultivars or used for crops, (2) there were at least 140,000 observations of BBCH 11, (3) to represent
88 over half of the total number of sites available (11,684), (4) there were observations for at least 65 out
89 of the 66 years of the study (1951-2016).

90 **Climate Data**

- 91 1. We collected daily gridded climate data from the European Climate Assessment & Dataset (ECA&D)
92 and used the E-OBS 0.25 degree regular latitude-longitude grid from version 16.
- 93 2. We used the daily minimum temperature dataset to determine if a false spring occurred.
- 94 3. False springs in this study were defined as temperatures at or below -2.2°C (Schwartz, 1993).
- 95 4. In order to capture regional climatic effects we calculated the mean spring temperature by using the
96 daily mean temperature from February 1 through April 30.
- 97 5. Mean spring temperature was calculated – likely after chilling was accumulated – in an attempt to
98 incorporate the general effects of spring forcing temperatures in our Bayesian hierarchical model and
99 to compare differences in spring across sites (Basler & Körner, 2012; Körner *et al.*, 2016).
- 100 6. We collected NAO-index data from the KNMI Climate Explorer annual NAO time series (Trouet *et al.*,
101 2009).
- 102 7. Since the primary aim of the study is to predict false spring incidence in a changing climate, we split
103 our data to before and after 1983 to capture reported temporal shifts in temperature trends (Stocker
104 *et al.*, 2013; Kharouba *et al.*, 2018).

105 **Data Analysis**

- 106 1. A false spring was determined if temperatures fell below -2.2°C at least once between budburst and
107 leafout.
- 108 (a) We scaled the elevation predictor by dividing it by 100 to be consistent with the other predictors
109 in the model.
- 110 (b) We used a space parameter, rather than a more traditional latitude parameter, to adjust for
111 spatial autocorrelation issues using a minimization of Moran's *I* of the residuals (David *et al.*,
112 2017) (Figure S1).
- 113 (c) We then took the calculated eigenvectors determined from the MIR approach and regressed these
114 against the number of false springs for each datapoint to establish a spatial parameter (space).
- 115 2. We used a Bayesian hierarchical model approach to analyze our data to best estimate the number of
116 false springs across-species levels.

- 117 (a) We fit a mixed-effects model using mean spring temperature, NAO, elevation, space, and climate
 118 change as predictors and all two-way interactions (fixed effects) and species as modeled groups on
 119 the main effects (random effects).
- 120 (b) (Although, we may find that space and elevation are collinear and may decide to take space out
 121 and use elevation instead - unless space is picking up more of the distance from the coast then
 122 we'll use the space parameter instead of elevation)
- 123 (c) The Bayesian hierarchical model was fit using the brms package (Bürkner, Paul-Christian , 2017),
 124 version 2.3.1, in R (R Development Core Team, 2017), version 3.3.1, and was written as follows:
 125 (subject to change as per above, this is just the ideal model)

$$y_i \sim N(\alpha(i) + \beta_{MeanSpringTemp_{sp(i)}} + \beta_{NAO_{sp(i)}} + \beta_{elevation_{sp(i)}} + \beta_{space_{sp(i)}} + \beta_{ClimateChange_{sp(i)}} \\ + \beta_{MeanSpringTemp \times ClimateChange_{(i)}} + \beta_{NAO \times ClimateChange_{(i)}} \\ + \beta_{elevation \times ClimateChange_{(i)}} + \beta_{space \times ClimateChange_{(i)}} + \sigma_{sp(i)})$$

- (d) The β coefficients and α were modeled at the species level:

$$1. \beta_{MeanSpringTemp_{sp}} \sim N(\mu_{MeanSpringTemp}, \sigma^2_{MeanSpringTemp}) \\ \dots \\ 5. \beta_{ClimateChange_{sp}} \sim N(\mu_{ClimateChange}, \sigma^2_{ClimateChange})$$

- 123 (e) We ran two chains, each with 4,000 warm-up iterations and 2,500 sampling iterations for a total
 124 of 10,000 posterior samples for each predictor.
- 125 (f) We evaluated our model performance on \hat{R} values that were close to 1 and assessed chain conver-
 126 gence and posterior predictive checks (Gelman & Hill, 2006).

127 References

- 128 Augspurger, C.K. (2009) Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate
 129 deciduous forest. *Functional Ecology* **23**, 1031–1039.
- 130 Augspurger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124
 131 years: Spring damage risk is increasing. *Ecology* **94**, 41–50.
- 132 Basler, D. & Körner, C. (2012) Photoperiod sensitivity of bud burst in 14 temperate forest tree species.
 133 *Agricultural and Forest Meteorology* **165**, 73–81.

- ¹³⁴ Bürkner, Paul-Christian (2017) brms: An R Package for Bayesia Multilevel Models. *Journal of Statistical Software* **80**, 1–28.
- ¹³⁶ 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.
- ¹³⁸ Chmielewski, F.M. & Rötzer, T. (2001) Response of tree phenology to climate change across europe. *Agricultural and Forest Meteorology* **108**, 101 – 112.
- ¹⁴⁰ 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.
- ¹⁴² David, B., Thomas, D., Stéphane, D. & Jason, V. (2017) Disentangling good from bad practices in the selection of spatial or phylogenetic eigenvectors. *Ecography* **0**.
- ¹⁴⁴ 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.
- ¹⁴⁷ Gelman, A. & Hill, J. (2006) *Data analysis using regression and multilevel/hierarchical models*. Cambridge university press.
- ¹⁴⁹ 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.
- ¹⁵¹ Hänninen, H. (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell & Environment* **14**, 449–454.
- ¹⁵³ 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.
- ¹⁵⁶ Inouye, D.W. (2008) Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* **89**, 353–362.
- ¹⁵⁸ IPCC (2015) *Climate change 2014: mitigation of climate change*, vol. 3. Cambridge University Press.
- ¹⁵⁹ 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.

- 162 Klosterman, S., Hufkens, K. & Richardson, A.D. (2018) Later springs green-up faster: the relation between
163 onset and completion of green-up in deciduous forests of north america. *International Journal of Biomete-*
164 *orology* .
- 165 Kollas, C., Körner, C. & Randin, C.F. (2014) Spring frost and growing season length co-control the cold
166 range limits of broad-leaved trees. *Journal of Biogeography* **41**, 773–783.
- 167 Körner, C., Basler, D., Hoch, G., Kollas, C., Lenz, A., Randin, C.F., Vitasse, Y. & Zimmermann, N.E. (2016)
168 Where, why and how? explaining the low-temperature range limits of temperate tree species. *Journal of*
169 *Ecology* **104**, 1076–1088.
- 170 Kramer, K. (1994) A modelling analysis of the effects of climatic warming on the probability of spring frost
171 damage to tree species in the netherlands and germany. *Plant, Cell & Environment* **17**, 367–377.
- 172 Kukal, M.S. & Irmak, S. (2018) U.s. agro-climate in 20th century: Growing degree days, first and last frost,
173 growing season length, and impacts on crop yields. *Scientific Reports* **8**.
- 174 Labe, Z., Ault, T. & Zurita-Milla, R. (2016) Identifying anomalously early spring onsets in the cesm large
175 ensemble project. *Climate Dynamics* **48**, 3949–3966.
- 176 Lenz, A., Hoch, G., Körner, C. & Vitasse, Y. (2016) Convergence of leaf-out towards minimum risk of freezing
177 damage in temperate trees. *Functional Ecology* **30**, 1–11.
- 178 Liu, Q., Piao, S., Janssens, I.A., Fu, Y., Peng, S., Lian, X., Ciais, P., Myneni, R.B., Peñuelas, J. & Wang, T.
179 (2018) Extension of the growing season increases vegetation exposure to frost. *Nature Communications* **9**.
- 180 Liu, X., Yin, Z., Shao, X. & Qin, N. (2006) Temporal trends and variability of daily maximum and minimum,
181 extreme temperature events, and growing season length over the eastern and central tibetan plateau during
182 1961–2003. *Journal of Geophysical Research: Atmospheres* **111**.
- 183 Martin, M., Gavazov, K., Körner, C., Hattenschwiler, S. & Rixen, C. (2010) Reduced early growing season
184 freezing resistance in alpine treeline plants under elevated atmospheric CO₂. *Global Change Biology* **16**,
185 1057–1070.
- 186 Meier, U. (2001) Growth stages of mono-and dicotyledonous plants BBCH Monograph Edited by Uwe Meier
187 Federal Biological Research Centre for Agriculture and Forestry. *Agriculture* **12**, 141—147 ST — Geo-
188 chemical study of the organic mat.
- 189 Menzel, A., Helm, R. & Zang, C. (2015) Patterns of late spring frost leaf damage and recovery in a european
190 beech (*fagus sylvatica* l.) stand in south-eastern germany based on repeated digital photographs. *Frontiers*
191 *in Plant Science* **6**, 110.

- 192 R Development Core Team (2017) R: A language and environment for statistical computing. *R Foundation
for Statistical Computing, Vienna, Austria* .
- 194 Richardson, A.D., Keenan, T.F., Migliavacca, M., Ryu, Y., Sonnentag, O. & Toomey, M. (2013) Climate
195 change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural
196 and Forest Meteorology* **169**, 156 – 173.
- 197 Sakai, A. & Larcher, W. (1987) *Frost Survival of Plants*. Springer-Verlag.
- 198 Scheifinger, H., Menzel, A., Koch, E. & Peter, C. (2003) Trends of spring time frost events and phenological
199 dates in Central Europe. *Theoretical and Applied Climatology* **74**, 41–51.
- 200 Schwartz, M.D. (1993) Assessing the onset of spring: A climatological perspective. *Physical Geography* **14(6)**,
201 536–550.
- 202 Sgubin, G., Swingedouw, D., Dayon, G., de Cortázar-Atauri, I.G., Ollat, N., Pagé, C. & van Leeuwen, C.
203 (2018) The risk of tardive frost damage in french vineyards in a changing climate. *Agricultural and Forest
204 Meteorology* **250-251**, 226 – 242.
- 205 Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V. &
206 Midgley, P.M. (2013) Climate change 2013: The physical science basis. contribution of working group i to
207 the fifth assessment report of the intergovernmental panel on climate change, 1535 pp.
- 208 Templer, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., Rutishauser, T., Busto, M.,
209 Chmielewski, F.M., Hájková, L., Hodžić, S., Kaspar, F., Pietragalla, B., Romero-Fresneda, R., Tolvanen,
210 A., Vučetić, V., Zimmermann, K. & Zust, A. (2018) Pan european phenological database (pep725): a single
211 point of access for european data. *International Journal of Biometeorology* **62**, 1109–1113.
- 212 Trouet, V., Esper, J., Graham, N., Baker, A., Scourse, J. & Frank, D. (2009) Persistent positive north atlantic
213 oscillation mode dominated the medieval climate anomaly. *Science* .
- 214 Vitasse, Y., Lenz, A. & KÄÄürner, C. (2014) The interaction between freezing tolerance and phenology in
215 temperate deciduous trees. *Frontiers in Plant Science* **5**.
- 216 Vitra, A., Lenz, A. & Vitasse, Y. (2017) Frost hardening and dehardening potential in temperate trees from
217 winter to budburst. *New Phytologist* **216**, 113–123.
- 218 Wolkovich, E.M., Cook, B.I., Allen, J.M., Crimmins, T.M., Betancourt, J.L., Travers, S.E., Pau, S., Regetz,
219 J., Davies, T.J., Kraft, N.J.B., Ault, T.R., Bolmgren, K., Mazer, S.J., McCabe, G.J., McGill, B.J., Parme-
220 san, C., Salamin, N., Schwartz, M.D. & Cleland, E.E. (2012) Warming experiments underpredict plant
221 phenological responses to climate change. *Nature* **485**, 18–21.

²²² Wypych, A., Ustrnul, Z., Sulikowska, A., Chmielewski, F.M. & Bochenek, B. (2016) Spatial and temporal
²²³ variability of the frost-free season in central europe and its circulation background. *International Journal*
²²⁴ of *Climatology* **37**, 3340–3352.

²²⁵ Zohner, C.M., Benito, B.M., Svenning, J.C. & Renner, S.S. (2016) Day length unlikely to constrain climate-
²²⁶ driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* **6**, 1120–1123.

²²⁷ **Tables and Figures**

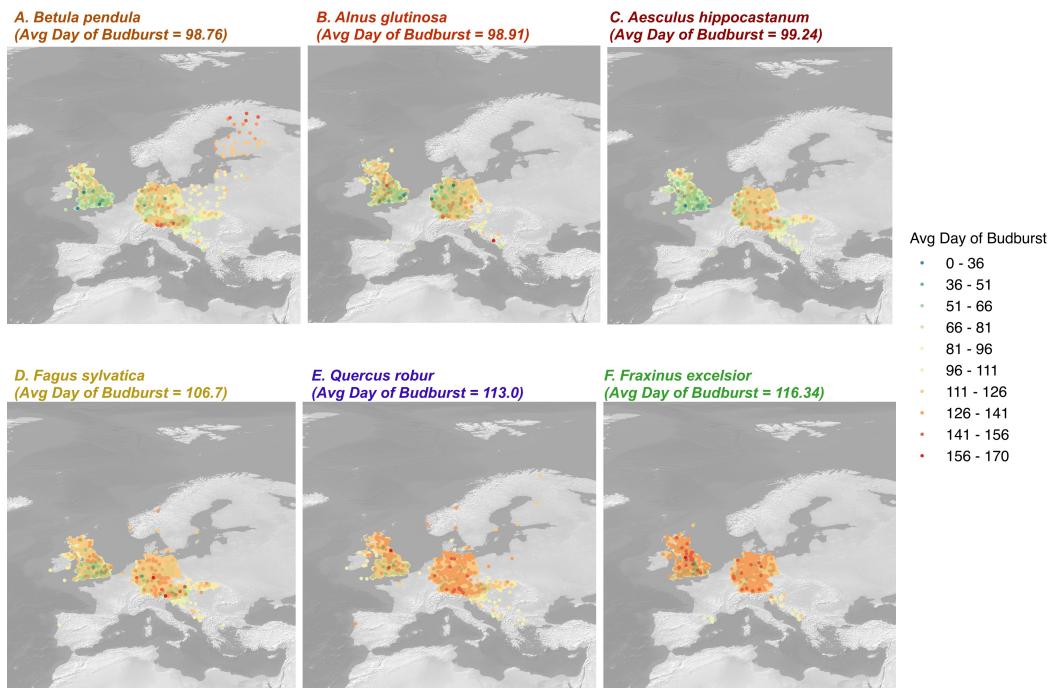


Figure 1: The average day of budburst is mapped by site for each species. Species are ordered by day of budburst starting with *Betula pendula* as the earliest budburst date to *Fraxinus excelsior*. Earlier budburst dates are blue and later budburst dates are in red.

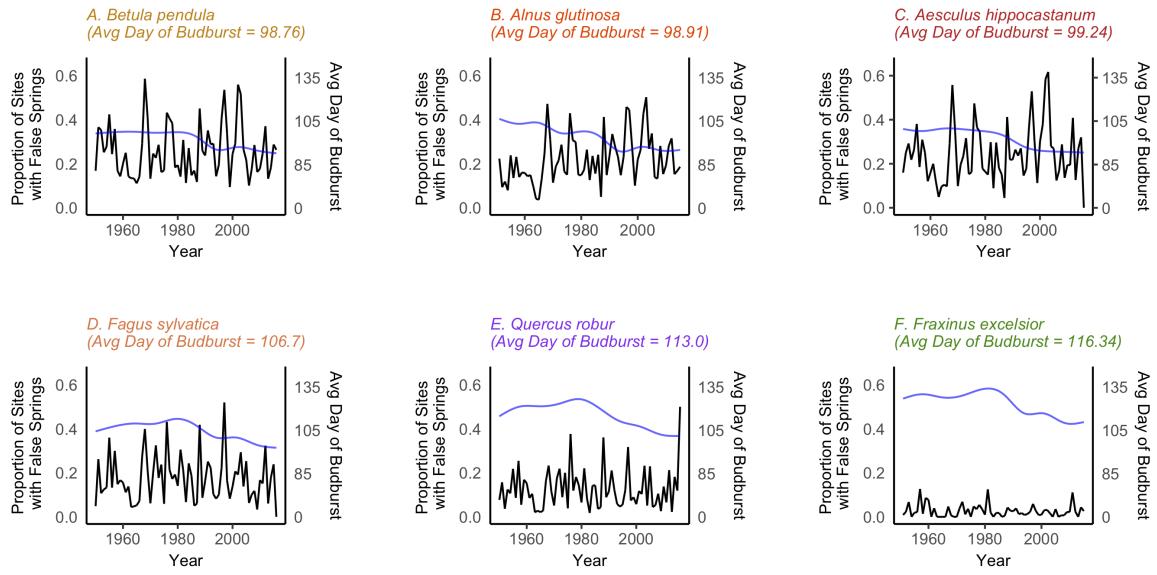


Figure 2: The black line indicates the proportion of sites that had false spring conditions for each year across all species. The blue line is a smoothing spline, indicating the trend of average day of budburst for each year for each species. Species are ordered by average day of budburst, with the earliest being *Betula pendula* and the latest being *Fraxinus excelsior*.

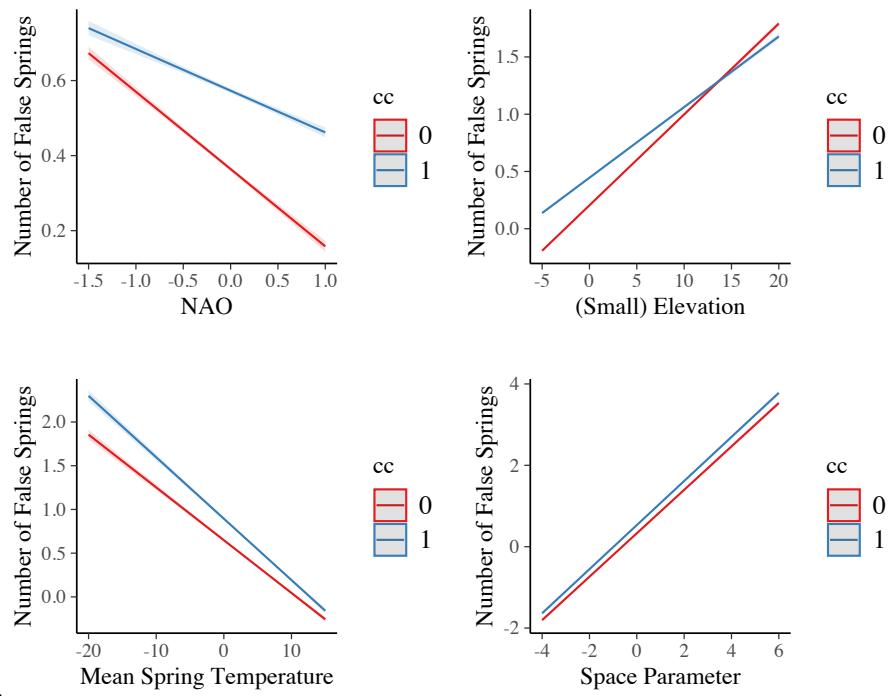


Figure 3

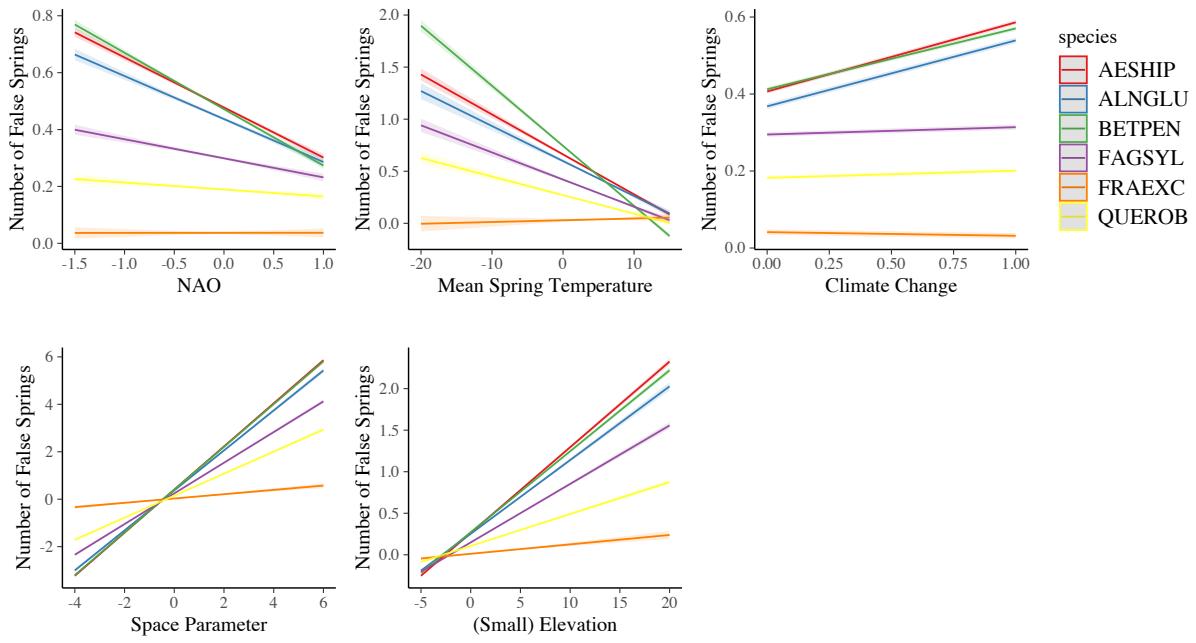


Figure 4

228 **Supplement: Tables and Figures**

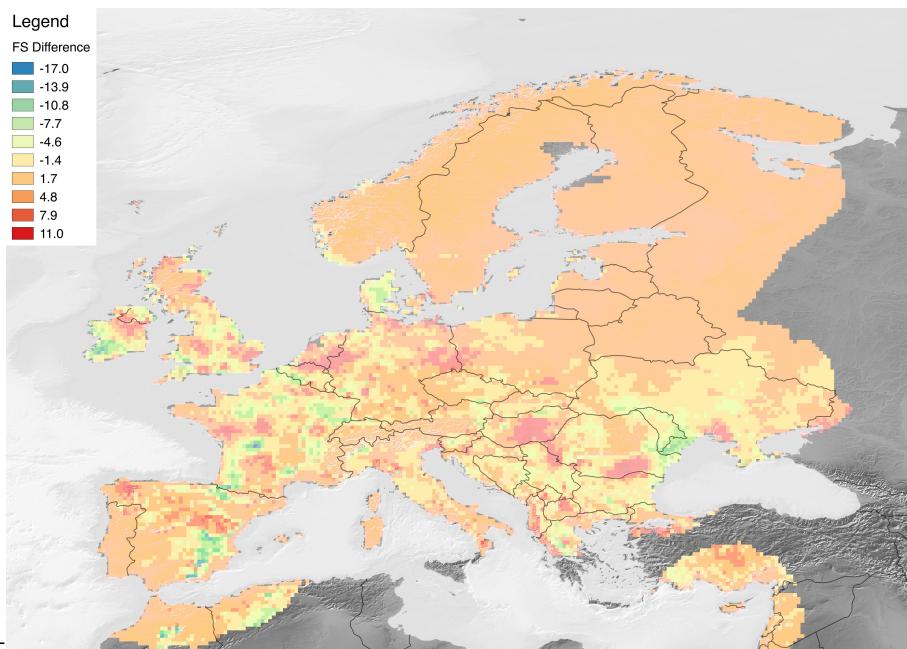


Figure 5: Number of years with freezing events that occurred before temperature shifts related to climate change began (1951-1983) as compared to after reported climate shifts (1984-2016). If temperatures fell below -2°C between March 1 and June 30, a year with a spring freeze was tallied. Some regions experienced more years with spring freezes after climate change began, whereas other years experienced the same number or even fewer years with spring freezes. Regions that had more years with spring freezes after climate change began are blue and green and regions that had fewer freezes are depicted in red.

229

Table 1: Data points collected for each species

Species	Num. of Observations	Num. of Sites	Num. of Years
<i>Aesculus hippocastanum</i>	216396	10158	66
<i>Alnus glutinosa</i>	136991	6775	66
<i>Betula pendula</i>	215729	10139	66
<i>Fagus sylvatica</i>	185949	9099	66
<i>Fraxinus excelsior</i>	143269	7327	65
<i>Quercus robur</i>	184406	8811	66

230

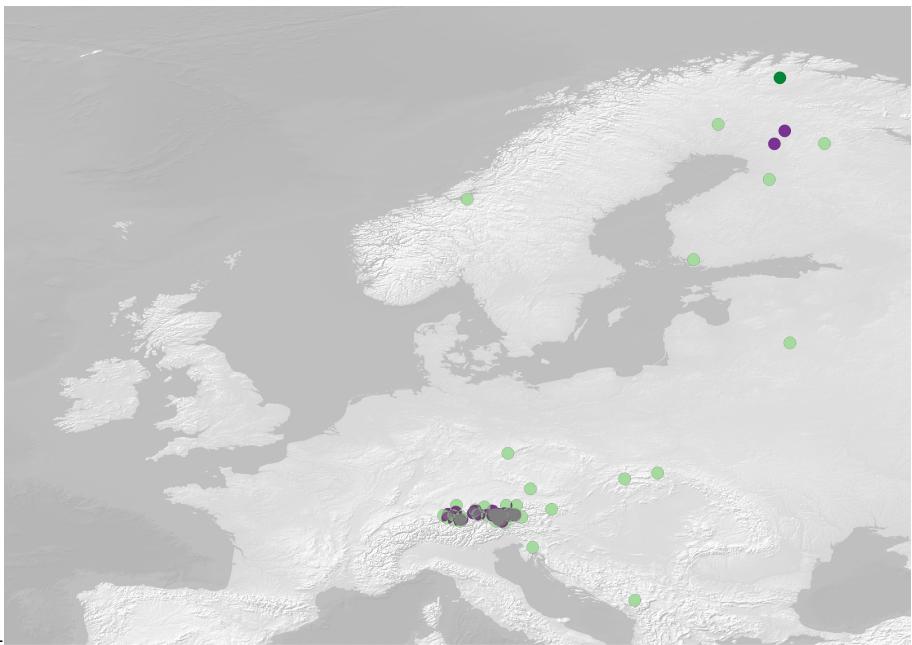


Figure 6: Space parameter values are mapped for each location to elucidate patterns in the parameter values.