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## Running head: Divergent trends in spring frost damage risk

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## Abstract

Frost events during the active growth period of plants can cause extensive frost damage with tremendous economic losses and dramatic ecological consequences. A common assumption is that climate warming may bring along a reduction in the frequency and severity of frost damage to vegetation. On the other hand, it has been argued that rising temperature in late winter and early spring might trigger the so called “false spring”, i.e., early onset of growth that is followed by cold spells, resulting in increased frost damage. By combining daily gridded climate data and 1489k *in situ* phenological observations of 27 tree species from 5565 phenological observation sites in Europe, we show here that temporal changes in the risk of spring frost damage with recent warming vary largely depending on the species and geographical locations. Species whose phenology was especially sensitive to climate warming tended to have increased risk of frost damage. Geographically, compared with continental areas, maritime and coastal areas in Europe were more exposed to increasing occurrence of frost and these late spring frosts were getting more severe in the maritime and coastal areas. Our results suggest that even though temperatures will be elevated in the future, some phenologically responsive species and many populations of a given species will paradoxically experience more frost damage in the future warming climate. More attention should be paid to the increased frost damage in responsive species and populations in maritime areas when developing strategies to mitigate the potential negative impacts of climate change on ecosystems in the near future.

## Introduction

While plants are highly resistant to below-freezing temperatures during the dormancy in winter, during the active growth, the sensitive tissues of plants that include buds, new leaves and flowers, are vulnerable to frosts (Inouye, 2000). The late spring frosts affect growth and reproduction of plants and thus can cause tremendous economic losses (Warmund *et al.*, 2008). For example, the economic loss for agricultural crops after the 2007 eastern US spring freeze was up to $112 million, with fruit crop loss of $86 million (Warmund *et al.*, 2008). In addition, through direct sub-lethal and potentially lethal damages to sensitive tissues of plants, frosts can affect plant fitness, alter species interactions (i.e., interspecific competition), and reduce carbon uptake, which consequently cause significant changes in the structure and function of terrestrial ecosystems (Gu *et al.*, 2008; Hufkens *et al.*, 2012; Vitasse *et al.*, 2014). The occurrence of frost damage is determined by the timing of frosts and that of phenological events. Due to climate warming in recent decades (Hansen *et al.*, 2006), extreme cold events are expected to occur less frequently (IPCC, 2012) and the date of the last spring frost has advanced (Schwartz *et al.*, 2006). A reduction in the frequency and severity of frost damage to plants is thus expected. Under the tremendous pressure from rapid climate change, plant species have been facing a tradeoff between early development (or growth) to maximize the length of the growing season (carbon gain) and late development to avoid frost damage (Bennie *et al.*, 2010; Augspurger, 2013). Varying strategies to cope with climate warming among species will have long-term effects on terrestrial ecosystems. Phenological tracking of climate change has been shown to improve the performance of many species as regards to standing biomass, plant cover, and individual growth, or to otherwise increase their fitness (Cleland *et al.*, 2012). However, climatic warming has also generally advanced phenological events (Menzel & Fabian, 1999; Parmesan & Yohe, 2003), which may increase the exposure of vulnerable plant tissues to subsequent spring frosts.

Cannell (1985) hypothesized, therefore, that climate warming in boreal and temperate zones increases the risk of frost damage to trees. This hypothesis has been addressed in several studies with modeling and experimental approaches (Hänninen, 1991; Schwartz & Chen, 2002; Bennie *et al.*, 2010; Augspurger, 2013; Ge *et al.*, 2013). Altogether, a consensus whether the risk of plants to encounter spring frost damage due to recent warming has increased, or decreased, has not been reached (Vitasse *et al.*, 2014; Hänninen, 2016).

Responses of phenological timing to climate warming indeed vary among species (Cleland *et al.*, 2012). In addition to the well-known advances of spring phenology, by reducing the exposure of temperate tree species to chilling, climatic warming may have a lower impact on the advance of spring phenology, or sometimes even cause a delay of it, in these tree species (Murray *et al.*, 1989; Ford *et al.*, 2016). Thus, the temporal changes in the risk of frost damage caused by climate warming might depend on species-specific phenological responses to warming. Those species which advance the phenological timing strongly (more responsive species) may experience increased risk of frost damage, whereas species that advance the phenological timing slowly or even have delayed spring phenology (less responsive species) may have decreased risk of frost damage (Hufkens *et al.*, 2012) (see Materials and methods for the definitions of more responsive and less responsive species).

Within species, phenological sensitivity to elevated temperature varies among populations in different geographical locations (Schwartz *et al.*, 2006; Chen *et al.*, 2018; Ma *et al.*, 2018). Furthermore, the influence of global climatic change on the frequency and distribution of frost events is also uncertain.

Frosts may become more frequent in some areas and less frequent in others (Inouye, 2000). Therefore, the temporal changes in the risk of spring frost damage to a given species as a consequence of global climate change may vary geographically. In all, comprehensive studies comparing temporal changes in the risk of spring frost damage to a large number of species over broad spatial scales are urgently needed.

We used long-term phenological records of the Pan European Phenology (PEP) network (www.pep725.eu (Templ *et al.*, 2018)) as well as a recent high-resolution daily gridded climate data (Haylock *et al.*, 2008) to explore the changes in the risk of spring frost damage to tree species in Europe during 1950 - 2013. We hypothesize that the temporal changes in the risk of spring frost damage with recent climate warming vary among species groups (more responsive vs less responsive species) and across geographical locations. The earliest phenophase of a given species has the highest risk of spring frost damage, so it was analyzed in this study. In total, 1,488,816 phenological observations of 27 tree species from 5565 phenological observation sites were used (see Table 1 for the studied species, and Fig. S1 for the geographical distribution of the *in situ* phenological observation sites). Based on selected phenophases (Table 1), this study focused on the frost damage to the buds, new leaves and flowers. This study aimed to examine the temporal changes in the risk of spring frost damage as a result of climate warming, rather than the survival and growth of the species in response to climate warming, which is not recorded in the dataset. Thus, the effect of the frost damage on the subsequent performance of the examined tree species was not addressed.

## Materials and methods

### Phenology and climate data

Phenology dataset was obtained from the Pan European Phenology (PEP) network (www.pep725.eu), which provides a free access to *in situ* phenology records for multiple phenophases of a variety of plant species across Europe (Templ *et al.*, 2018). The phenological timing was recorded as the day of year (DOY). Currently, PEP provides the phenology data grouped by phenological site, without any information on the number of trees and buds per tree at each site.

For a given species, the earliest phenophase during spring was analyzed, because it is the one where the risk of frost damage is highest. If the timing for the earliest phenophase was not recorded in the PEP dataset, then a later phenophase recorded was used instead. For each selected species, the following screening criteria of the data were applied: (i) We removed extreme phenological records that lied far away from the bulk of observations: [Q1 - k (Q3 - Q1), Q3 + k (Q3 - Q1)], where Q1 and Q3 are the lower and upper quartiles of the DOYs of the phenological events, respectively, and k = 5; (ii) We kept in the analyzed dataset only species that were recorded at least at 10 phenological observation sites with a minimum of 10 years' observations at each site. A total of 27 tree species from 5565 phenological observation sites were analyzed (Table 1). For most species, there was a similar number of observations across the study period. The overall mean DOY for each species was computed as the mean phenological timing across all years and all sites, thus describing in general the species earliness in the phenological development in relation to other species. Fig. S1 shows the geographical distribution of all PEP phenological observation sites used in the study.

We used daily temperature data from a gridded climate dataset E-OBS, which is based on EU-FP6 project ENSEMBLES (http://ensembles-eu.metoffice.com) and the ECA&D project (http://www.ecad.eu) (Haylock *et al.*, 2008). Data in the E-OBS are derived through interpolation of observed daily temperature data from weather stations across Europe (Haylock et al., 2008). E-OBS data files contain daily minimum temperature since January 1st, 1950, with a spatial resolution of 0.25 degrees. The mean altitude for the climate grid cell is provided as well. Due to the coarse-resolution of the grid cell data, particularly in mountain areas the altitude of the observation sites may be vastly different from the mean altitude of the climate grid. To better capture the temperature variation in each site, temperature data were adjusted using elevation difference between the site and the climate grid cell, based on a temperature lapse rate of 6.4°C/km (Olsson & Jönsson, 2014).

## Calculation of variables for frost and frost damage risk

**Last spring frost (LSF)** date is defined as the last calendar day (DOY) prior to 15th July, with the daily minimum temperature below -2.2 °C (Schwartz *et al.*, 2006; Peterson & Abatzoglou, 2014). **The probability of potential frost damage** is computed as the proportion of those populations of a given species where at least one frost event (daily minimum temperature below -2.2°C) occurred between the date of the phenological event and 15th July (Schwartz *et al.*, 2006; Peterson & Abatzoglou, 2014). Post-dormant minimum temperature ($T_{PD}$) is the minimum of the daily minimum temperatures occurring between the date of the phenological event and 15th July, indicating the heaviest freezing stress the plants will be exposed to during the active growth period (Hänninen, 1991; Hänninen, 2016).

In order to facilitate comparisons with the probability of potential frost damage, the **severity of potential frost damage** is quantified as -$T_{PD}$.

## Advancing rates of phenological timing and LSF date over years

Using ‘lme4’ package (Bates *et al.*, 2014) of R (R Development Core Team, 2015), linear mixed effects models including phenological site as a random intercept were run to compute the long-term advancing rates of phenological timing and the LSF date over years for each species in Table 1:

$$y_{ij} = \alpha + \beta x_{ij} + a_j + \varepsilon_{ij} \quad (1)$$

where $y_{ij}$ is the phenological timing or LSF date in year i at the site j, $x_{ij}$ is the year i at the site j, $\alpha$ is the intercept with the y-axis, $\beta$ is the slope, $a_j$ is the random effect of the site j, and $\varepsilon_{ij}$ is the error term. $-\beta$, the opposite number of the slope, is the advancing rate of phenological timing or LSF date. Species whose advancing rate of phenological timing was higher (slower) than that of the LSF date were defined as more (less) responsive species (Table 1).

Then, paired t-test was used to determine if there was a statistically significant difference between advancing rates of timing of the phenological event and that of the LSF date. Simple linear regression analyses were applied to separately examine how the advancing rates of phenological timing and LSF date were related to the earliness of the tree species, represented as the overall mean DOY.

## Temporal changes in the probability and severity of potential spring frost damage

Mixed effects logistic regression, also known as generalized linear mixed effects model with logit link function, including phenological site as a random variable, was applied for each species to test whether the probability of potential frost damage increased or decreased during the studied period:

$$logit(p_{ij}) = log\left(\frac{p_{ij}}{1-p_{ij}}\right) = \alpha + \beta x_{ij} + a_j \qquad (2)$$

where $p_{ij}$ is the probability of potential frost damage of a given species in year i at the site j, and $1-p_{ij}$ is the probability of no frost damage occurring. $x_{ij}$ is the year i at the site j, α is the intercept with the y-axis, β is the slope, $a_j$ is the random effect of the site j.

A linear mixed effects model (see Eq. (1)), including phenological site as a random variable, was applied to compute the changes in the severity of potential frost damage over years. In the equation the variable $y_{ij}$ indicates the value of the severity of potential frost damage ($=-T_{PD}$) in year i at the site j.

Simple linear regression analyses were performed to examine the changes in the probability and the severity of potential spring frost damage in relation to the overall mean DOY that represents the species earliness in the phenological development.

## Temporal changes in the probability and severity of potential spring frost damage of trees in various geographical locations

We further analyzed the geographical variation of the temporal changes in the probability and the severity of potential frost damage for 19 species with observations over a large geographical region where the phenological observations were recorded at more than 1000 observation sites (for the observation sites of the different species, see Table 1). We gridded the whole region into 2 by 2 degree cells. Using the phenological and climate data in each single grid cell, mixed effects logistic regression (see Eq. (2)), including phenological site as a random variable, was used to compute the temporal changes in the probability of potential spring frost damage. A linear mixed effects model (see Eq. (1)), including phenological site as a random variable, was applied to compute the temporal changes in the severity of potential frost damage ($-T_{PD}$) over years.

## Changes in advancing rates of phenological timing and last spring frost (LSF) date along altitude

For each species at each observation site, simple linear regression analyses were performed to compute the advancing rate of phenological timing and LSF date over years. Then, using ‘mgcv’ package (Wood, 2001) of R (Wood, 2001), generalized additive mixed models with random intercepts for each species were run to examine the changes in advancing rates of phenological timing and LSF date along altitude.

### Sensitivity analysis

The present study used -2.2 °C (Schwartz *et al.*, 2006; Peterson & Abatzoglou, 2014) as the threshold to determine the occurrence of spring frost. Additionally, we carried out a sensitivity analysis by using 0 °C, -1 °C, -3 °C, -4 °C and -5 °C as the threshold.

In all data analyses, residuals from regressions were tested to confirm normality. All data analyses were conducted with the R software (R Development Core Team, 2015).

## Results

For each species, we first computed the advancing rate of the phenological timing and the advancing rate of the last spring frost (LSF) date at sites where the phenological timing of that species was recorded. The spring phenological timing advanced at a mean rate of 0.13 days/year, ranging from 0.43 days (advance) to -0.13 days/year (delay, Fig. 1a). The spring phenological timing was advanced significantly in 21 out of the 27 species, delayed significantly in four species, and in two species it remained unchanged. Consistent with previous studies (Murray *et al.*, 1989; Menzel & Fabian, 1999; Parmesan & Yohe, 2003), the majority of spring phenological events advanced, and unchanged and delayed spring phenology was also observed. LSF date advanced at a mean rate of 0.12 days/year, varying from 0.31 (advance) to -0.04 days/year (delay, Fig. 1a). A paired t-test showed that the average advancing rates of phenological timing and LSF date did not differ significantly ($p = 0.73$). However, phenological timing advanced faster than LSF date in some species (defined as more responsive species), whereas LSF date advanced faster in others (defined as less responsive species), indicating divergent changes in the risk of potential frost damage.

For each species, we then calculated two indicators, i.e., the probability and the severity, for the temporal changes in the risk of spring frost damage. Divergent trends in both the probability and the severity of potential spring frost damage were revealed among the species examined (Fig. 1b). Linear regression analyses between the probability and severity of spring frost damage and overall mean DOY suggest that the early species were more likely to have increased probability of potential frost damage (slope = -0.0008, $p < 0.001$) and more severe frost damage (slope = -0.001, $p < 0.001$) than the late species.

A paired comparison between the advancing rates of phenological timing and LSF date indicated that changes in the risk of frost damage of a given species were strongly related to the two advancing rates. Species whose phenology was more responsive to climate change, i.e., species where the advancing rate of phenology was higher than that of the LSF date, tended to have an increased probability of potential spring frost damage (Fig. 2a) and also an increased severity of potential spring frost damage (Fig. 2b). The opposite was true for less responsive species where the advancing rate of phenology was lower than that of the LSF date (Fig. 2).

We also examined the spatial variation in the temporal changes of the risk of spring frost damage in 19 species with observations over a wide geographical range where phenology was recorded at more than 1000 phenological sites (for the phenological observation sites of the different species, see Table 1). The temporal changes in the probability and severity of potential spring frost damage of 6 species in various geographical locations are shown in Figs. 3 & 4, respectively. The corresponding graphs for the other 13 species are presented in Figs. S2&S3. The results indicate obvious geographical differences, with maritime and coastal areas (low-altitude areas) being prone to increased risk (both probability and severity) of potential spring frost damage, and continental high-altitude areas having a reduced risk of frost damage.

As the risk of frost damage is closely related to the advancing rates of phenological timing and LSF date, we further examined the changes in the two advancing rates along altitudes across all species (Fig. 5). Overall, the advancing rate of phenological timing decreased slightly with altitude. However, the advancing rate of LSF date increased drastically along altitude. At low altitudes, the phenological timing advanced more rapidly than the LSF date, resulting in an increased risk of spring frost damage. At high altitudes, the advancing of the LSF date was faster than that of phenological timing, leading to a decreased risk of frost damage.

We carried out a sensitivity analysis by using alternative frost temperature thresholds including 0 °C, -1 °C, -3 °C, -4 °C and -5 °C. No matter which frost temperature threshold was used, the phenologically more responsive species were more prone to increased risk of potential spring frost damage than the less responsive ones (Fig. S4), and the maritime and coastal areas in Europe were more exposed to increased risk of frost potential spring frost damage than continental areas (Figs. S5-S9).

## Discussion

By combining daily gridded climate data and long-term phenological observation data, a comprehensive multi-species study over a large geographical area on the effects of recent warming on the risk of potential spring frost damage to trees was conducted for the first time. Our results revealed divergent trends in the warming-induced risk of spring frost damage among species, and geographical differences among populations within species. Species whose phenology was more sensitive to climate warming tended to have increased occurrence and severity of potential frost damage (Fig. 2). Geographically, compared with continental areas, maritime and coastal areas in Europe were more exposed to increasing occurrence of frost and these late frosts were getting more severe in the maritime and coastal areas (Figs. 3&4). Even though temperatures will be elevated in the future, some more species and some populations in maritime areas will paradoxically experience increased frost damage in the future warming climate.

Previous studies have suggested that the phenologically responsive species tend to have improved performances in standing biomass, plant cover and individual growth and thus have increased fitness (Cleland *et al.*, 2012). However, our results suggest that the species whose phenology was more sensitive to climate warming tended to experience increased risk of frost damage, which may offset the benefits of advanced phenology. The species-specific differences in the risk of spring frost damage may affect fitness of tree species and consequently have significant implications on the structure and function of terrestrial ecosystems (Inouye, 2000; Gu *et al.*, 2008; Vitasse *et al.*, 2014), as even slight differences in the frost damage among species can be magnified by other processes, such as interspecific competition, in natural ecosystems (Hänninen, 2016).

As the warming continues, the phenological sensitivity of temperate trees to elevated temperature is expected to decline (Fu *et al.*, 2015). The declined sensitivity is probably attributable to reduced chilling, and photoperiodic limitations, both of which prevents the premature phenological development during early spring (Fu *et al.*, 2015). As a result, under the future climate warming more species will be expected to show an advancement rate of spring phenology that is slower than that of the LSF date. Some species that used to suffer from frost damages will probably be better adapted to escape spring frost with continued warming.

The strong geographical pattern in the temporal changes of the risk of spring frost damage suggests that tree populations are better adapted to avoid spring frost damage in continental high-altitude areas than in maritime and coastal areas (low-altitude areas). The decreased risk of frost damage at high-altitude areas is possibly caused by the more dramatic climatic warming in these areas than at low altitudes (Pepin *et al.*, 2015). Frost damage will continue to be an issue for forest regeneration and management in areas where the risk of frost damage is increased (Woldendorp *et al.*, 2008). The geographical variation in the temporal changes of the risk of spring frost damage may affect the survival and growth of trees differently depending on the geographical locations, and thus influence the distribution of tree species, which may further alter the forest structure and function over a large geographical region (Inouye, 2000).

The results presented in this study were based on using daily minimum temperatures below -2.2 °C in determining the occurrence of frosts for all species and all sites. However, there can be differences among tree species and among tree provenances (geographical regions) of a given species in their frost hardiness after the occurrence of the observed phenological events. However, we do not know any literature for addressing this issue, especially over a large geographical region. Accordingly, we carried out a sensitivity analysis by using alternative frost temperature thresholds in the calculations. Regardless of the frost temperature threshold used, the phenologically more responsive species were always more prone to increased risk of spring frost damage, and the maritime and coastal areas in Europe were more exposed to increased risk of spring frost damage than the continental areas. These consistent results based on different frost temperature thresholds indicate that our results are robust and the temporal trends remain even if the thresholds vary among species and among provenances.

The present study was based on the phenology dataset provided by the PEP network (Templ *et al.*, 2018). The dataset involves some shortcomings, such as lacking information about the number of trees and buds per tree observed at each site, or the position of the buds observed. However, despite these shortcomings, the dataset has been proved to be a valuable source of information in earlier large-scale studies sharing a partly similar approach with the present study (Fu *et al.*, 2015; Piao *et al.*, 2015; Templ *et al.*, 2018).

This study used the gridded climate dataset E-OBS (Haylock *et al.*, 2008), derived through interpolation of the daily temperature records from the most complete weather station network in Europe. Ideally, real observed climate data from weather stations at or near the phenological observation sites should be used. However, observed climate data for the thousands of phenological observation sites is unfortunately not available. Despite the potential bias in grids with limited observed climate data, the gridded data set is still usable when addressing such large geographical areas as in the present study.

A recent work of Liu *et al.* (2018), based mainly on remote-sensed data, found that the frost days when the daily minimum temperature dropped below 0° C have increased during the growing season in recent decades in the Northern Hemisphere. While being in broad agreement with the large-scale results of Liu *et al.* (2018), our species-specific analysis additionally shows that there have been great differences among species in the temporal changes of frost damage risk. These differences should be taken into account when projecting the future effects of climate change on plants and ecosystems, otherwise oversimplified projections will be arrived at. Furthermore, we addressed not only the probability of potential frost damage, but also its severity, and the phenology of both leafing out and flowering. In all, our approach is between the large-scale remote sensing-based approach of Liu *et al.* (2018), and the small-scale approaches addressing experimentally the ecophysiological details of the effects of climatic warming, such as the responses of dormancy release to various chilling temperatures under a warming climate (Cannell, 1985; Murray *et al.*, 1989; Hänninen, 2016). For that reason the shortcomings of the PEP dataset discussed in the previous paragraph are not critical to our approach. A well-balanced combination of all these and other approaches is needed for projecting the ecological effects of climate change.

Within the context of global warming, a better understanding of occurrence and severity of potential frost damage to tree species over time and space is critical to assessing and predicting the survival, growth and distribution of tree species and the impact of climate change on forest structure and function. Our findings may help policymakers to develop strategies to mitigate the potential negative impacts of extreme climatic conditions on the earth ecosystems and human beings in the near future.

**References:**

Augspurger, C.K. (2013) Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology*, **94**, 41-50.

Bates, D., Mächler, M., Bolker, B. & Walker, S. (2014) Fitting linear mixed-effects models using lme4. *arXiv preprint arXiv:1406.5823*,

Bennie, J., Kubin, E., Wiltshire, A., Huntley, B. & Baxter, R. (2010) Predicting spatial and temporal patterns of bud ‐ burst and spring frost risk in north ‐ west Europe: the implications of local adaptation to climate. *Global Change Biology*, **16**, 1503-1514.

Cannell, M.G. (1985) Analysis of risks of frost damage to forest trees in Britain. *Crop physiology of forest trees/compiled and edited by Peter MA Tigerstedt, Pasi Puttonen and Veikko Koski*,

Chen, L., Huang, J.G., Ma, Q., Hänninen, H., Rossi, S., Piao, S. & Bergeron, Y. (2018) Spring phenology at different altitudes is becoming more uniform under global warming in Europe. *Global change biology*, **24**, 3969-3975.

Cleland, E.E., Allen, J.M., Crimmins, T.M., Dunne, J.A., Pau, S., Travers, S.E., Zavaleta, E.S. & Wolkovich, E.M. (2012) Phenological tracking enables positive species responses to climate change. *Ecology*, **93**, 1765-1771.

Ford, K.R., Harrington, C.A., Bansal, S., Gould, P.J. & St Clair, J.B. (2016) Will changes in phenology track climate change? A study of growth initiation timing in coast Douglas ‐ fir. *Global Change Biology*, **22**, 3712-3723.

Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A. & Peñuelas, J. (2015) Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, **526**, 104-107.

Ge, Q., Wang, H. & Dai, J. (2013) Shifts in spring phenophases, frost events and frost risk for woody plants in temperate China. *Climate Research*, **57**, 249-258.

Gu, L., Hanson, P.J., Mac Post, W., 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**, 253-262.

Hänninen, H. (1991) Does climatic warming increase the risk of frost damage in northern trees? *Plant, Cell & Environment*, **14**, 449-454.

Hänninen, H. (2016) *Boreal and Temperate Trees in a Changing Climate: Modelling the Ecophysiology of Seasonality*. Springer.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D.W. & Medina-Elizade, M. (2006) Global temperature change. *Proceedings of the National Academy of Sciences*, **103**, 14288-14293.

Haylock, M., Hofstra, N., Klein Tank, A., Klok, E., Jones, P. & New, M. (2008) A European daily high‐resolution gridded data set of surface temperature and precipitation for 1950–2006. *Journal of Geophysical Research: Atmospheres*, **113**

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. (2000) The ecological and evolutionary significance of frost in the context of climate change. *Ecology Letters*, **3**, 457-463.

IPCC (2012) Summary for policymakers. Managing the risks of extreme events and disasters to advance climate change adaptation (ed. by Field, C.B., Barros, V., Stocker, T.F., Quin, D., Dokken, D.J., Ebi, K.L., Mastrandrea, M., Mach, K., Plattner, G.-K., Allen, S., Tignor, M. and Midgley, P.), pp. 1-19.

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**, 426.

Ma, Q., Huang, J.-G., Hänninen, H. & Berninger, F. (2018) Reduced geographical variability in spring phenology of temperate trees with recent warming. *Agricultural and Forest Meteorology*, **256-257C**, 526-533.

Menzel, A. & Fabian, P. (1999) Growing season extended in Europe. *Nature*, **397**, 659-659.

Murray, M., Cannell, M. & Smith, R. (1989) Date of budburst of fifteen tree species in Britain following climatic warming. *Journal of Applied Ecology*, 693-700.

Olsson, C. & Jönsson, A.M. (2014) Process‐based models not always better than empirical models for simulating budburst of Norway spruce and birch in Europe. *Global Change Biology*, **20**, 3492-3507.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37-42.

Pepin, N., Bradley, R., Diaz, H., Baraër, M., Caceres, E., Forsythe, N., Fowler, H., Greenwood, G., Hashmi, M. & Liu, X. (2015) Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, **5**, 424-430.

Peterson, A.G. & Abatzoglou, J.T. (2014) Observed changes in false springs over the contiguous United States. *Geophysical Research Letters*, **41**, 2156-2162.

Piao, S., Tan, J., Chen, A., Fu, Y.H., Ciais, P., Liu, Q., Janssens, I.A., Vicca, S., Zeng, Z. & Jeong, S.-J. (2015) Leaf onset in the northern hemisphere triggered by daytime temperature. *Nature communications*, **6**

R Development Core Team (2015) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing.

Schwartz, M.D. & Chen, X. (2002) Examining the onset of spring in China. *Climate Research*, **21**, 157-164.

Schwartz, M.D., Ahas, R. & Aasa, A. (2006) Onset of spring starting earlier across the Northern Hemisphere. *Global Change Biology*, **12**, 343-351.

Templ, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., Busto, M., Chmielewski, F.-M., Hájková, L. & Hodzić, S. (2018) Pan European Phenological database (PEP725): a single point of access for European data. *International Journal of Biometeorology*, 1-5.

Vitasse, Y., Lenz, A. & Körner, C. (2014) The interaction between freezing tolerance and phenology in temperate deciduous trees. *Frontiers in Plant Science*, **5**, 541.

Warmund, M.R., Guinan, P. & Fernandez, G. (2008) Temperatures and cold damage to small fruit crops across the eastern United States associated with the April 2007 freeze. *HortScience*, **43**, 1643-1647.

Woldendorp, G., Hill, M.J., Doran, R. & Ball, M.C. (2008) Frost in a future climate: modelling interactive effects of warmer temperatures and rising atmospheric [CO2] on the incidence and severity of frost damage in a temperate evergreen (Eucalyptus pauciflora). *Global Change Biology*, **14**, 294-308.

Wood, S.N. (2001) mgcv: GAMs and generalized ridge regression for R. *R news*, **1**, 20-25.

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## Author contributions

J.H, Q.M. and F.B. designed the study. Q.M. performed the analysis and wrote the manuscript with assistance from J.H, H.H and F.B. All authors discussed and commented on the manuscript.

## Competing financial interests

The authors declare no competing financial interests.

## Data accessibility statement

All phenology data used in this study are openly available at Pan European Phenology (PEP) network (www.pep725.eu). Climate data are freely accessible at the ECA&D (http://www.ecad.eu)

## Tables

**Table 1** The 27 tree species addressed in the study. The phenophase is identified by the BBCH code: 7 (beginning of sprouting), 10 (first leaves separated), 11 (leaf unfolding), and 60 (beginning of flowering). Species are ordered according to their overall mean DOY (day of year) which is computed for each species as the mean of the phenological timings across all years and sites. SD of DOY for each species is the standard deviation of the phenological timings across all years and sites. Note: Species whose advancing rate of phenological timing was higher (slower) than that of the LSF date were defined as more (less) responsive species. [a] denotes more responsive species, and [b] denotes less responsive species.

| ID | Name | BBCH | #observations | #sites | Study years | Overall mean DOY | SD of DOY |
|---|---|---|---|---|---|---|---|
| 1 | *Alnus glutinosa*[a] | 60 | 73392 | 2854 | 1951-2013 | 76 | 25 |
| 2 | *Alnus incana*[a] | 60 | 563 | 22 | 1960-2013 | 86 | 18 |
| 3 | *Sorbus aucuparia*[b] | 7 | 24039 | 1451 | 1991-2010 | 94 | 13 |
| 4 | *Syringa vulgaris*[b] | 11 | 1134 | 77 | 1953-2013 | 102 | 13 |
| 5 | *Larix decidua*[a] | 10 | 98051 | 3613 | 1950-2013 | 106 | 14 |
| 6 | *Prunus armeniaca*[b] | 60 | 451 | 26 | 1950-2013 | 107 | 17 |
| 7 | *Prunus persica*[b] | 60 | 37859 | 1899 | 1951-1991 | 109 | 14 |
| 8 | *Betula pendula*[a] | 60 | 28937 | 1651 | 1951-2013 | 110 | 12 |
| 9 | *Prunus spinosa*[a] | 60 | 103145 | 3692 | 1950-2013 | 110 | 15 |
| 10 | *Acer platanoides*[a] | 60 | 85957 | 3322 | 1951-2013 | 111 | 15 |
| 11 | *Aesculus hippocastanum*[a] | 11 | 137038 | 4735 | 1950-2013 | 112 | 12 |
| 12 | *Betula pubescens*[b] | 60 | 375 | 23 | 1971-2000 | 114 | 14 |
| 13 | *Prunus avium*[a] | 60 | 7776 | 356 | 1950-2013 | 116 | 13 |
| 14 | *Fraxinus excelsior*[a] | 60 | 63834 | 2605 | 1951-2013 | 118 | 15 |
| 15 | *Prunus domestica*[b] | 60 | 96269 | 4239 | 1950-2013 | 119 | 13 |
| 16 | *Fagus sylvatica*[a] | 11 | 110547 | 4044 | 1950-2013 | 119 | 10 |
| 17 | *Prunus cerasus*[b] | 60 | 112885 | 4096 | 1951-2010 | 120 | 11 |
| 18 | *Acer pseudoplatanus*[b] | 11 | 2413 | 147 | 1950-2013 | 120 | 14 |
| 19 | *Tilia platyphyllos*[b] | 11 | 75909 | 3586 | 1951-2012 | 121 | 12 |
| 20 | *Pyrus communis*[b] | 60 | 6097 | 296 | 1950-2002 | 121 | 13 |
| 21 | *Tilia cordata*[b] | 11 | 49528 | 2379 | 1951-2013 | 125 | 12 |
| 22 | *Quercus robur*[a] | 11 | 113998 | 4148 | 1950-2013 | 126 | 11 |
| 23 | *Populus tremula*[b] | 11 | 911 | 41 | 1964-2005 | 127 | 14 |
| 24 | *Prunus padus*[b] | 60 | 28883 | 1540 | 1951-1990 | 128 | 14 |
| 25 | *Picea abies*[a] | 10 | 106745 | 3866 | 1951-2013 | 129 | 11 |
| 26 | *Pinus sylvestris*[a] | 10 | 83453 | 3350 | 1951-2010 | 132 | 12 |
| 27 | *Robinia pseudoacacia*[b] | 7 | 38627 | 1992 | 1951-1990 | 136 | 12 |

## Figure captions

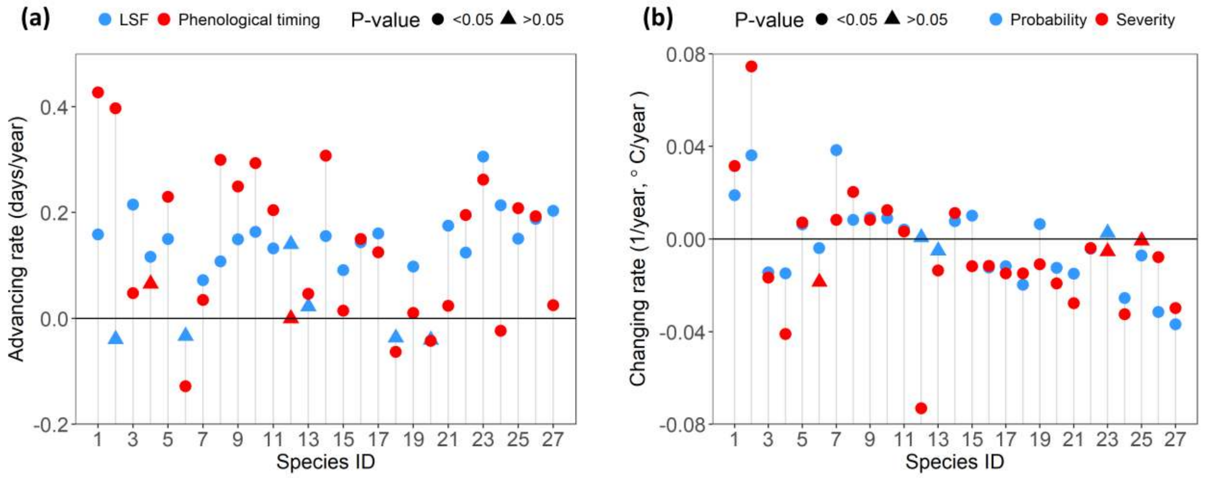
**Figure 1** Effects of climatic warming during recent decades in Europe. (a) Advancing rates of phenological timing of the 27 studied tree species, and the last spring frost date (LSF date) at the sites where phenological timing of each species was recorded (for the tree species ID and years included, see Table 1). Negative advancing rate indicates a trend towards later phenological timing, or later LSF date. (b) Changing rates of the probability and the severity of potential spring frost damage. Negative changing rate indicates a decrease in the probability (or severity) of potential spring frost damage. See Materials and methods for the definitions of LSF, and the probability and the severity of potential spring frost damage.

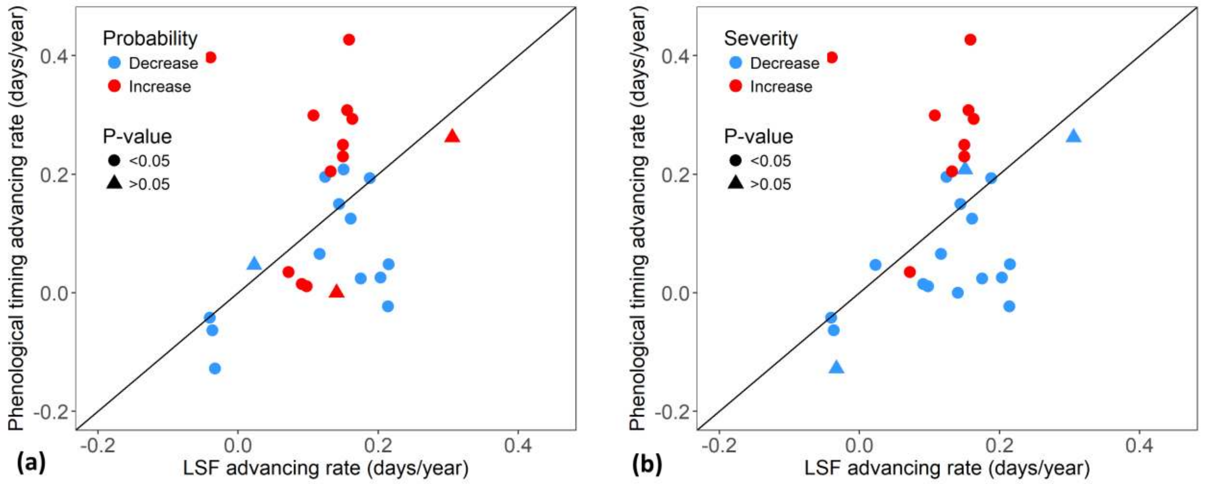
**Figure 2** Temporal changes in (a) the probability and (b) the severity of potential spring frost damage of trees species during recent decades in Europe, in relation to the species-specific advancing rates of phenological timing (vertical axes) and the last spring frost date (LSF, horizontal axes). See Material and methods for definitions of LSF, and the probability and the severity of potential spring frost damage. The straight black line represents y = x. Points above (below) the line represent more (less) responsive species when advancing rate of phenological timing is higher (lower) than the advancing rate of LSF.

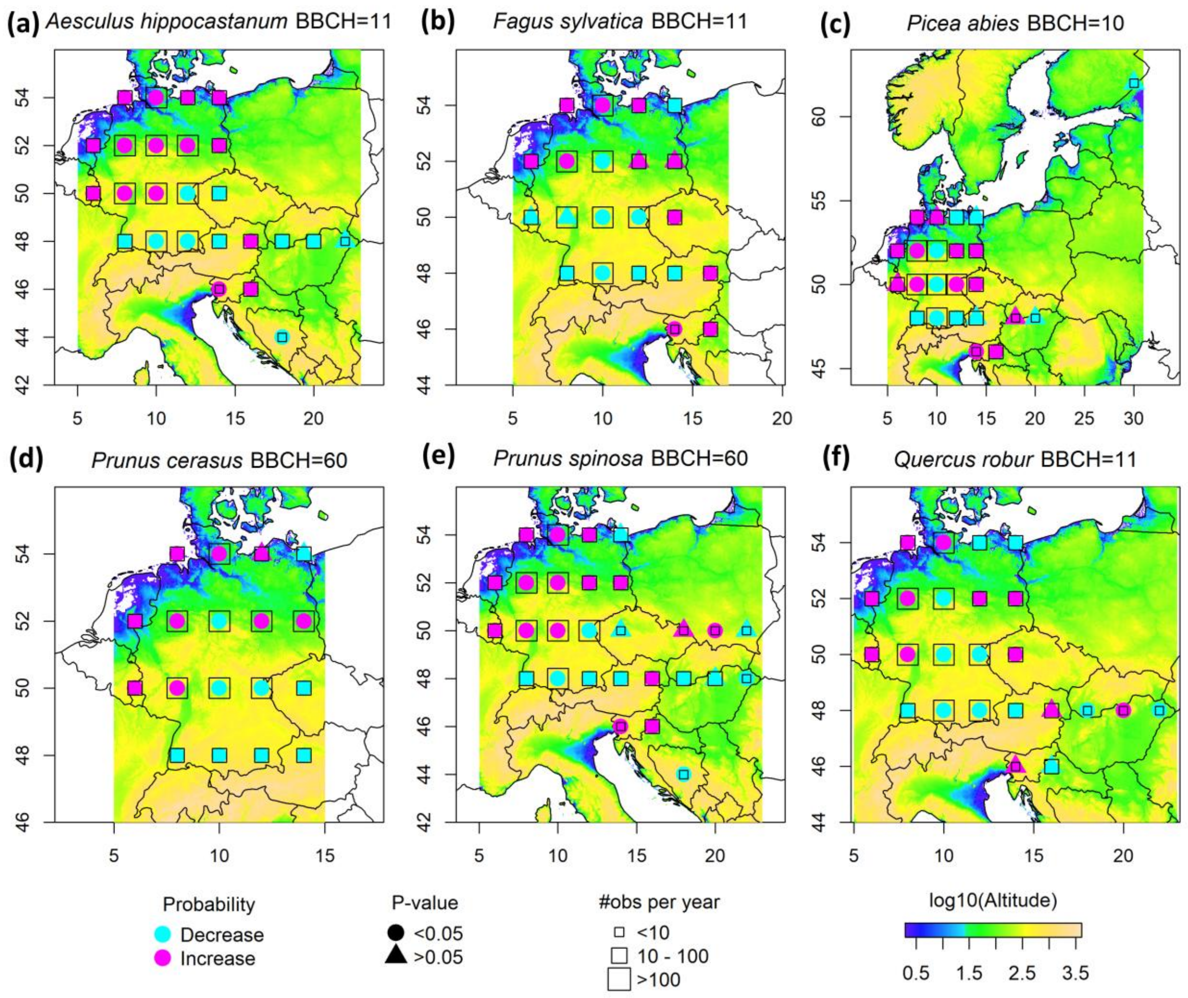
**Figure 3** Temporal changes in the probability of potential spring frost damage of 6 tree species caused by climatic warming during recent decades in various geographical locations in Europe. The notation #obs per year indicates the mean number of phenological observations per year. Phenophase is denoted by the BBCH code: 10 (first leaves separated), 11 (leaf unfolding), and 60 (beginning of flowering). For calculation of the probability of potential spring frost damage, see Materials and methods. Corresponding graphs for the rest of the species are presented in Fig. S2.

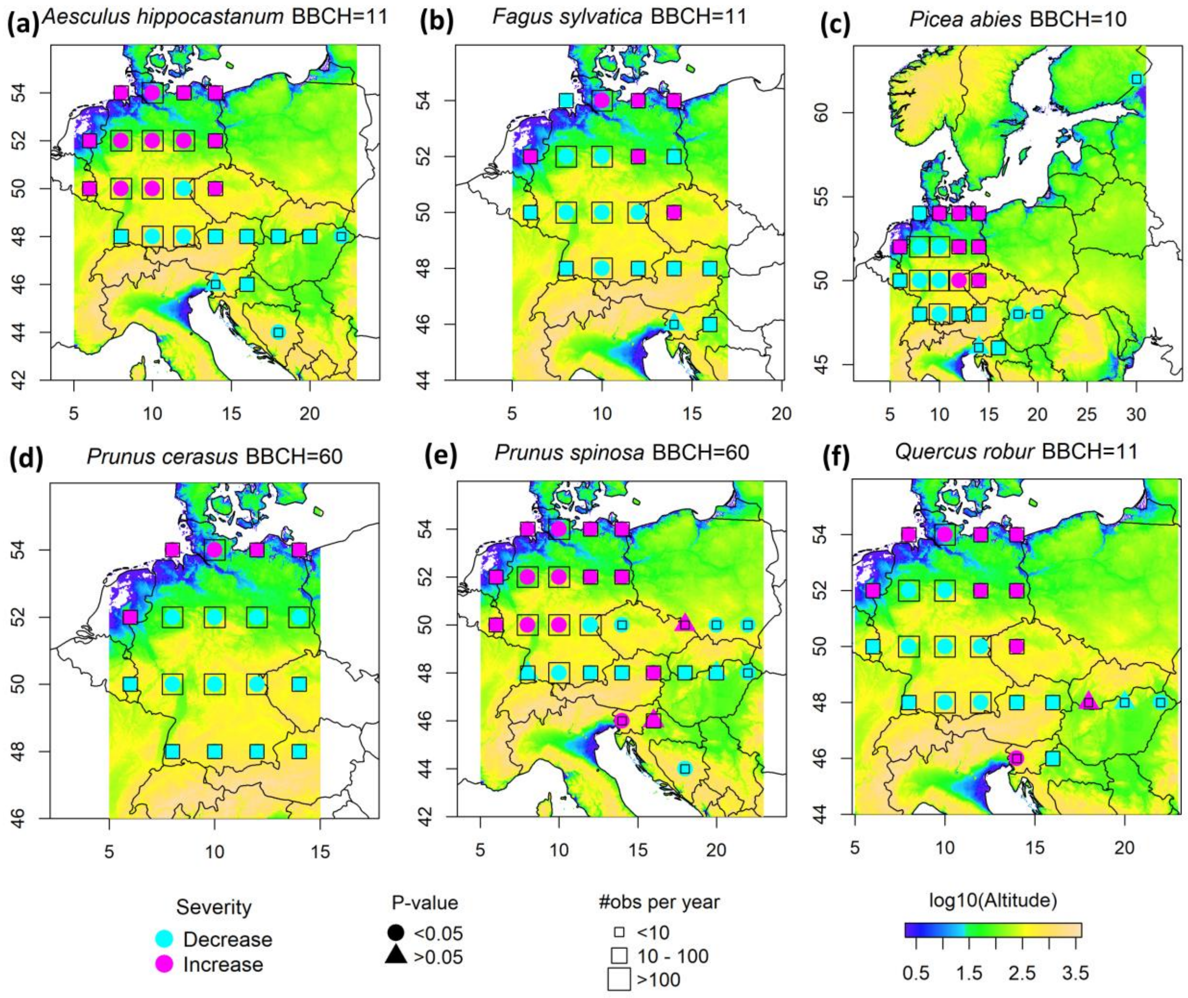
**Figure 4** Temporal changes in the severity of potential spring frost damage of 6 tree species caused by climatic warming during recent decades in various geographical locations in Europe. The notation #obs per year indicates the mean number of phenological observations per year. Phenophase used in the calculations is denoted by the BBCH code: 10 (first leaves separated), 11 (leaf unfolding), and 60 (beginning of flowering). For calculation of the severity of potential spring frost damage, see Materials and methods. Corresponding graphs for the rest of the species are presented in Fig. S3.

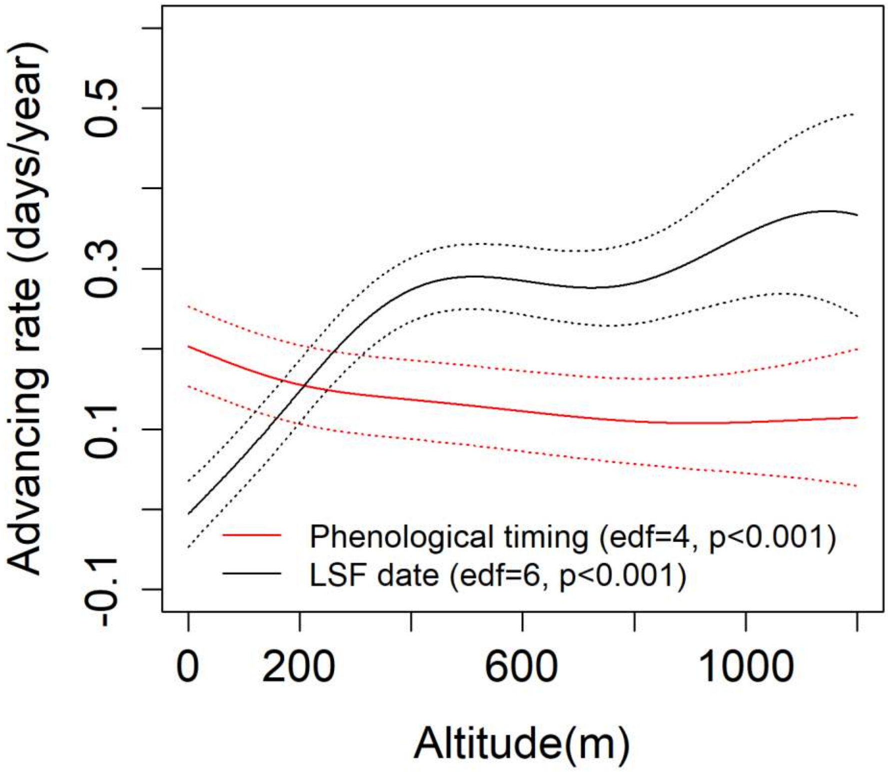
**Figure 5** Advancing rates of phenological timing of trees and the last spring frost date (LSF date) caused by climatic warming during recent decades at different altitudes in Europe. Dotted lines represent the 95% confidence intervals. LSF date is defined as the last calendar day prior to 15th July with the daily minimum temperature below -2.2°C.


(a)
LSF
Phenological timing
P-value
<0.05
>0.05
Advancing rate (days/year)
0.4
0.2
0.0
-0.2
1 3 5 7 9 11 13 15 17 19 21 23 25 27
Species ID
(b)
P-value
<0.05
>0.05
Probability
Severity
Changing rate (1/year, ° C/year )
0.08
0.04
0.00
-0.04
-0.08
1 3 5 7 9 11 13 15 17 19 21 23 25 27
Species ID


Probability
Decrease
Increase
P-value
<0.05
>0.05
Phenological timing advancing rate (days/year)
0.4
0.2
0.0
-0.2
-0.2
0.0
0.2
0.4
(a)
LSF advancing rate (days/year)
Severity
Decrease
Increase
P-value
<0.05
>0.05
Phenological timing advancing rate (days/year)
0.4
0.2
0.0
-0.2
-0.2
0.0
0.2
0.4
(b)
LSF advancing rate (days/year)


(a) Aesculus hippocastanum BBCH=11
(b) Fagus sylvatica BBCH=11
(c) Picea abies BBCH=10
(d) Prunus cerasus BBCH=60
(e) Prunus spinosa BBCH=60
(f) Quercus robur BBCH=11
42
44
46
48
50
52
54
55
60
45
5
10
15
20
25
30
Probability
Decrease
Increase
P-value
<0.05
>0.05
#obs per year
<10
10 - 100
>100
log10(Altitude)
0.5
1.5
2.5
3.5


(a) Aesculus hippocastanum BBCH=11
(b) Fagus sylvatica BBCH=11
(c) Picea abies BBCH=10
(d) Prunus cerasus BBCH=60
(e) Prunus spinosa BBCH=60
(f) Quercus robur BBCH=11
Severity
Decrease
Increase
P-value
<0.05
>0.05
#obs per year
<10
10 - 100
>100
log10(Altitude)
0.5
1.5
2.5
3.5


Advancing rate (days/year)
-0.1
0.1
0.3
0.5
0
200
600
1000
Altitude(m)
Phenological timing (edf=4, p<0.001)
LSF date (edf=6, p<0.001)