

## Research paper

## Increase in the risk of exposure of forest and fruit trees to spring frosts at higher elevations in Switzerland over the last four decades

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## ABSTRACT

Winters and early springs are predicted to become warmer in temperate climates under continued global warming, which in turn is expected to promote earlier plant development. By contrast, there is no consensus about the changes in the occurrence and severity of late spring frosts. If the frequency and severity of late spring frosts remain unchanged in the future or change less than spring phenology of plants does, vulnerable plant organs (dehardened buds, young leaves, flowers or young fruits) may be more exposed to frost damage. Here we analyzed long-term temperature data from the period 1975–2016 in 50 locations in Switzerland and used different phenological models calibrated with long-term series of the flowering and leaf-out timing of two fruit trees (apple and cherry) and two forest trees (Norway spruce and European beech) to test whether the risk of frost damage has increased during this period. Overall, despite the substantial increase in temperature during the study period, the risk of frost damage was not reduced because spring phenology has advanced at a faster rate than the date of the last spring frost. In contrast, we found that the risk of frost exposure and subsequent potential damage has increased for all four species at the vast majority of stations located at elevations higher than 800 m while remaining unchanged at lower elevations. The different trends between lower and higher elevations are due to the date of the last spring frost moving less at higher altitudes than at lower altitudes, combined with stronger phenological shifts at higher elevations. This latter trend likely results from a stronger warming during late compared to earlier spring and from the increasing role of other limiting factors at lower elevations (chilling and photoperiod). Our results suggest that frost risk needs to be considered carefully when promoting the introduction of new varieties of fruit trees or exotic forest tree species adapted to warmer and drier climates or when considering new plantations at higher elevations.

## 1. Introduction

In temperate climates, the greatest risk of frost injury to herbaceous and woody plant species occurs during the period of vegetation onset in spring, and this risk appears to be a strong driver of evolution (Inouye, 2000; Vitasse et al., 2014b). In early spring, prior to bud break, buds of forest species in temperate climatic zones are in a phase of ecdormancy and their resistance to frost decreases progressively as temperature rises (dehardening period) reaching a minimum as new leaves emerge (Lenz et al., 2013b; Sakai and Larcher, 1987; Vitasse et al., 2014b). The timing of vegetation onset is therefore decisive in minimizing the risk of frost injury (Lenz et al., 2016). This is why late spring frost events are climatic extremes with high ecological and evolutionary importance, likely controlling the latitudinal and elevational limits of

temperate trees (Kollas et al., 2014; Körner et al., 2016).

Destruction of foliage, flowers and unripe fruits due to late spring frost is a considerable loss for trees since it negatively affects nutrient storage, growth, reproduction, leaf development, and ultimately survival in subsequent years (Vanoni et al., 2016). In addition, late spring frosts may cause important economic losses, in particular when they affect the flower or fruit tissue in orchards and vineyards, which can dramatically reduce fruit production (Rodrigo, 2000). In forest trees, frost injury can affect the production of biomass (Dittmar et al., 2006), which is a loss for the timber industry, and may eventually weaken trees, resulting in them becoming more vulnerable to pathogens (Wargo, 1996). Temperate trees have thus adapted their spring phenology to begin their development in spring in connection to the mean-long term probability of late spring frost events (Lenz et al., 2016).

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Fig. 1. Frost damage observed on European beech on June 22, 2016 induced by a late spring frost event on April 28, 2016 in the Swiss Jura Mountains at 1100 m a.s.l. (© photo: left M.R., right Y.V. June 22, 2016).

Nevertheless, wild trees seldom experience serious frost injury to developing leaves and flowers within their natural distribution ranges (e.g. Fig. 1). In orchards, breeding objectives are prioritized to increase fruit production so that the current and future cultivated varieties may not be well synchronized with the long-term probability of late spring frosts. A challenging issue for fruit growers today is to assess whether promoting new varieties adapted to warmer and drier climates during summer time (generally having earlier spring phenology), could be more profitable in future decades. This would occur if the latest potentially damaging frost in spring would advance (i.e. occur earlier in the year) to a greater extent than the advance of spring phenology. Similarly, in forestry, the challenge is to determine which species or local provenances are most suitable to grow under future warmer conditions in future decades. In contrast to crop plants, which can be irrigated, forest trees must be able to cope with severe droughts, the frequency and intensity of which are expected to increase in future decades in Switzerland (Scherler et al., 2016). Thus, forest managers are currently turning towards the scientific community to get insights on which climatic extremes, with which frequency, will affect trees, and whether exotic species more able to withstand such climatic extremes should be considered for plantations (Lindner et al., 2010). In such discussions, the focus has often been placed on the ability of the future trees to withstand extreme drought whereas the relationship between spring phenology and potential frosts has largely been ignored.

Widespread frost damage to natural vegetation and crops has recently been reported. For instance the frost event that occurred in the eastern United States in early April 2007 caused extensive damage to crops and wild vegetation across large areas (Augsburger, 2009; Gu et al., 2008). Three years later, in spring 2010, another important frost event affected forests in the northeastern United States, with a strong negative impact on productivity (Hufkens et al., 2012). In Europe, significant frost damage to cultivated and forest trees was reported in 1995 in France (Ningre and Colin, 2007), in 2011, 2016 and 2017 in Switzerland (Fig. 1), and in south Germany and northeastern France (Kreyling et al., 2012a). In the majority of these examples, frost damage occurred after an unusually warm period that triggered precocious spring phenology. However, it is still unclear whether the risk of natural

and cultivated trees encountering frost damage has recently changed, because both spring phenology and minimum temperatures need to be analyzed simultaneously over a long period, which is limited by the amount of available data. Only a few studies have addressed whether plants have been at higher or lower risk from spring frosts in recent decades (Augsburger, 2013; Bennie et al., 2010; Hänninen, 1991; Rigby and Porporato, 2008; Scheifinger et al., 2003). While it is very likely that overall frost frequency has been reduced and will continue to decline in the future (IPCC, 2013), this does not necessarily mean that the risk of frost damage to natural and cultivated trees is decreasing. Temperate forest trees are most vulnerable to frost when the leaves are emerging from buds in spring (Vitasse et al., 2014b), and this period of vulnerability has advanced substantially in response to warmer temperatures. For instance, using ground observations of forest trees from over 3'800 locations in Western Europe, Fu et al. (2014) showed that the leaf-out date of temperate trees has advanced by about 13 days during the period 1982–2011.

The phenological shift of spring onset in response to climate change has considerable implications for crop management, especially in agriculture and forestry, human health (transport of allergens and disease vectors), as well as in numerous supporting and regulating ecosystem services such as nutrient cycle and carbon storage (Polgar and Primack, 2011; Richardson et al., 2013). In addition, foresters, farmers and fruit growers may adapt to warmer and drier climate during summer by using earlier new varieties, provenances or alternative species, potentially resulting in greater exposure to frost damage.

Since the mid-1980s, there has been an unresolved debate over whether the risk of frost damage on temperate plants will increase in future decades under continued climate change. For instance, Hänninen (1991) predicted an increased risk of frost damage under an expected warmer climate in Finland. Augsburger (2013) drew the same conclusion when focusing on 20 woody species in Illinois (USA), while no change or even a decreased risk was expected in the future decades in other studies in the Netherlands and Italy (Eccel et al., 2009b; Kramer, 1994a). Overall, late spring frosts were predicted to generally occur earlier but the stochasticity of such events is such that plants might be at higher risk of encountering frost damage, especially in more continental areas (Kreyling et al., 2012b). These contradictory predictions are likely due to the lack of sites where long time series of phenological observations have been recorded along with temperature. In addition, when both datasets are available, frost damage is too rare to investigate whether its frequency has changed in recent decades. A robust alternative is to quantify the safety margin against frost by comparing the timing of the last spring frost event with the observed or predicted date of flowering or leaf-out dates (Lenz et al., 2016; Lenz et al., 2013b) and testing whether this safety margin has changed over the last decades (Scheifinger et al., 2003). There are three alternative hypotheses associated with climate change and frost damage: (i) the risk of frost damage remains unchanged because both phenology and the frost-free period advance to the same extent (Fig. 2, hypothesis a); (ii), the risk of frost damage decreases because phenology advances less than the frost-free period.

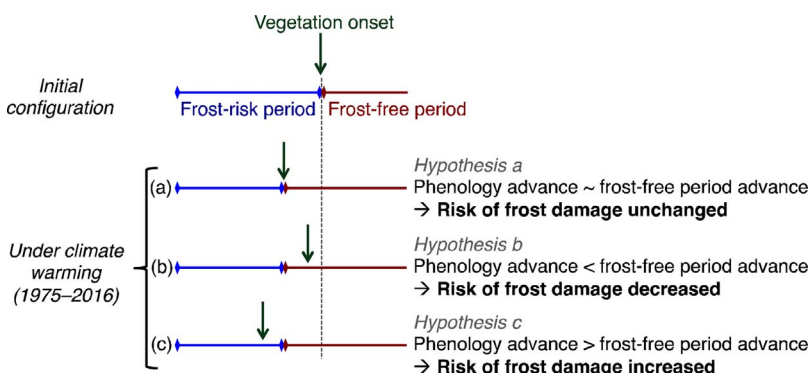


Fig. 2. Theoretical hypotheses on how the risk of spring frost damage to trees could change under climate warming.

Hypothesis a, the risk of frost damage remains unchanged because both phenology and the frost-free period advance to the same extent.

Hypothesis b, the risk of frost damage decreases because phenology advances less than the frost-free period.

Hypothesis c, the risk of frost damage increases because phenology advances more than the frost-free period.

free period (Fig. 2, hypothesis b); (iii) the risk of frost damage increases because phenology advances more than the frost-free period (Fig. 2, hypothesis c). We tested these hypotheses over the period 1975–2016 at sites throughout Switzerland at various elevations between 203 m asl. and 2283 m asl., focusing on the two dominant forest tree species in Switzerland, European beech (*Fagus sylvatica* L.) and Norway spruce (*Picea abies* (L.) Karst.), and on two widely cultivated fruit trees, cherry (*Prunus avium* L. or *Prunus cerasus* L.) and apple tree (*Malus domestica* Borkh.), for which long-term series of phenological observations are available.

## 2. Data and methods

### 2.1. Study sites and phenological data

We selected all weather stations managed by MeteoSwiss situated below the treeline (i.e. ~2400 m in Switzerland, Gehrig-Fasel et al., 2007) with daily minimum and maximum temperatures recorded since 1975. This selection resulted into 50 stations covering elevations between 203 m and 2283 m and located in all climatic regions of Switzerland, i.e. the Alps (Northern, Western central, Eastern central, and Southern Alps), Jura Mountains and Swiss Plateau (Fig. 3).

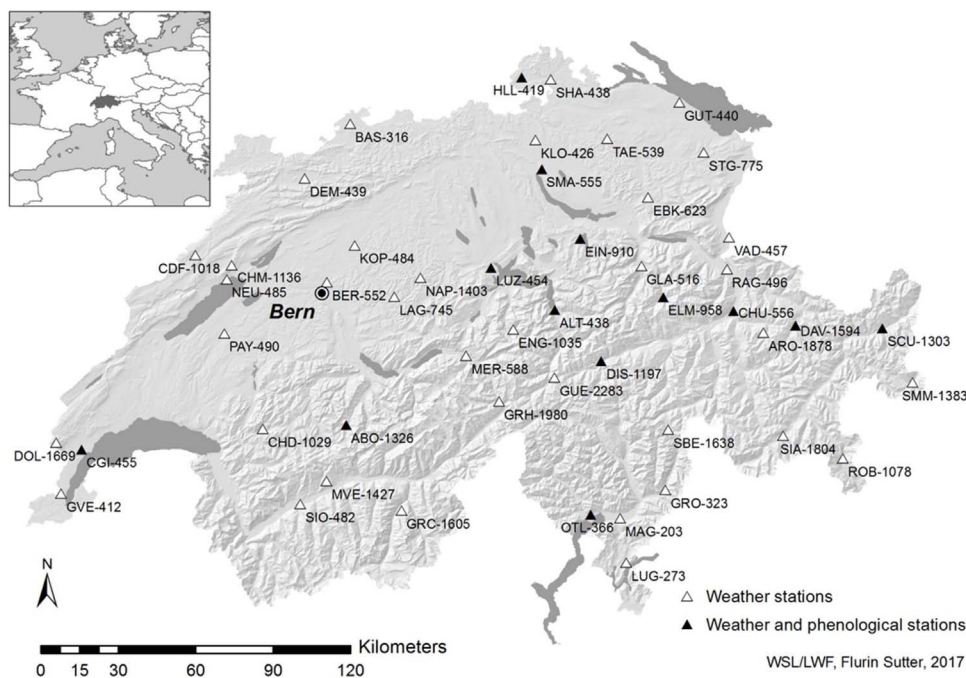
Although some of the 50 sites were above the current distribution of the selected species, in particular for fruit trees, it is interesting to test whether these species would be more exposed to frost when planted beyond their current upper elevation limit.

In 8 of the 50 selected sites, long-term series of flowering observations containing at least 35 years of data during the period 1975–2016 were available for two representative orchard fruit trees in Switzerland: cherry tree and apple tree. Similarly, long-term series of leaf-out observations containing at least 35 years of observations were available in 8–11 of the selected sites for two representative and dominant forest tree species in Switzerland: Norway spruce and European beech (see Appendix A in Supplementary material). Phenological observations were conducted weekly on single or several individuals by 1–8 observers per site applying a protocol for phenological monitoring made available by MeteoSwiss. For fruit trees, we selected the date when full flowering was recorded, corresponding to 50% of flowers open with some petals possibly fallen. For forest trees, we selected the date of leaf-out for beech and needle elongation for spruce, corresponding to more

than half of the canopy of a given individual reaching this stage. For apple trees, phenological monitoring was conducted on the cultivar ‘Belle de Boskoop’ at most of the sites, except at one site (CGI) where mostly the cultivar ‘Golden delicious’ was recorded during the study period. The cultivar was unknown at two sites (ABO and ALT). For cherry trees, phenology was monitored on wild ecotypes at two study sites (CHU, ELM), on three different varieties at one site (CGI) depending on years (‘Burlat’, ‘Hedelfingen’, ‘Durone nero 1’), on the variety ‘Alfa’ at one site (LUZ), on sour cherry (*Prunus cerasus* L.) at one site (ABO), and on unknown variety in three sites (DIS, SMA and HLL). Only minor differences in the timing of full flowering among the different selected varieties and sour cherry have been observed in Switzerland (Dubuis et al., 2011). For clarity and brevity, we refer to each of the selected species by its genus in the following account.

### 2.2. Phenology modeling

Phenological data were checked for outliers prior to conducting the analyses. Within a station, observations corresponding to more than 2.5 times the median absolute deviation (moderately conservative threshold) across the study period were removed, as recommended by Leys et al. (2013). We calibrated six different phenological models on the sites where both phenological observations and temperature records were available in order to simulate flowering (*Prunus* and *Malus*) and leaf-out dates (*Fagus* and *Picea*) in all the 50 study sites. We first used a classical growing degree day model with an arbitrary date to accumulate daily mean temperature, fixed as January 1st and a temperature base threshold of 5 °C, as typically applied in numerous studies. The average GDD values reached at the time of flowering/leaf-out were 147 degree days for *Prunus*, 219 degree days for *Malus*, 185 degree days for *Fagus* and 236 degree days for *Picea*. Because a significant trend was found between the GDD reached at the time of flowering/leaf-out and elevation of the station for all the four species, we used the slope of the corresponding linear relationships to adjust the required GDD according to elevation ( $-5.65$  degree days  $100\text{ m}^{-1}$  for *Prunus*  $-5.02$  degree days  $100\text{ m}^{-1}$  for *Malus*,  $-10.33$  degree days  $100\text{ m}^{-1}$  for *Fagus* and  $-12.31$  degree days  $100\text{ m}^{-1}$  for *Picea*). These different GDD thresholds (adjusted for elevation) were then applied to simulate flowering and leaf-out dates at all selected weather stations for each species. This simple model is referred to hereafter as GDD<sub>fixed</sub>. We then



**Fig. 3.** Locations, names and elevations of the 50 MeteoSwiss weather stations and phenological stations used in the analyses. Open symbols represent weather stations without phenology observations. Filled symbols represent weather stations where long-term of phenological observations were available for at least one of the four study species (see also Appendix A in Supplementary material).



used the software PMP (Phenological Modeling Platform, Chuine et al., 2013) to calibrate five different models available in the literature to our phenological dataset: two 1-phase models (accounting only for the forcing temperature accumulation during the ecodormancy phase) and three 2-phase models (accounting for both chilling temperatures during the endodormancy and forcing temperatures during the ecodormancy). The 1-phase models were (i) a classical growing degree days model, also called a thermal time model or spring warming model (Cannell and Smith, 1983), with three fitted parameters, referred to hereafter as  $GDD_{fit}$  and (ii) the Sigmoid model with four fitted parameters (Chuine and Cour, 1999). The 2-phase models were (i) the UniChill model with 7 fitted parameters (Chuine, 2000; Chuine et al., 2013), (ii) the parallel model with 11 fitted parameters (Kramer, 1994b; Landsberg, 1974) and (iii) the Utah model with 8 fitted parameters (Richardson, 1974). For this latter model we used the smooth Utah function (Bonhomme et al., 2010) implemented in the PMP software for modeling the endodormancy phase and a classical GDD function for modeling the ecodormancy phase, both phases acting sequentially. Detailed equations for the functions used in the different models are presented in Appendix B in Supplementary material. Model parameters were derived using a simulated annealing algorithm (Chuine and Cour, 1999; Chuine et al., 1998) implemented in the PMP software. To assess the robustness of the models, a 2-fold cross-validation was performed for each model and species, fitting the parameters on even years (training set) and validating them on the odd years (validation set). We compared the model accuracies using three criteria, with the first being the Nash–Sutcliffe Efficiency index (NSE, Nash and Sutcliffe, 1970). A negative NSE value indicates that the model performs worse than the null model (mean dates of leaf-out/flowering), whereas a positive NSE value indicates that the model explains more variance than the null model, with a maximum value of 1 indicating a perfect match between the model and observations. The second criterion was the root means squared error, which gives the mean error of the prediction in days and third was the corrected Akaike Information Criterion (AICc, Burham and Anderson, 2002) which rates models in terms of parsimony and efficiency, where the lowest value is associated with the best model. We selected the model with the lowest AICc value when calibrating on the whole dataset, ensuring that predictions were not altered in the two cross-validations based on RMSE and NSE values. For *Malus*, models were calibrated on sites sharing the same cultivar and very similar results were found concerning model parameters when comparing with the model calibration conducted on all observations, including the different cultivars.

### 2.3. Safety margin against frost and minimum temperatures around flowering/leaf-out time

The time lag between the predicted dates of flowering or leaf-out and the latest spring frost  $< 0^\circ\text{C}$  was calculated for each year, station and species during the study period 1975–2016. This time lag is referred to hereafter as the safety margin against frost, as denominated by Lenz et al. (2013b). Linear regressions were used to determine whether the safety margin has changed over the last four decades for each site and species. Although young leaves of temperate trees have been shown to resist to temperatures below between  $-8^\circ\text{C}$  to  $-3^\circ\text{C}$  in the laboratory (Lenz et al., 2013b; Vitasse et al., 2014a), temperatures below  $0^\circ\text{C}$  as recorded in a standard weather station can potentially damage emerging leaves, flowers and young fruits. During clear and windless nights, radiative cooling may lead to temperatures in plant tissues several degrees lower (from 4 to  $8^\circ\text{C}$  lower) than those measured at 2 m height under the sheltered conditions of a Stevenson screen (Ducrey, 1998). It is therefore common, under clear night conditions, to observe frost damage to wild and cultivated trees in spring when the measured dry air temperature is close to  $0^\circ\text{C}$  (Ducrey, 1998; Osaer et al., 1998; Perraudin and Fellay, 1975), especially for trees at the forest edge. This is also why in orchards, water aspersion of tree canopies to protect

flowers and juvenile fruits against frost is typically applied as soon as temperatures reach  $0^\circ\text{C}$  (Perraudin and Fellay, 1975; Quénot, 1998). Note that we obtained similar results using  $-3^\circ\text{C}$  as a threshold for frost in our analyses for the safety margin trends in recent decades or when using the other non-selected models for predicting phenology. As substantial differences were found between stations below and above  $\sim 800\text{ m}$  (Appendix C in Supplementary material), in the following all results are split into two elevation classes: stations located below  $800\text{ m}$  ( $n = 29$ ) and stations located above  $800\text{ m}$  ( $n = 21$ ).

We also examined the lowest minimum temperature occurring from two weeks before to 4 weeks after the predicted flowering and leaf-out time, as we assumed dehardened buds, emerging leaves, flowers and developing fruits to be most vulnerable to frost during this time window (Rodrigo, 2000; Vitasse et al., 2014b).

All data analyses were performed using Rstudio version 0.99.489 (R Core Team, 2015).

## 3. Results

### 3.1. Trends in minimum and maximum temperature and latest spring frost

Spring maximum temperatures increased almost twice faster than minimum temperatures during the period 1975–2016, by  $0.63^\circ\text{C}.\text{decade}^{-1}$  and  $0.37^\circ\text{C}.\text{decade}^{-1}$  on average across sites, respectively (Fig. 4a & b). Warming trends in maximum (Fig. 4a) and minimum (Fig. 4b) temperatures were slightly enhanced at higher

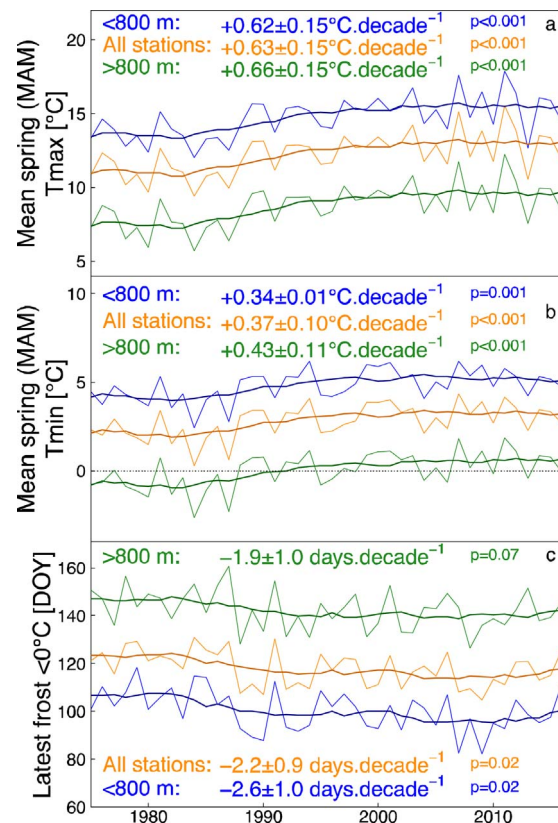


Fig. 4. Trends in spring temperatures and in the occurrences of the latest spring frost across the 50 meteorological stations during the period 1975–2016.

a. spring (MAM) daily maximum temperatures across all stations and across stations below or above  $800\text{ m}$  a.s.l.  
b. spring (MAM) daily minimum temperatures across all stations and across stations below or above  $800\text{ m}$  a.s.l.  
c. Time of occurrence of the latest spring frost across all stations and across stations below or above  $800\text{ m}$  a.s.l.  
11-year moving averages were applied and slopes of the linear regressions were reported on the graphs.

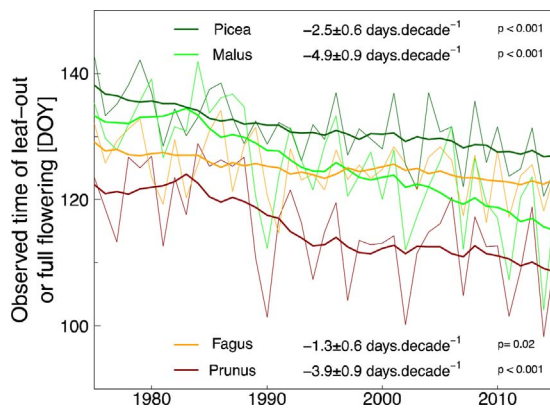


Fig. 5. Mean date of full flowering for *Malus* and *Prunus* and of leaf-out for *Fagus* and *Picea* during the period 1975–2016, averaged from 8 to 11 sites, depending on species, with more than 35 years of observations. 11-year moving averages were applied and slopes of the linear regressions were reported.

elevations. Across all stations, the latest spring frost event below 0 °C has significantly advanced by 2.2 days.decade<sup>-1</sup> on average across stations, yet with a high variability (Fig. 4c). The advance was not significant at stations located above 800 m (−1.9 days.decade<sup>-1</sup> p = 0.07, Fig. 4c), whereas trends were significant on average for lower elevations (−2.6 days.decade<sup>-1</sup> p = 0.02, Fig. 4c).

### 3.2. Trends in spring flowering and leaf-out timing between 1975 and 2016

Long-term series of phenological observations available across 8 sites for *Prunus* and *Malus* showed a significant advance in flowering by  $-3.9 \pm 0.1$  and  $-4.9 \pm 0.1$  days.decade<sup>-1</sup>, respectively (Fig. 5). Full flowering occurred on average 10 days later in *Malus* compared to *Prunus*, although this difference has declined in recent years (Fig. 5). In contrast, trends in the leaf-out dates of forest tree species across the 8–11 sites were less pronounced but still significant, on average  $-1.3 \pm 0.1$  and  $-2.5 \pm 0.1$  days.decade<sup>-1</sup> for *Fagus* and *Picea*, respectively (Fig. 5). A breakpoint was detected around 1987–1989 for all species, particularly visible for fruit tree species (Fig. 5). Interestingly, the phenological ranking among the four study species has changed over time because of their different sensitivity to climate: spring phenology of *Fagus* occurred in second position after *Prunus* flowering and before *Malus* flowering from 1975 to ~1995, whereas it occurred in third position, substantially after *Malus* flowering during the following period.

### 3.3. Performance of the phenological models

Fitted across the whole data set, the different models provided high NSE values for all species, from 0.70 to 0.79, with root mean square errors (RMSE) from 6.53 to 7.83 days and negligible bias, except for GDD<sub>fixed</sub> which gives NSE < 0.5 and RMSE > 10 when calibrating on the *Fagus* and *Picea* datasets (Table 1). Overall, the 2-phase models that account for the duration of chilling to release endodormancy and for modulating heat requirement, performed as well as the 1-phase models accounting for the ecodormancy phase only (Table 1). Regarding the AICc values, the Sigmoid model outperformed the other models for *Prunus*, *Malus* and *Picea*, whereas the parallel model performed better for *Fagus* (Table 1). We therefore used these two models in all further analyses. Overall, the performance of the models was not altered between the validation and the training set, showing that the models were robust and that the number of data points was sufficient to avoid over-parameterization issues (Table 1).

### 3.4. Trends in the safety margin against frost

Overall the safety margin against the latest frost, defined as the difference between the latest frost event and predicted date of flowering (fruit trees) or leaf-out (forest trees), has remained unchanged at lower elevation sites (Fig. 6a), whereas it has significantly declined at sites above 800 m asl. from  $-1.7 \pm 0.9$  days.decade<sup>-1</sup> to  $-2.4 \pm 0.9$  days.decade<sup>-1</sup> for *Picea* and *Malus*, respectively (Fig. 6b). In other words, the risk that young leaves or flowers encounter freezing temperatures has remained unchanged at lower elevations but has increased at higher elevations over the last decade in connection with earlier phenology.

In detail, using the best model to predict phenology, the safety margin declined at less than 40% of the lower elevation sites, irrespective of species, and none of these trends were significant, whereas the safety margin increased significantly at 7% of the sites (Table 2). In contrast, it declined at ~90% of the higher elevation sites, significantly so (P < 0.05) at about 15% of sites (Table 2 & Appendix C in Supplementary material).

### 3.5. Trends in the lowest minimum temperature occurring after flowering/leaf-out

The lowest minimum temperature occurring from two weeks before to a month after the predicted date of flowering or leaf-out has remained unchanged for all four species, irrespective of elevation (Fig. 7), although trends tend to be positive at lower elevation sites (Fig. 7a) and negative at higher elevation sites (Fig. 7b).

## 4. Discussion

The occurrences of freezing temperatures in spring in a mid-latitude region such as Switzerland are highly unpredictable and the spring phenology of temperate zone vegetation must be well-adapted to escape frost damage over long time-scales by having a large safety margin against frost (Lenz et al., 2013a; Lenz et al., 2016). Since the mid-1970s, climate warming in Switzerland has been particularly pronounced in spring and summer compared to the other seasons (Matiu et al., 2016; Rebetez and Reinhard, 2008). With data up to 2016 and 50 stations, our results confirm that the warming trend was still very pronounced in spring over the last 4 decades, especially for maximum temperatures (0.63 °C.decade<sup>-1</sup>), which have increased almost twice as much as minimum temperatures (0.37 °C.decade<sup>-1</sup>). We hypothesized that this temperature increase and the differences between the increases in minimum and maximum temperatures may have disrupted the synchrony between spring tree phenology and long-term probability of injury by late spring frost. Consistently, our results show that the risk that vulnerable tissues (emerging leaves, flowers and young fruits) will encounter late spring frosts has increased significantly over the last four decades at higher elevations, while it has remained unchanged at lower elevations.

### 4.1. Advance of spring frost versus spring phenology

Our results show that the sequence of phenological events among species may change over time. On average across sites, leaf-out of *Fagus* occurred earlier than the flowering of *Malus* in the 1970s and 1980s, whereas the reverse was detected for the 2000s and 2010s. The change in the spring phenology order among co-existing species is not unusual due to species-specific climatic requirements to break dormancy but is more expected under warmer climate when chilling may become limiting. A similar result has been observed in Morocco between almond and olive trees (El Yaacoubi et al., 2014) and has been predicted to occur for an array of forest tree species in UK (Roberts et al., 2015). In the same way, the flowering time of apple trees var. *Golden Delicious* has remained unchanged in recent decades in southern France where

**Table 1**

Performance of the phenological models fitted on the whole data set along with the 2 fold cross-validation (even vs. odd years).

<i>Malus</i>										
Whole data set (n = 295)					Training set (n = 146)			Validation set (n = 149)		
Models	RMSE	NSE	Bias	AICc	RMSE	NSE	Bias	RMSE	NSE	Bias
GDD <sub>fixed</sub>	7.72	0.70	1.43	1208	7.96	0.70	1.73	7.19	0.73	−0.13
GDD <sub>fitted</sub>	7.19	0.74	0.03	1171	7.47	0.74	−0.16	7.46	0.69	−1.33
<b>Sigmoid</b>	<b>7.09</b>	<b>0.75</b>	<b>0.03</b>	<b>1163</b>	<b>7.31</b>	<b>0.75</b>	<b>−0.52</b>	<b>7.05</b>	<b>0.72</b>	<b>−1.20</b>
UniChill	7.11	0.75	0.43	1376	6.63	0.79	0.86	6.71	0.77	0.78
Parallel	7.19	0.74	0.11	1391	7.35	0.74	0.13	7.17	0.72	−0.47
Utah	7.08	0.75	0.28	1170	7.24	0.75	−0.09	6.90	0.75	−0.68

<i>Prunus</i>										
Whole data set (n = 307)					Training set (n = 148)			Validation set (n = 159)		
Models	RMSE	NSE	Bias	AICc	RMSE	NSE	Bias	RMSE	NSE	Bias
GDD <sub>fixed</sub>	7.83	0.70	1.21	1266	7.86	0.71	1.36	7.71	0.70	−0.22
GDD <sub>fitted</sub>	7.05	0.76	0.45	1205	7.24	0.75	−0.03	6.93	0.75	−0.08
<b>Sigmoid</b>	<b>6.53</b>	<b>0.79</b>	<b>0.13</b>	<b>1160</b>	<b>6.62</b>	<b>0.79</b>	<b>−0.38</b>	<b>6.54</b>	<b>0.78</b>	<b>−0.68</b>
UniChill	6.56	0.79	0.84	1382	6.58	0.79	0.85	6.50	0.78	0.73
Parallel	6.89	0.77	−0.11	1421	6.90	0.77	−0.35	6.82	0.76	−0.50
Utah	6.65	0.78	0.61	1181	6.69	0.79	0.07	6.67	0.77	0.03

<i>Fagus</i>										
Whole data set (n = 416)					Training set (n = 213)			Validation set (n = 203)		
Models	RMSE	NSE	Bias	AICc	RMSE	NSE	Bias	RMSE	NSE	Bias
GDD <sub>fixed</sub>	12.34	0.39	1.78	2093	12.75	0.32	1.06	12.12	0.44	0.38
GDD <sub>fitted</sub>	8.68	0.70	0.13	1804	8.27	0.71	0.06	9.12	0.68	0.67
Sigmoid	8.57	0.71	0.18	1792	8.12	0.72	0.23	9.06	0.69	0.93
UniChill	8.59	0.70	0.86	1795	8.20	0.72	1.18	9.26	0.67	1.93
<b>Parallel</b>	<b>8.48</b>	<b>0.71</b>	<b>0.11</b>	<b>1789</b>	<b>7.90</b>	<b>0.74</b>	<b>0.06</b>	<b>9.02</b>	<b>0.69</b>	<b>1.03</b>
Utah	8.55	0.71	0.64	1796	8.05	0.73	0.66	9.04	0.69	1.22

<i>Picea</i>										
Whole data set (n = 302)					Training set (n = 152)			Validation set (n = 153)		
Models	RMSE	NSE	Bias	AICc	RMSE	NSE	Bias	RMSE	NSE	Bias
GDD <sub>fixed</sub>	10.41	0.47	1.53	1417	10.61	0.44	0.58	10.05	0.51	1.60
GDD <sub>fitted</sub>	7.80	0.70	−0.07	1246	7.56	0.72	−0.12	8.05	0.69	0.89
<b>Sigmoid</b>	<b>7.47</b>	<b>0.73</b>	<b>−0.01</b>	<b>1223</b>	<b>7.30</b>	<b>0.73</b>	<b>−0.01</b>	<b>7.72</b>	<b>0.71</b>	<b>0.62</b>
UniChill	7.50	0.73	0.64	1229	7.25	0.74	1.15	7.92	0.70	1.70
Parallel	7.44	0.73	0.10	1233	7.09	0.75	−0.41	7.87	0.70	0.49
Utah	7.45	0.73	0.24	1227	7.20	0.74	0.34	7.85	0.70	0.98

RMSE, root mean square error; NSE, Nash–Sutcliffe Efficiency index; Bias, mean difference between the observed and the predicted dates. Values of the selected model for the analysis were highlighted in bold.

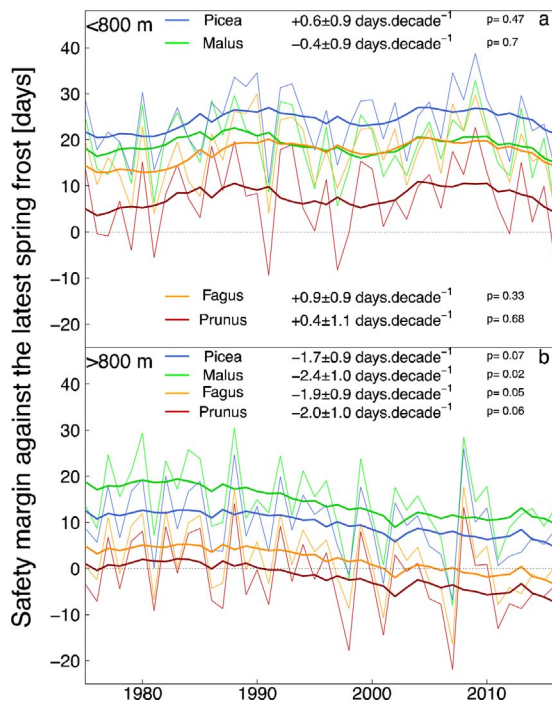
chilling and photoperiod may have been limiting factors, whereas it advanced substantially in northern France, Switzerland and Germany (Legave et al., 2015).

Spring vegetation phenology was recently reported to respond more to temperatures during daytime than nocturnal temperatures (Fu et al., 2016; Peng et al., 2013). Our study highlights that maximum temperatures have increased almost twice faster than minimum temperatures, which is in line with a greater advance of spring phenology over frost events. This result contrasts with an earlier study conducted at 50 sites spread over Germany, Austria and Switzerland (Scheffinger et al., 2003), which reported a greater increase in minimum compared to maximum temperatures and a greater advance of latest frosts ( $-2.0$  days.decade<sup>−1</sup> over the period 1951–1997) compared to the advance of spring phenology of temperate forest trees and shrubs ( $-2$  to  $0$  days.decade<sup>−1</sup> depending on species). This contrast with our results is probably due to the earlier time period considered during which minimum temperatures were generally observed to increase more than maximum temperatures in the Northern hemisphere (Hansen et al., 1995; Karl et al., 1993), including Switzerland (Rebetez, 2001). This reduction in diurnal temperature range (DTR) was due in part to the

increase in air pollution and aerosols during the 20th century, through their impact on solar radiation (Wild et al., 2005), contributing to warmer nights and fewer warming days, especially at lower elevations. It was also due in part to a series of high North Atlantic Oscillation (NAO) index values (Hurrell and Deser, 2009; Hurrell and Van Loon, 1997) at the end of the 20th century impacting parts of Europe, including Switzerland (Rebetez, 2001). Our study covered the period 1975–2016, which did not exhibit this reduction in DTR. It shows a more constant and homogenous warming compared to previous decades, making it an ideal study period to test whether the risk of frost injury has been increasing during a continuous warming trend. In line with our results, Matiu et al. (2016) also observed that maximum temperatures had increased more than minimum temperatures during the period 1973–2012 in the UK, Switzerland and Germany, especially in spring where the mean trend in minimum temperatures was approximately half the trend of maximum temperatures, as roughly found here.

Using a modified version of the Utah model, Eccel et al. (2009b) reported a reduction in the risk of frost damage to apple trees in northern Italy 1966–2005 and predicted a further decrease or





**Fig. 6.** Trends in the safety margin against the latest frost ( $< 0^{\circ}\text{C}$ ) for the four study species using the best model to predict spring phenology (model Sigmoid for *Prunus*, *Malus* and *Picea* and model Parallel for *Fagus*) across all 50 sites during the period 1975–2016 at lower (a) and higher (b) elevations. The safety margin was calculated as the difference between the latest frost  $< 0^{\circ}\text{C}$  and the predicted date of flowering (*Malus* and *Prunus*) or leaf-out (*Fagus* and *Picea*). Note that a reduction of the safety margin against frost means an increasing risk to frost exposure. 11-year moving averages were applied and slopes of the linear regressions were reported.

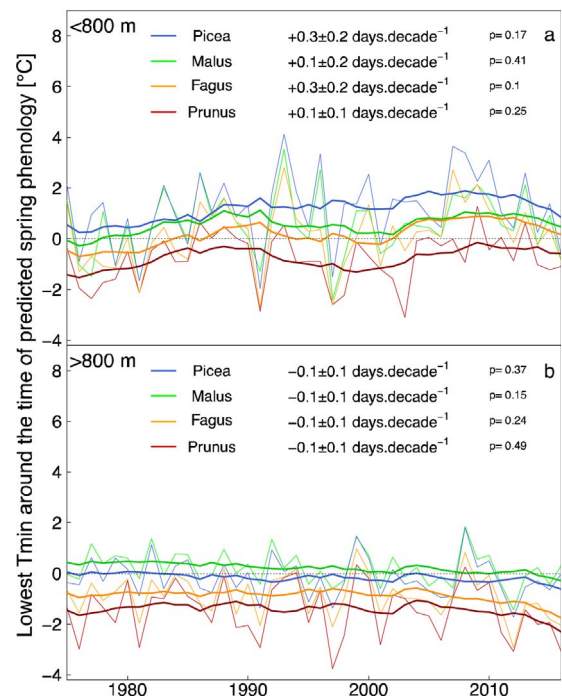
**Table 2**

Number of lower and higher elevation stations (below or above 800 m asl.) for which the safety margin against frost has decreased (negative trends) or increased (positive trends) for each study species.

	Stations < 800 m (n = 29)		Stations > 800 m (n = 21)	
	Negative	Positive	Negative	Positive
<i>Prunus</i>	10 (0)	19 (1)	17 (3)	4 (0)
<i>Malus</i>	16 (0)	13 (0)	20 (4)	1 (0)
<i>Fagus</i>	8 (0)	21 (5)	19 (3)	2 (0)
<i>Picea</i>	9 (0)	20 (3)	19 (3)	2 (0)

The number of stations presenting significant trends at  $P < 0.05$  is reported in brackets. The safety margin has been calculated as the day of the predicted flowering dates (using the best phenological model) subtracted by the day of the latest frost  $< 0^{\circ}\text{C}$ . The best model used for *Prunus*, *Malus* and *Picea* was the Sigmoid model, whereas for *Fagus* it was the Parallel model.

unchanged risk for the coming decades. It is likely that the increase in temperatures may result in different patterns for spring frost, depending on the specific climatic conditions of the area. As a result, it may be necessary to study this phenomenon at regional scales rather than at larger scales. For instance, phenology is expected to advance more in colder areas than in warmer areas, where chilling and photoperiod may become limiting and therefore may reduce the sensitivity of vegetation spring phenology to temperature increases (Fu et al., 2015). The region studied by Eccel et al. (2009a) covers a warmer region in northern Italy, on the southern side of the Alps; our results show that the warmer the temperature, the less significant the increase in late spring frost risk (Appendix C in Supplementary material).



**Fig. 7.** Trends in the intensity of frost around the time of the predicted flowering or leaf-out dates in all 50 stations during the period 1975–2016 at lower (a) and higher (b) elevations. Lowest minimum temperatures from 14 days before to 1 month after the predicted spring phenology were reported using the best phenological model. 11-year moving averages were applied and slopes of the linear regressions were reported.

#### 4.2. Different trends between low and high elevations

Our study suggests that the strong shift in spring phenology observed in recent years has led to a decline in the safety margin against frost exposure at higher elevations, whereas it has remained more or less unchanged at lower elevations. We suggest that the differences in trends at lower and higher elevations can be attributed to two main causes. Firstly, the last spring frost events, although on average occurring earlier in the year, have not advanced significantly at stations located above 800 m. Secondly, during the study period, a stronger phenological shift has occurred at higher elevations (predicted mean across species and all 50 stations:  $-3.9 \text{ days/decade}^{-1}$ , data not shown) compared to lower elevations ( $-2.2 \text{ days/decade}^{-1}$ , data not shown), consistent with long-term observations in the same area (Güsewell, 2014). This stronger shift at higher elevations in turn may be connected to the greater temperature increase during late spring compared to early spring during the study period (mean temperature increase February–March:  $0.15^{\circ}\text{C/decade}^{-1}$ , April–May:  $0.62^{\circ}\text{C/decade}^{-1}$ , Appendix D in Supplementary material) and/or to fewer limiting factors such as insufficient chilling requirements or too short a photoperiod (Fu et al., 2015; Vitasse and Basler, 2013).

#### 4.3. Modeling spring phenology

Growing degree days (GDD) is a widely-used metric to predict spring phenology in agricultural and forest lands. Although the GDD requirement for triggering vegetation onset is expected to increase progressively with climate change due to a progressive lack of chilling (Fu et al., 2015), it has been shown to be an excellent proxy for spring phenology in the past decades for crops (eg. Miller et al., 2001; Sacks and Kucharik, 2011; Wang and Engel, 1998), forest trees (Vitasse et al., 2011), fruit trees such as apple trees (Rivero et al., 2016) and vineyards (Jones et al., 2010). Our results confirm that the timing of flowering or leaf-out of fruit and forest trees can be predicted well using an accumulation of heat in spring, either with a linear function (GDD) or a

sigmoid function (Sigmoid model). However, the arbitrary use of 1st January and a temperature threshold of 5 °C for GDD accumulation seems inappropriate in comparison to fitting these parameters, especially for the two forest tree species ( $GDD_{\text{fitted}}$  performed way better than  $GDD_{\text{fixed}}$ ). The one-phase models tested here performed as well as the two-phase models, suggesting no major chilling limitation in recent years in Switzerland, except for *Fagus*, for which the parallel model performed better. This is consistent with *Fagus* having a significant chilling requirement, which may not be entirely fulfilled during the warmest winters at lower elevations (Vitasse and Basler, 2013). Albuquerque et al. (2008) reported that chilling requirements seem to be currently satisfied for seven cherry cultivars in south-east Spain above 650 m asl. In Switzerland, chilling temperatures are obviously more frequent than in south-east Spain, especially as we used a large range of elevations. However 1-phase models should only be used to predict future phenological changes with caution as chilling requirements may be progressively unfulfilled under continued climate warming in temperate latitudes, the endodormancy break may be delayed and there may be increasing heat requirements for bud break in temperate wild (Chuine et al., 2016) and crop tree species (Darbyshire et al., 2017; Legave et al., 2008; Shi et al., 2017). For instance, using different models for the flowering time of apple trees in France, Legave et al. (2008) showed that the period of chilling accumulation has been extended (later dormancy release) and the period of GDD accumulation compressed over the period 1976–2002.

As spring phenology is advancing in response to spring warming, the photoperiod at the time of flowering or budburst is becoming shorter, which may progressively reduce bud sensitivity to warming (Basler and Körner, 2014; Blümel and Chmielewski, 2012; Fu et al., 2015). Although the risk of frost injury has increased at higher elevations due to the strong shift in phenology, a progressive decline in the phenological shift in response to temperature is expected at lower elevations, due either to chilling or photoperiod limitations (Fu et al., 2015). This may increase the safety margin against frost injury at lower elevations and enhance the discrepancy between lower and higher elevations. Plant species having low chilling requirements to break dormancy will be at greater risk. While simple 1-phase models seem appropriate to test whether the risk of frost injury has increased in the past, more sophisticated phenological models that involve chilling and photoperiod interactions could be useful in assessing future risks of frost injury and damage under different climatic scenarios.

#### 4.4. Implications of spring frost risk for fruit and forest trees under climate warming

Some varieties of perennial crops such as orchard trees or vineyards are becoming poorly adapted to their local environment, which is expected to get warmer, and most importantly, drier during summer. However, the changing climatic conditions are also creating suitable conditions for new crop varieties adapted to warmer and drier environments. Similarly, forest trees are vulnerable to extreme climatic events such as severe summer drought and frost (Vanoni et al., 2016); such events are expected to increase substantially in the coming decades in Switzerland (Scherler et al., 2016). Consequently, forest managers are being encouraged to plant new tree species or provenances from drier and warmer environments (Lindner et al., 2010). However, the promotion of new varieties from warmer climates should take into account their chilling requirements to break dormancy and their heat requirement to budburst or flowering in spring, as a warmer climate could lead to higher vulnerability against frost exposure. Similarly, despite the general upward vegetation shift in mountainous regions (Lenoir et al., 2008), our results suggest that planting current species at higher altitudes will entail a greater risk of frost injury.

#### 4.5. Limitations of the study

While our study provides robust data to assess whether the safety margin against late spring frost has changed in recent decades, it also includes some limitations. Firstly, we examined the risk of frost damage at full flowering rather than earlier, such as during bud swelling. With winters expected to become progressively milder, and an increasing risk of exceptionally warm spells, there could be a rise in the incidence of premature dehardening associated with warmer spells, and thus an increased risk of subsequent freezing injury to buds in late winter and early spring (Hänninen, 2016; Pagter and Arora, 2013; Vitasse et al., 2014b; Vitra et al., 2017). The duration of flowering, which was not available in our dataset, would also help to determine whether the risk of frost damage was more important for flowers or for young fruits and would enable an examination of whether the length of frost-sensitive periods has changed in recent decades (Legave et al., 2013). Secondly, we calibrated models on populations from various elevations assuming they share similar heat and chilling requirements. However, populations from higher and lower elevations are often genetically differentiated in their spring phenology, as revealed in common garden experiments (Vitasse et al., 2009a; Vitasse et al., 2013; vonWuehlisch et al., 1995), and it is still unclear whether the differences are due to different chilling or forcing requirements (e.g. Dantec et al., 2014; Kramer et al., 2017; Vitasse et al., 2009b; Vitasse et al., 2013; vonWuehlisch et al., 1995). Nevertheless, the dominance of environmental effects over genetic effects is overwhelming (Vitasse et al., 2010; Vitasse et al., 2013), so genetic differentiation in the phenology of different populations growing at different elevations should not substantially affect predictions from phenological models calibrated at the species scale. Finally, we focused our study on all sites below the treeline where maximum and minimum temperatures were available over the study period in Switzerland. Although several sites were considerably above the current distribution of the four selected species, especially for fruit trees, it was interesting to test whether these species would be more exposed to frost when planted at these higher elevations, assuming no phenological adaptation. Our results clearly warn against planting fruit trees at upper elevations because compared to lower elevations the safety margin against frost is smaller and is declining, despite the general warming.

#### 5. Conclusions

Our study suggests an increasing risk of frost exposure to fruit and forest trees at elevations above 800 m and unchanged risk at lower elevations over the period 1975–2016. The differing results between higher and lower elevations is likely explained by a stronger phenological shift at higher elevations as a result of stronger warming during late rather than early spring and the increasing role of limiting factors (insufficient chilling and photoperiod) at lower elevations, as well as by an insignificant change in the occurrence of the latest spring frost event at higher elevations. The increasing risk of frost exposure might accentuate in the future as maximum temperatures are currently still rising faster than minimum temperatures (Matiu et al., 2016).

Farmers, fruit growers and forest managers may adapt to climate change by planting plant varieties or species with higher summer stress resistance (FAO, 2007; Lindner et al., 2010) or plant trees at higher elevations. However, any consideration of the planting of new varieties, provenances or species needs to take into account the trade-off between the potential higher profitability associated with the use of summer-adapted varieties/species and the cost of protecting plants from frost damage. New summer-adapted varieties/species may exhibit lower spring thermal requirements, which may lead to increasing risks of frost risk damage. For fruit growers, breeding initiatives should focus on varieties exhibiting late flowering to minimize exposure of sensitive tissues to late spring frost, but which are also better adapted to overall warmer conditions.



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## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.agrformet.2017.09.005>.

## References

- Albuquerque, N., García-Montiel, F., Carrillo, A., Burgos, L., 2008. Chilling and heat requirements of sweet cherry cultivars and the relationship between altitude and the probability of satisfying the chill requirements. *Environ. Exp. Bot.* 64 (2), 162–170.
- Augspurger, C.K., 2009. Spring 2007 warmth and frost: phenology, damage and refoliation in a temperate deciduous forest. *Funct. Ecol.* 23 (6), 1031–1039.
- Augspurger, C.K., 2013. Reconstructing patterns of temperature, phenology, and frost damage over 124 years: spring damage risk is increasing. *Ecology* 94 (1), 41–50.
- Basler, D., Körner, C., 2014. Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiol.* 34 (4), 377–388.
- 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 Biol.* 16 (5), 1503–1514.
- Blümel, K., Chmielewski, F.-M., 2012. Shortcomings of classical phenological forcing models and a way to overcome them. *Agric. Forest Meteorol.* 164 (0), 10–19.
- Bonhomme, M., Rageau, R., Lacombe, A., 2010. Optimization of endodormancy release models, using series of endodormancy release data collected in France. *Acta Hort.* 872, 51–60.
- Burham, K.P., Anderson, D.P., 2002. Information Theory and Loglikelihood Models: a Basis for Model Selection and Inference, Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer, Berlin, pp. 33–74.
- Cannell, M.G.R., Smith, R.I., 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *J. Appl. Ecol.* 20 (3), 951–963.
- Chuine, I., Cour, P., 1999. Climatic determinants of budburst seasonality in four temperate-zone tree species. *New Phytol.* 143 (2), 339–349.
- Chuine, I., Cour, P., Rousseau, D.D., 1998. Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant. Cell Environ.* 21 (5), 455–466.
- Chuine, I., García de Cortázar Atauri, I., Kramer, K., Hänninen, H., 2013. Plant development models. In: Schwarz, M.D. (Ed.), *Phenology: An Integrative Environmental Science*. Springer, Dordrecht, Netherlands, pp. 275–293.
- Chuine, I., Bonhomme, M., Legave, J.-M., García de Cortázar-Atauri, I., Charrier, G., Lacombe, A., Améglio, T., 2016. Can phenological models predict tree phenology accurately in the future? the unrevealed hurdle of endodormancy break. *Global Change Biol.* 22 (10), 3444–3460.
- Chuine, I., 2000. A unified model for budburst of trees. *J. Theor. Biol.* 207 (3), 337–347.
- Dantec, C.F., Vitasse, Y., Bonhomme, M., Louvet, J.M., Kremer, A., Delzon, S., 2014. Chilling and heat requirements for leaf unfolding in European beech and sessile oak populations at the southern limit of their distribution range. *Int. J. Biometeorol.* 1–12.
- Darbyshire, R., Farrera, I., Martínez-Lüscher, J., Leite, G.B., Mathieu, V., El Yaacoubi, A., Legave, J.-M., 2017. A global evaluation of apple flowering phenology models for climate adaptation. *Agric. Forest Meteorol.* 240–241, 67–77.
- Dittmar, C., Fricke, W., Elling, W., 2006. Impact of late frost events on radial growth of common beech (*Fagus sylvatica* L.) in Southern Germany. *Eur. J. Forest Res.* 125 (3), 249–259.
- Dubuis, P.-H., Fabre, A.-L., Bloesch, B., Viret, O., 2011. Agrometeo: une plate-forme très appréciée. *Revue Suisse de Vitic. Arboric. Hortic.* 43 (5), 324.
- Ducrey, M., 1998. Aspects écophysiologiques de la réponse et de l'adaptation des sapins méditerranéens aux extrêmes climatiques: gélées printanières et sécheresse estivale.
- Eccel, E., Rea, R., Caffarra, A., Crisci, A., 2009a. Risk of spring frost to apple production under future climate scenarios: the role of phenological acclimation. *Int. J. Biometeorol.* 53 (3), 273–286.
- Eccel, E., Rea, R., Caffarra, A., Crisci, A., 2009b. Risk of spring frost to apple production under future climate scenarios: the role of phenological acclimation (vol 53, pg 273, 2009). *Int. J. Biometeorol.* 53 (4) 375–375.
- El Yaacoubi, A., Malagi, G., Oukabli, A., Hafidi, M., Legave, J.-M., 2014. Global warming impact on floral phenology of fruit trees species in Mediterranean region. *Sci. Hort.* 180, 243–253.
- FAO, 2007. *Adaptation to Climate Change in Agriculture, Forestry, and Fisheries: Perspective, Framework and Priorities*. FAO, Rome.
- Fu, Y.H., Piao, S., Op de Beeck, M., Cong, N., Zhao, H., Zhang, Y., Menzel, A., Janssens, I.A., 2014. Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecol. Biogeogr.* 23 (11), 1255–1263.
- Fu, Y.H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., Ciais, P., Huang, M., Menzel, A., Penuelas, J., Song, Y., Vitasse, Y., Zeng, Z., Janssens, I.A., 2015. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526 (7571), 104–107.
- Fu, Y.H., Liu, Y., De Boeck, H.J., Menzel, A., Nijs, I., Peaucelle, M., Peñuelas, J., Piao, S., Janssens, I.A., 2016. Three times greater weight of daytime than of night-time temperature on leaf unfolding phenology in temperate trees. *New Phytol.* 212 (3), 590–597.
- Güsewell, S., 2014. Phenological Responses to Changing Temperatures: Representativeness and Precision of Results from the Swiss Phenological Network, Zurich. 146 pp.
- Gehrig-Fasel, J., Guisan, A., Zimmermann, N.E., 2007. Tree line shifts in the Swiss Alps: climate change or land abandonment? *J. Veg. Sci.* 18 (4), 571–582.
- 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 freezes: increased cold damage in a warming world? *Bioscience* 58 (3), 253–262.
- Hänninen, H., 1991. Does climatic warming increase the risk of frost damage in northern trees? *Plant Cell Environ.* 14 (5), 449–454.
- Hänninen, H., 2016. The Annual Cycle Under Changing Climatic Conditions, Boreal and Temperate Trees in a Changing Climate: Modelling the Ecophysiology of Seasonality. Springer, Netherlands, Dordrecht, pp. 263–335.
- Hansen, J., Sato, M., Ruedy, R., 1995. Long-term changes of the diurnal temperature cycle: implications about mechanisms of global climate change. *Atmos. Res.* 37 (1–3), 175–209.
- 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 Biol.* 18 (7), 2365–2377.
- Hurrell, J.W., Deser, C., 2009. North Atlantic climate variability: the role of the north Atlantic oscillation. *J. Mar. Syst.* 78 (1), 28–41.
- Hurrell, J.W., Van Loon, H., 1997. *Decadal Variations in Climate Associated with the North Atlantic Oscillation, Climatic Change at High Elevation Sites*. Springer, pp. 69–94.
- IPCC, et al., 2013. Summary for policymakers. In: Stocker, T.F. (Ed.), *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, pp. pp. 1–30.
- Inouye, D.W., 2000. The ecological and evolutionary significance of frost in the context of climate change. *Ecol. Lett.* 3 (5), 457–463.
- Jones, G.V., Duff, A.A., Hall, A., Myers, J.W., 2010. Spatial analysis of climate in wine-grape growing regions in the western United States. *Am. J. Enol. Vitic.* 61 (3), 313–326.
- Körner, C., Basler, D., Hoch, G., Kollas, C., Lenz, A., Randin, C., Vitasse, Y., Zimmermann, N.E., 2016. Where, why and how? explaining the low temperature range limits of temperate tree species. *J. Ecol.* 104 (4), 1076–1088.
- Karl, T.R., Knight, R.W., Gallo, K.P., Peterson, T.C., Jones, P.D., Kukla, G., Plummer, N., Razuvayev, V., Lindsey, J., Charlson, R.J., 1993. A new perspective on recent global warming: asymmetric trends of daily maximum and minimum temperature. *Bull. Am. Meteorol. Soc.* 74 (6), 1007–1023.
- Kollas, C., Körner, C., Randin, C.F., 2014. Spring frost and growing season length co-control the cold range limits of broad-leaved trees. *J. Biogeogr.* 41 (4), 773–783.
- Kramer, K., Ducousso, A., Gömöry, D., Hansen, J.K., Ionita, L., Liesebach, M., Lorent, A., Schüller, S., Sulkowska, M., de Vries, S., von Wühlisch, G., 2017. Chilling and forcing requirements for foliage bud burst of European beech (*Fagus sylvatica* L.) differ between provenances and are phenotypically plastic. *Agric. Forest Meteorol.* 234–235, 172–181.
- Kramer, K., 1994a. 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 Environ.* 17 (4), 367–377.
- Kramer, K., 1994b. Selecting a model to predict the onset of growth of *Fagus sylvatica*. *J. Appl. Ecol.* 31 (1), 172–181.
- Kreyling, J., Stahlmann, R., Beierkuhnlein, C., 2012a. Spatial variation in leaf damage of forest trees and the regeneration after the extreme spring frost event in May 2011. *Allg. Forst Jagdztg.* 183 (1–2), 15–22.
- Kreyling, J., Thiel, D., Simmnacher, K., Willner, E., Jentsch, A., Beierkuhnlein, C., 2012b. Geographic origin and past climatic experience influence the response to late spring frost in four common grass species in central Europe. *Ecography* 35 (3), 268–275.
- Landsberg, J., 1974. Apple fruit bud development and growth: analysis and an empirical model. *Ann. Bot.* 38 (5), 1013–1023.
- Legave, J.M., Farrera, I., Almeras, T., Calleja, M., 2008. Selecting models of apple flowering time and understanding how global warming has had an impact on this trait. *J. Hortic. Sci. Biotechnol.* 83 (1), 76–84.
- Legave, J.M., Blanke, M., Christen, D., Giovannini, D., Mathieu, V., Oger, R., 2013. A comprehensive overview of the spatial and temporal variability of apple bud dormancy release and blooming phenology in Western Europe. *Int. J. Biometeorol.* 57 (2), 317–331.
- Legave, J.-M., Guédon, Y., Malagi, G., El Yaacoubi, A., Bonhomme, M., 2015. Differentiated responses of apple tree floral phenology to global warming in contrasting climatic regions. *Front. Plant Sci.* 6, 1054.
- Lenoir, J., Gegout, J.C., Marquet, P.A., de Ruffray, P., Brisse, H., 2008. A significant upward shift in plant species optimum elevation during the 20th century. *Science* 320 (5884), 1768–1771.
- Lenz, A., Hoch, G., Körner, C., 2013a. Early season temperature controls cambial activity and total tree ring width at the alpine treeline. *Plant Ecol. Divers.* 1–11.
- Lenz, A., Hoch, G., Vitasse, Y., Körner, C., 2013b. European deciduous trees exhibit

- similar safety margins against damage by spring freeze events along elevational gradients. *New Phytol.* 200 (4), 1166–1175.
- Lenz, A., Hoch, G., Körner, C., Vitasse, Y., 2016. Convergence of leaf-out timing towards minimum risk of freezing damage in temperate trees. *Funct. Ecol.* 30 (9), 1480–1490.
- Leys, C., Ley, C., Klein, O., Bernard, P., Licata, L., 2013. Detecting outliers: do not use standard deviation around the mean, use absolute deviation around the median. *J. Exp. Soc. Psychol.* 49 (4), 764–766.
- Lindner, M., Maroschek, M., Netherer, S., Kremer, A., Barbati, A., Garcia-Gonzalo, J., Seidl, R., Delzon, S., Corona, P., Kolstrom, M., Lexer, M.J., Marchetti, M., 2010. Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For. Ecol. Manage.* 259 (4), 698–709.
- Matiu, M., Ankerst, D.P., Menzel, A., 2016. Asymmetric trends in seasonal temperature variability in instrumental records from ten stations in Switzerland, Germany and the UK from 1864 to 2012. *Int. J. Climatol.* 36 (1), 13–27.
- Miller, P., Lanier, W., Brandt, S., 2001. Using Growing Degree Days to Predict Plant Stages. Ag/Extension Communications Coordinator, Communications Services, Montana State University-Bozeman, Bozeman, MO.
- Nash, J.E., Sutcliffe, J.V., 1970. River flow forecasting through conceptual models part I—a discussion of principles. *J. Hydrol.* 10 (3), 282–290.
- Ningre, F., Colin, F., 2007. Frost damage on the terminal shoot as a risk factor of fork incidence on common beech (*Fagus sylvatica* L.). *Ann. Forest Sci.* 64 (1), 79–86.
- Osaer, A., Vaysse, P., Berthoumieu, J., Audubert, A., Trillot, M., 1998. Gel de printemps. Protection des vergers. Centre technique interprofessionnel des fruit et légumes, Paris.
- Pagter, M., Arora, R., 2013. Winter survival and deacclimation of perennials under warming climate: physiological perspectives. *Physiol. Plant.* 147 (1), 75–87.
- Peng, S., Piao, S., Ciais, P., Myneni, R.B., Chen, A., Chevallier, F., Dolman, A.J., Janssens, I.A., Penuelas, J., Zhang, G., Vicca, S., Wan, S., Wang, S., Zeng, H., 2013. Asymmetric effects of daytime and night-time warming on Northern Hemisphere vegetation. *Nature* 501 (7465), 88–92.
- Perraudin, G., Fellay, D., 1975. Les moyens de lutte. La lutte contre le gel. *Revue Suisse de Vitic. Arboric. Hortic.* 7, 31–54.
- Polgar, C.A., Primack, R.B., 2011. Leaf-out phenology of temperate woody plants: from trees to ecosystems. *New Phytol.* 191 (4), 926–941.
- Quénol, H., 1998. Gel de printemps: protection des vergers. *Hortipratic*.
- R Core Team, 2015. *CianR: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Rebetez, M., Reinhard, M., 2008. Monthly air temperature trends in Switzerland 1901–2000 and 1975–2004. *Theor. Appl. Climatol.* 91 (1–4), 27–34.
- Rebetez, M., 2001. Changes in daily and nightly day-to-day temperature variability during the twentieth century for two stations in Switzerland. *Theor. Appl. Climatol.* 69 (1–2), 13–21.
- 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. *Agric. Forest Meteorol.* 169, 156–173.
- Richardson, E., 1974. A model for estimating the completion of rest for Redhaven and Elberta peach trees. *HortSci* 9, 331–332.
- Rigby, J.R., Porporato, A., 2008. Spring frost risk in a changing climate. *Geophys. Res. Lett.* 35 (12), 5.
- Roberts, A.M., Tansey, C., Smithers, R.J., Phillimore, A.B., 2015. Predicting a change in the order of spring phenology in temperate forests. *Global Change Biol.*
- Rodrigo, J., 2000. Spring frosts in deciduous fruit trees—morphological damage and flower hardiness. *Sci. Hort.* 85 (3), 155–173.
- Sacks, W.J., Kucharik, C.J., 2011. Crop management and phenology trends in the U.S. Corn Belt: impacts on yields, evapotranspiration and energy balance. *Agric. Forest Meteorol.* 151 (7), 882–894.
- Sakai, A., Larcher, W., 1987. Frost survival of plants: responses and adaptation to freezing stress. *Ecological Studies*. Springer, Berlin, Germany.
- Scheffinger, H., Menzel, A., Koch, E., Peter, C., 2003. Trends of spring time frost events and phenological dates in Central Europe. *Theor. Appl. Climatol.* 74 (1–2), 41–51.
- Scherler, M., Remund, J., Walther, L., 2016. Wasserhaushalt von Wäldern bei zunehmender Trockenheit. In: Pluess, A.R., Augustin, S., Brang, P., B. Bundesamt für Umwelt BAFU, B. Eidgenössische Forschungsanstalt WSL (Eds.), *Wald im Klimawandel. Grundlagen für Adaptationsstrategien*. Haupt, Bern, Stuttgart, Vienne.
- Shi, P., Chen, Z., Reddy, G.V.P., Hui, C., Huang, J., Xiao, M., 2017. Timing of cherry tree blooming: contrasting effects of rising winter low temperatures and early spring temperatures. *Agric. Forest Meteorol.* 78–89.
- Vanoni, M., Bugmann, H., Nötzli, M., Bigler, C., 2016. Drought and frost contribute to abrupt growth decreases before tree mortality in nine temperate tree species. *For. Ecol. Manage.* 382, 51–63.
- Vitasse, Y., Basler, D., 2013. What role for photoperiod in the bud burst phenology of European beech. *Eur. J. Forest Res.* 132 (1), 1–8.
- Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., Kremer, A., 2009a. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can. J. For. Res.* 39 (7), 1259–1269.
- Vitasse, Y., Delzon, S., Bresson, C.C., Michalet, R., Kremer, A., 2009b. Altitudinal differentiation in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Can. J. Forest Res.* 39 (7), 1259–1269.
- Vitasse, Y., Bresson, C.C., Kremer, A., Michalet, R., Delzon, S., 2010. Quantifying phenological plasticity to temperature in two temperate tree species. *Funct. Ecol.* 24 (6), 1211–1218.
- Vitasse, Y., Francois, C., Delpierre, N., Dufrene, E., Kremer, A., Chuine, I., Delzon, S., 2011. Assessing the effects of climate change on the phenology of European temperate trees. *Agric. Forest Meteorol.* 151 (7), 969–980.
- Vitasse, Y., Hoch, G., Randin, C.F., Lenz, A., Kollas, C., Scheepens, J.F., Körner, C., 2013. Elevational adaptation and plasticity in seedling phenology of temperate deciduous tree species. *Oecologia* 171 (3), 663–678.
- Vitasse, Y., Lenz, A., Hoch, G., Körner, C., 2014a. Earlier leaf-out rather than difference in freezing resistance puts juvenile trees at greater risk of freeze damage than adult trees. *J. Ecol.* 102 (4), 981–988.
- Vitasse, Y., Lenz, A., Koerner, C., 2014b. The interaction between freezing tolerance and phenology in temperate deciduous trees. *Front. Plant Sci.* 5 (541), 1–12.
- Vitra, A., Lenz, A., Vitasse, Y., 2017. Frost hardening and dehardening potential in temperate trees from winter to budburst. *New Phytol.* 216 (1), 113–123.
- Wang, E.L., Engel, T., 1998. Simulation of phenological development of wheat crops. *Agric. Syst.* 58 (1), 1–24.
- Wargo, P., 1996. Consequences of environmental stress on oak: predisposition to pathogens. *Ann. For. Sci.* 53 (2–3), 359–368.
- Wild, M., Gilgen, H., Roesch, A., Ohmura, A., Long, C.N., Dutton, E.G., Forgan, B., Kallis, A., Russak, V., Tsvetkov, A., 2005. From dimming to brightening: decadal changes in solar radiation at Earth's surface. *Science* 308 (5723), 847–850.
- vonWuehlisch, G., Krusche, D., Muhs, H.J., 1995. Variation in temperature sum requirement for flushing of beech provenances. *Silvae Genet.* 44 (5–6), 343–346.