

2021

## Photoperiod decelerates the advance of spring phenology of six deciduous tree species under climate warming

Lin Meng

Yuyu Zhou

Lianhong Gu

Andrew D. Richardson

Josep Peñuelas

*See next page for additional authors*

---

**Authors**

Lin Meng, Yuyu Zhou, Lianhong Gu, Andrew D. Richardson, Josep Peñuelas, Yongshuo Fu, Yeqiao Wang, Ghasserm R. Asrar, Hans G. De Boeck, Jiafu Mao, Yongguang Zhang, and Zhousen Wang

---

## PRIMARY RESEARCH ARTICLE

## Photoperiod decelerates the advance of spring phenology of six deciduous tree species under climate warming

Lin Meng<sup>1</sup>  | Yuyu Zhou<sup>1</sup>  | Lianhong Gu<sup>2</sup>  | Andrew D. Richardson<sup>3,4</sup> |  
Josep Peñuelas<sup>5,6</sup>  | Yongshuo Fu<sup>7</sup>  | Yeqiao Wang<sup>8</sup> | Ghasserm R. Asrar<sup>9</sup> |  
Hans J. De Boeck<sup>10</sup> | Jiafu Mao<sup>2</sup> | Yongguang Zhang<sup>11,12,13</sup>  | Zhuosen Wang<sup>14,15</sup>

<sup>1</sup>Department of Geological and Atmospheric Sciences, Iowa State University, Ames, IA, USA

<sup>2</sup>Environmental Sciences Division and Climate Change Science Institute, Oak Ridge National Laboratory, Oak Ridge, TN, USA

<sup>3</sup>School of Informatics, Computing and Cyber Systems, Northern Arizona University, Flagstaff, AZ, USA

<sup>4</sup>Center for Ecosystem Science and Society, Northern Arizona University, Flagstaff, AZ, USA

<sup>5</sup>CSIC, Global Ecology Unit CREAM-CSIC-UAB, Bellaterra, Spain

<sup>6</sup>CREAF, Cerdanyola del Vallès, Spain

<sup>7</sup>Beijing Key Laboratory of Urban Hydrological Cycle and Sponge City Technology, College of Water Sciences, Beijing Normal University, Beijing, China

<sup>8</sup>Department of Natural Resources Science, University of Rhode Island, Kingston, RI, USA

<sup>9</sup>Universities Space Research Association, Columbia, MD, USA

<sup>10</sup>PLECO (Plants and Ecosystems, Department of Biology, University of Antwerp, Wilrijk, Belgium

<sup>11</sup>International Institute for Earth System Science, Nanjing University, Nanjing, China

<sup>12</sup>Jiangsu Center for Collaborative Innovation in Geographical Information Resource Development and Application, Nanjing, China

<sup>13</sup>Collaborative Innovation Center of Novel Software Technology and Industrialization, Nanjing, China

<sup>14</sup>NASA Goddard Space Flight Center, Greenbelt, MD, USA

<sup>15</sup>Earth System Science Interdisciplinary Center, University of Maryland, College Park, MD, USA

## Correspondence

Yuyu Zhou, Department of Geological and Atmospheric Sciences, Iowa State University, Ames, IA, USA.  
Email: yuyuzhou@iastate.edu

## Funding information

NASA, Grant/Award Number: 80NSSC19K1356; College of Liberal Arts and Science; NSF, Grant/Award Number: EF-1702697; European Research Council, Grant/Award Number: ERC-SyG-2013-610028; US Department of Energy, Grant/Award Number: DE-AC05-1008 00OR22725

## Abstract

Vegetation phenology in spring has substantially advanced under climate warming, consequently shifting the seasonality of ecosystem process and altering biosphere-atmosphere feedbacks. However, whether and to what extent photoperiod (i.e., day-length) affects the phenological advancement is unclear, leading to large uncertainties in projecting future phenological changes. Here we examined the photoperiod effect on spring phenology at a regional scale using in situ observation of six deciduous tree species from the Pan European Phenological Network during 1980–2016. We disentangled the photoperiod effect from the temperature effect (i.e., forcing and chilling) by utilizing the unique topography of the northern Alps of Europe (i.e., varying day-length but uniform temperature distribution across latitudes) and examining phenological changes across latitudes. We found prominent photoperiod-induced shifts in spring leaf-out across latitudes (up to 1.7 days per latitudinal degree). Photoperiod regulates spring phenology by delaying early leaf-out and advancing late leaf-out caused by temperature variations. Based on these findings, we proposed two phenological models

This is an open access article under the terms of the Creative Commons Attribution-NonCommercial License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2021 The Authors. *Global Change Biology* published by John Wiley & Sons Ltd.

that consider the photoperiod effect through different mechanisms and compared them with a chilling model. We found that photoperiod regulation would slow down the advance in spring leaf-out under projected climate warming and thus mitigate the increasing frost risk in spring that deciduous forests will face in the future. Our findings identify photoperiod as a critical but understudied factor influencing spring phenology, suggesting that the responses of terrestrial ecosystem processes to climate warming are likely to be overestimated without adequately considering the photoperiod effect.

#### KEYWORDS

chilling, climate change, daylength, phenological model, spring leaf-out, temperature

## 1 | INTRODUCTION

Phenological stages, such as leaf-out and flowering, are sensitive to weather and climate variability, serving as indicators of integrative biological impacts of climate change (Menzel & Fabian, 1999). Finely tuned to the seasonality of the surrounding environment, phenology plays two apparently conflicting but equally important roles in minimizing the risk of damage from late frost events and maximizing the length of the growing season for carbon fixation (Basler & Körner, 2012; Larcher, 2003). Temperature directly drives the developmental rates of deciduous trees in spring but has large interannual variations (Peñuelas & Filella, 2001). In contrast, photoperiod (i.e., daylength) is astronomically controlled and predictable, serving as a reliable cue for seasonal progression and changing of freezing risk (Körner & Basler, 2010). Greater incidence of extreme climate events and climate warming has pushed spring phenology to new limits of interannual variation, exposing deciduous trees to increased risks on both ends (Richardson et al., 2018). However, it is unclear whether photoperiod would constrain the warming-induced variation of spring phenology (Basler & Körner, 2012; Way & Montgomery, 2015), leading to considerable uncertainties in the projection of phenological changes and associated land-atmosphere interactions and feedbacks (Peñuelas & Filella, 2009; Richardson et al., 2013). These uncertainties have hindered the development of effective adaptation strategies to reduce ecosystem vulnerability under the ongoing climate change (Gu et al., 2008; Hufkens et al., 2012).

Empirical evidence is inconclusive with respect to the photoperiod effect on spring phenology (Flynn & Wolkovich, 2018; Way & Montgomery, 2015; Zohner et al., 2016). Temperate and boreal forests experience dormancy in winter to withstand unfavorable environmental conditions. Environmental factors, including the degree of winter chilling, photoperiod, and spring forcing (degree-day accumulation), trigger the dormancy release and onset of the growing season (Richardson et al., 2013). Under the same daily forcing temperature, manipulated longer photoperiod was found to advance spring phenology of late-successional species by counterbalancing the effects of lack of chilling (Caffarra & Donnelly, 2011; Laube, Sparks, Estrella, Höfler, et al., 2014). Photoperiod may also constrain the phenological development until daylength exceeds a threshold (Heide, 1993; Wareing, 1953; Zohner & Renner, 2015).

In addition, the phenological variability of some species seems not to be strongly constrained by photoperiod (Richardson et al., 2018; Zohner et al., 2016). Besides the physiological variations among tree species, such divergent results could also be caused by the design of experimental manipulations, for example, the use of seedlings or cuttings cultivated indoors as a substitute for mature trees and the use of fixed, rather than gradually extended daylength under controlled conditions (Saxe et al., 2001). Experimental studies are also limited to certain species and locations, leaving potentially large discrepancies across species and space in the photoperiod effect to be poorly understood.

Observational datasets that cover a wide geographic range and include abundant tree species allow for regional-scale investigations of the photoperiod effect on phenology (Vitasse & Basler, 2013). For example, the spring phenology of European beech (*Fagus sylvatica*) was found to be mainly controlled by photoperiod for southern and lower elevation populations and by temperature for northern and higher elevation populations (Wareing, 1953). Photoperiod effects are also found to be highly species-specific across European temperate zone tree species (Fu et al., 2019). However, the photoperiod effects from these studies are often challenging to interpret, given the covariation of temperature and photoperiod within a year (Flynn & Wolkovich, 2018). As a result, the complex interactions of temperature and photoperiod on spring phenology remain unclear (Chuine et al., 2010).

The topography of central Europe, from the Alps to northern Germany, offers a unique opportunity to disentangle the photoperiod and temperature effects on spring phenology in a natural setting. The coincidence of the increase in latitude but the decrease in elevation provides a relatively uniform temperature distribution in the background of gradual changes in daylength across latitudes. Taking advantage of this coincidence, we aim to answer the following questions: (1) Is there a photoperiod-induced latitudinal change in spring leaf-out of deciduous forests? (2) To what extent does photoperiod interact with temperature in affecting spring leaf-out? (3) How does photoperiod affect the spring leaf-out and frost risk under the projected future climate warming?

To answer these questions, we used the geographical characteristics of the study area combined with a stratification approach to maximally constrain the effects of temperature variation and isolate the effects of photoperiod on phenology. Specifically, we

stratified all data into nine temperature groups and examined the latitudinal changes in spring leaf-out of six deciduous tree species in each temperature group. To test whether photoperiod causes the temperature-independent phenological changes across latitudes, we developed two photoperiod-enabled phenology models and compared them with a conventional chilling-alone model (without photoperiod effect) in predicting the changes in spring leaf-out. Finally, we examined the photoperiod effect on frost risk of the deciduous tree under future warming scenarios by projecting spring leaf-out and frost days (days from spring leaf-out to the summer solstice when daily minimum temperature  $<0^{\circ}\text{C}$ ) until 2100 using temperatures from the Coupled Model Intercomparison Project 5 (CMIP5).

## 2 | MATERIALS AND METHODS

### 2.1 | Study area

Study sites of phenological observations are located in central Europe, from the Alps to northern Germany ( $47\text{--}55^{\circ}\text{N}$ , Figure 1), spanning an elevation range of 0–1100 m above the sea level. Elevation in this region decreases with latitude increases, resulting in similar temperatures but gradually changing daylength (Figure 2). The long-term mean spring temperature (January 1 to April 30) during 1980–2016 only ranges between  $3.0$  and  $4.2^{\circ}\text{C}$  in 50% of the study sites (Figure S1). Seasonal changes in daylength are larger in the north compared to in the south of the study region (Figure S2). For example, the ranges of daylength in a given year at  $55^{\circ}\text{N}$  and  $45^{\circ}\text{N}$  are 10.2 and 6.9 h respectively.

### 2.2 | Datasets

Phenological observations were collected from the Pan European Phenological Network (PEP725; Templ et al., 2018), which is a

large, long time series, and open access phenology dataset. This dataset has been widely used to investigate the effects of environmental factors on phenology. Spring leaf-out of six deciduous tree species, comprising *Aesculus hippocastanum* (horse chestnut), *Alnus glutinosa* (alder), *Betula pendula* (birch), *Fagus sylvatica* (beech), *Fraxinus excelsior* (Ash), and *Quercus robur* (oak), was analyzed. These species have the most complete records during the study period 1980–2016, and have been used in a variety of phenology studies (Fu et al., 2019). In total, 8653 site-year-species observations at 1851 sites were used in this study. We used the phenophase leaf-out (first visible leaf stalk) in this study. We excluded records of spring leaf-out later than June 30 to reduce potential bias due to outliers.

The time series of daily mean air temperature for the study sites during the period 1980–2016 was derived from the E-OBS gridded observational dataset version 19.0 at a  $0.1^{\circ}$  spatial resolution (Cornes et al., 2018). The temperature was used to calculate forcing and chilling accumulations, mean temperature during winter and spring, and to run phenological models.

Future daily minimum and mean temperatures during the period 2006–2100 for the study area were derived from the CMIP5 for the experiment of Representative Concentration Pathway 8.5 (RCP 8.5) scenario from the model of Community Climate System Model (CCSM) 4.0 of U.S. National Center for Atmospheric Research (NCAR). We used the experiment of RCP 8.5 to show the largest possible phenological changes under projected future climate warming. We calculated the regional mean time series of daily mean and minimum temperatures. The daily minimum temperature was then used to calculate frost days and the daily mean temperature was used to run phenological models.

We used a 90 m digital elevation dataset that provides continuous topography surfaces (Jarvis, 2008) from NASA's Shuttle Radar Topography Mission (SRTM).

Daylength was calculated as a function of latitude (L) and day of the year (DOY) using Equation (1; Forsythe et al., 1995):

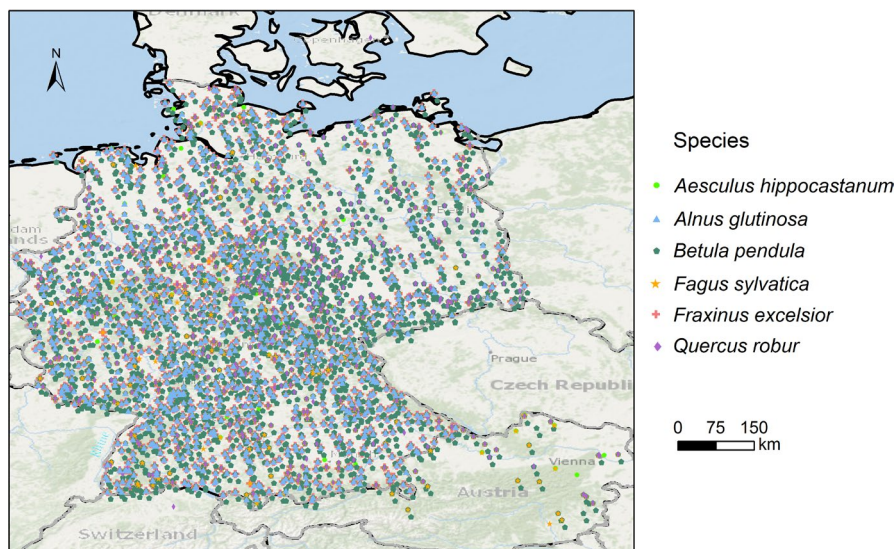
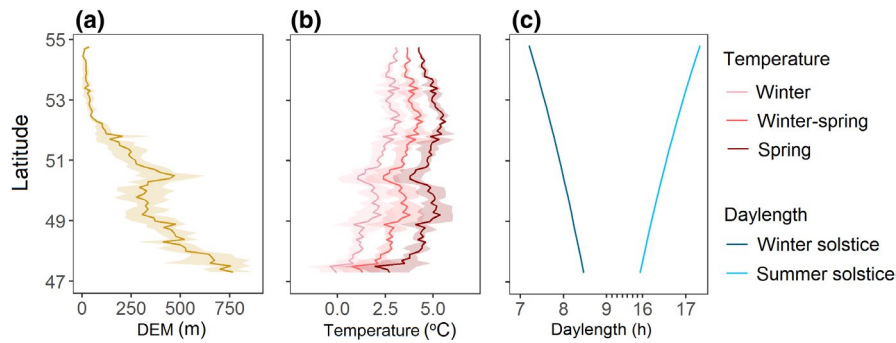


FIGURE 1 Location of phenological observations for six species



**FIGURE 2** Latitudinal variations of elevation (a), temperatures (b), and daylength (c). Winter-spring temperature is the mean temperature from November 1 in the preceding year to April 30. Winter temperature is the mean temperature from November 1 in the preceding year to January 31 and spring temperature is the mean temperature from February 1 to April 30. Solid lines and shaded areas in (a) and (b) represent mean and variation (i.e., 25% and 75% quantiles) at 0.1° latitude bin, respectively

$$D = 24 - \frac{24}{\pi} \times \cos^{-1} \left( \frac{\sin \frac{0.8333\pi}{180} + \sin \frac{\pi}{180} \sin \varphi}{\cos \frac{L\pi}{180} \times \cos \varphi} \right), \quad (1)$$

$$\varphi = \sin^{-1} (0.29795 \times \cos \theta), \quad (2)$$

$$\theta = 0.2163108 + 2 \tan^{-1} (0.9671396 \times \tan (0.0086 \times (\text{DOY} - 186))), \quad (3)$$

where  $D$  is daylength,  $\varphi$  is the sun's declination angle,  $\theta$  is revolution angle, and  $\varphi$  and  $\theta$  are measured in radians.

### 2.3 | Experimental design

To minimize the temperature effect on spring leaf-out across latitudes, we stratified the data into nine temperature groups based on three forcing and three chilling accumulations at high, medium, and low levels for each deciduous tree species. Forcing accumulation was defined as an integration of daily mean temperature above a temperature threshold (5°C) throughout the pre-season (from November 1 in the preceding year to leaf-out; Fu et al., 2015). Chilling accumulation was defined as the number of days when the daily mean temperature was below 5°C (Kramer, 1994). First, we divided all data into three forcing levels using 33.3% and 66.6% quantiles of all forcing accumulations during the period 1980–2016. Then, within each forcing level, we further divided data into three chilling levels using 33.3% and 66.6% quantiles of all chilling accumulations of that forcing level during the period 1980–2016. We analyzed changes in spring leaf-out across latitudes in each temperature group. This stratification approach also enables us to investigate the interaction between photoperiod and temperature by comparing the magnitude of latitudinal leaf-out changes across temperature groups.

To evaluate phenological models in terms of predicting the latitudinal trend of spring leaf-out, we ran models and compared model performance using data from the 65%–75% quantiles of forcing accumulations and 25%–35% quantiles of chilling accumulations. These criteria were used because we found the delay trends of spring leaf-out across latitudes were the most pronounced in high forcing and low chilling groups. We also examined the latitudinal trends in

forcing and chilling to test whether there are effects of forcing and chilling on the latitudinal trends in spring leaf-out. We further conducted two sensitivity analyses using a wider band (60%–80% quantiles of forcing accumulations and 20%–40% quantiles of chilling accumulations) and a narrower band (70%–75% quantiles of forcing accumulations and 25%–30% quantiles of chilling accumulations) to test the effect of samples size on results.

Frost risk was represented by the number of frost days during the first half of the growing season, that is, from spring leaf-out to the summer solstice on June 22. Frost days were calculated as days when the daily minimum temperature was below 0°C (Liu et al., 2018). To quantify the role of photoperiod in mitigating frost risks, we compared the spring leaf-out and total frost days using daily minimum temperatures from CMIP5 during the period 2007–2100 predicted by three phenological models.

### 2.4 | Phenological models

We proposed two photoperiod-enabled models, comprising a photo-threshold model and a photo-chilling model, which incorporated the photoperiod effect in predicting spring leaf-out. The photo-threshold model includes photoperiod and forcing processes while the photo-chilling model includes photoperiod (but different from the photo-threshold model), chilling, and forcing processes. Specifically, the photo-threshold model assumes the forcing process starts when the daylength is above a minimum threshold; spring leaf-out is predicted to occur when (1) forcing accumulation reaches its threshold or (2) daylength is above a maximum threshold (Melaas et al., 2016). The photo-threshold model was developed from the growing-degree-day model that only considers the forcing process, which used an arbitrary date (e.g., January 1) as the start date for the forcing accumulation. We replaced the arbitrary date with a minimum daylength threshold to account for the spatial variation of the start of the forcing process. We also added a maximum daylength threshold as the latest end date of the forcing process to ensure spring leaf-out could be triggered in the case when forcing cannot reach its requirement

in extreme cold years. The photo-chilling model assumes trees accumulate forcing and chilling starting from winter, and spring leaf-out is predicted to occur when forcing accumulation reaches a threshold (determined by chilling accumulation). The effectiveness of forcing accumulation is affected by photoperiod, which is chilling-dependent (i.e., strong photoperiod effect under low chilling; Caffarra et al., 2011). The photo-chilling model was developed from a widely used chilling model, that is, parallel model, which considers the forcing and chilling processes (Hänninen, 1990), and we added a chilling-dependent photoperiod variable to this model to adjust the efficiency of forcing accumulation. We also include the original parallel chilling model as a representation of a modeling scheme without consideration of the photoperiod effect and hereafter termed it as chilling-alone model.

We calibrated models using 80% of observations (i.e., data during the period 1980–2010 across all sites) for each deciduous tree species respectively. The objective function of the calibration process was the minimum root mean square error (RMSE) between prediction and observation. The calibrated parameters are shown in Table 1. We evaluated models using the remaining 20% of observations (i.e., data during the period 2011–2016 across all sites) for each deciduous tree species, and then applied three models to predict spring leaf-out and its latitudinal trends. We further compared the model performance in simulating the historical interannual variation in phenology in terms of RMSE for each species. We also used the models to project future changes in spring leaf-out using projected daily average temperatures from CMIP5 for the period 2007–2100. We then used the predicted spring leaf-out to calculate frost days.

The phenological models are shown below.

## 2.5 | Photo-threshold model

$$R_f(t) = \begin{cases} x(t) - T_{\text{base}} & x(t) > T_{\text{base}} \\ 0 & x(t) \leq T_{\text{base}} \end{cases},$$

$$S_f(t) = \sum_{t_0} R_f(x(t)).$$

Spring leaf-out is predicted to occur when  $S_f(t) \geq F^*$  or  $DL(t) \geq DL_{\text{end}}^*$ . The forcing process starts at  $t_0$ , that is when  $D(t) \geq DL_{\text{start}}^*$ .  $t$  is day of year,  $x(t)$  is daily temperature,  $DL(t)$  is daily daylength,  $DL_{\text{start}}^*$  is the minimum daylength threshold to trigger the forcing process,  $DL_{\text{end}}^*$  is the maximum daylength threshold,  $F^*$  is the forcing requirement,  $R_f(t)$  is the rate of forcing.  $S_f(t)$  is the state of forcing, calculated as the summation of  $R_f(t)$  from  $DL_{\text{start}}^*$  to the predicted spring leaf-out.  $T_{\text{base}}$  is base temperature (5°C).  $DL_{\text{start}}^*$ ,  $DL_{\text{end}}^*$ , and  $F^*$  are parameters to be calibrated.

## 2.6 | Photo-chilling model

$$R_f(t) = \begin{cases} \frac{28.4}{1 + \exp(3.4 - 0.185 * x(t))} & x(t) > T_{\text{base}} \\ 0 & x(t) \leq T_{\text{base}} \end{cases},$$

$$S_f(t) = \sum_{t_0} R_f(x(t)) \times R_p,$$

$$R_c(t) = \begin{cases} 0 & x(t) \geq 10.4 \text{ or } x(t) \leq -3.4 \\ \frac{x(t) + 3.4}{T_{\text{opt}} + 3.4} & -3.4 < x(t) \leq T_{\text{opt}} \\ \frac{x(t) - 10.4}{T_{\text{opt}} - 10.4} & T_{\text{opt}} < x(t) < 10.4 \end{cases},$$

$$S_c(t) = \sum_{t_0} R_c(x(t)),$$

$$R_p(t) = \frac{DL(t)}{12} \times e^{c \times S_c(t)}.$$

Spring leaf-out is predicted to occur when  $S_f(t) \geq a * \exp(b * S_c(t))$ , where  $b < 0$ .  $t$  is the day of year,  $x(t)$  is daily temperature,  $DL(t)$  is daily daylength,  $T_{\text{opt}}$  is the optimum temperature for chilling accumulation,  $S_f(t)$  and  $S_c(t)$  are the states of forcing and chilling respectively.  $R_f(t)$ ,  $R_c(t)$ , and  $R_p(t)$  are the rates of forcing, chilling, and photoperiod respectively. Forcing and chilling accumulations start at  $t_0$ , that is, November 1 in the preceding year in this study.  $T_{\text{base}}$  is base temperature (5°C).  $a$ ,  $b$ ,  $c$ , and  $T_{\text{opt}}$  are parameters to be calibrated.

TABLE 1 Parameters and statistics of model calibration

Models	Photo-threshold model				Photo-chilling model					Chilling-alone model			
	Species	$D_{\text{start}}^*$	$D_{\text{end}}^*$	$F^*$	RMSE	$a$	$b$	$c$	$T_{\text{opt}}$	RMSE	$a$	$b$	$T_{\text{opt}}$
<i>Aesculus hippocastanum</i>	10.7	15.5	90	9.92	518	-0.008	-0.12	-2.5	9.53	515	-0.0055	-3	12.04
<i>Alnus glutinosa</i>	10.7	15.5	86	14.30	500	-0.007	-0.01	-3.2	13.76	515	-0.0055	-3.2	15.87
<i>Betula pendula</i>	10.7	15.5	86	9.15	509	-0.008	-0.21	-3.2	8.92	515	-0.0055	-3.2	11.9
<i>Fagus sylvatica</i>	11.9	15.3	107	9.41	629	-0.011	-0.89	-3.2	8.81	579	-0.0055	-3	11.8
<i>Fraxinus excelsior</i>	11.7	15.5	176	9.95	630	-0.008	-0.9	-3.3	9.95	667	-0.0055	-3.2	11.66
<i>Quercus robur</i>	11.6	15.6	152	8.83	640	-0.008	-0.3	-3.3	8.82	635	-0.0055	-3.3	10.7

Abbreviation: RMSE, root mean square error.



## 2.7 | Chilling-alone model

$$R_f(t) = \begin{cases} \frac{28.4}{1 + \exp(3.4 - 0.185 * x(t))} & x(t) > T_{base} \\ 0 & x(t) \leq T_{base} \end{cases}$$

$$S_f(t) = \sum_{t_0} R_f(x(t)),$$

$$R_c(t) = \begin{cases} 0 & x(t) \geq 10.4 \text{ or } x(t) \leq -3.4 \\ \frac{x(t) + 3.4}{T_{opt} + 3.4} & -3.4 < x(t) \leq T_{opt} \\ \frac{x(t) - 10.4}{T_{opt} - 10.4} & T_{opt} < x(t) < 10.4 \end{cases}$$

Spring leaf-out is predicted to occur when  $S_f(t) \geq a * \exp(b * S_c(t))$ , where  $b < 0$ . This model shares the same parameters with the photo-chilling model but without the photoperiod variable.

## 3 | RESULTS

### 3.1 | Photoperiod-induced shifts in spring leaf-out

We found significant latitudinal shifts in spring leaf-out ( $p < 0.05$ ) in 49 of the 54 temperature–species groups (i.e., 9 temperature  $\times$  6 species groups, Table 2). Among these 49 groups, spring leaf-out delayed with increasing latitude in 44 groups (i.e., earlier spring leaf-out in the southern region), as indicated by positive slopes (day  $^{\circ}\text{L}^{-1}$ , i.e., number of days delayed in spring leaf-out per latitudinal degree increase,  $p < 0.05$ ). The greatest delays occurred in the medium forcing and low chilling groups, that is, spring leaf-out delayed  $>1.2$  day  $^{\circ}\text{L}^{-1}$  across the six deciduous tree species (largest delay in *Q. robur*: 1.7 day  $^{\circ}\text{L}^{-1}$ ,  $p < 0.05$ , Figure 3; Table 2). In contrast, spring leaf-out advanced, up to  $-0.3$  day  $^{\circ}\text{L}^{-1}$ , in the high forcing and high chilling groups of *A. hippocastanum*,

*A. glutinosa*, *F. excelsior*, *Q. robur*, and in the low forcing and high chilling group for *B. pendula* ( $p < 0.05$ , Figures S3 and S4; Table 2). The degree of latitudinal changes was very different among species, ranging from  $0.8 \pm 0.6$  day  $^{\circ}\text{L}^{-1}$  (mean  $\pm$  standard deviation, *Q. robur*) to  $0.5 \pm 0.5$  day  $^{\circ}\text{L}^{-1}$  (*A. glutinosa*) across all temperature groups (Table 2).

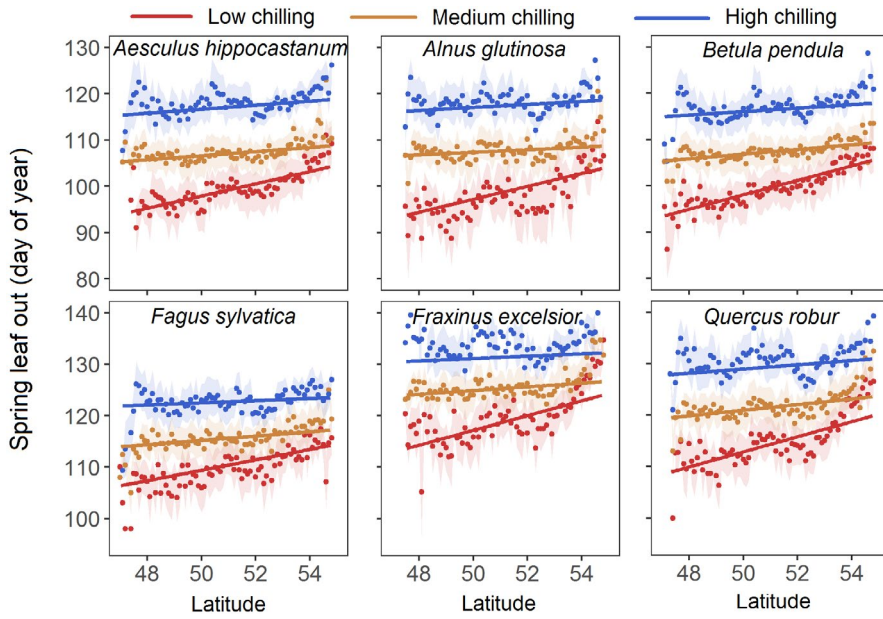
Modeling results directly supported that the photoperiod effect is the main contributor to the temperature-independent latitudinal shifts in spring leaf-out. All three models captured the historical interannual variation of spring leaf-out (Figure S5; Table S1). Both photoperiod-enabled models showed improvements in predicting spring leaf-out for all six deciduous tree species in terms of RMSE (photo-threshold:  $8.3 \pm 1.1$  days; photo-chilling:  $8.3 \pm 0.9$  days) and correlation (photo-threshold:  $0.62 \pm 0.07$ ; photo-chilling:  $0.60 \pm 0.06$ ), compared to the chilling-alone model (RMSE:  $9.7 \pm 0.8$  days; correlation:  $0.55 \pm 0.07$ ; Figure 4). More importantly, both photoperiod-enabled models reproduced the observed latitudinal delay in spring leaf-out (i.e., positive slopes) for all six deciduous tree species ( $p < 0.01$ ; Figure 5; see Section 4), although the photo-chilling model underestimated and the photo-threshold model overestimated the magnitude of the latitudinal delay for most species. In contrast, the chilling-alone model only reproduced 30% ( $0.39$  day  $^{\circ}\text{L}^{-1}$ ) and 32% ( $0.33$  day  $^{\circ}\text{L}^{-1}$ ) of magnitudes of the latitudinal delay for *F. excelsior* and *Q. robur* ( $p < 0.01$ , respectively, and predicted no trends for the remaining four species (Figure 5). The differences in slope between the photo-chilling and chilling-alone models (Figure 5) indicate the photoperiod effect, since these two models are the same except that the former considers the photoperiod effect. The chilling-alone model predicted no trends in spring leaf-out across latitudes, which was expected because the chilling-alone model depends solely on forcing and chilling and neither of them showed a trend across latitudes (Table S2). Such homogenous distribution of forcing and chilling further supports that the latitudinal shifts in spring leaf-out were not caused by a temperature effect.

**TABLE 2** Slopes of spring leaf-out across latitudes in nine temperature groups. Slopes represent the number of days changed in spring leaf-out per latitudinal degree increase. Positive or negative slopes represent delayed or advanced spring leaf-out northward respectively. Forcing accumulation was defined as an integration of daily mean temperature above  $5^{\circ}\text{C}$  from November 1 in the preceding year to leaf-out. Chilling was calculated as the number of days when daily mean temperature is below  $5^{\circ}\text{C}$  from November 1 in the preceding year to leaf-out

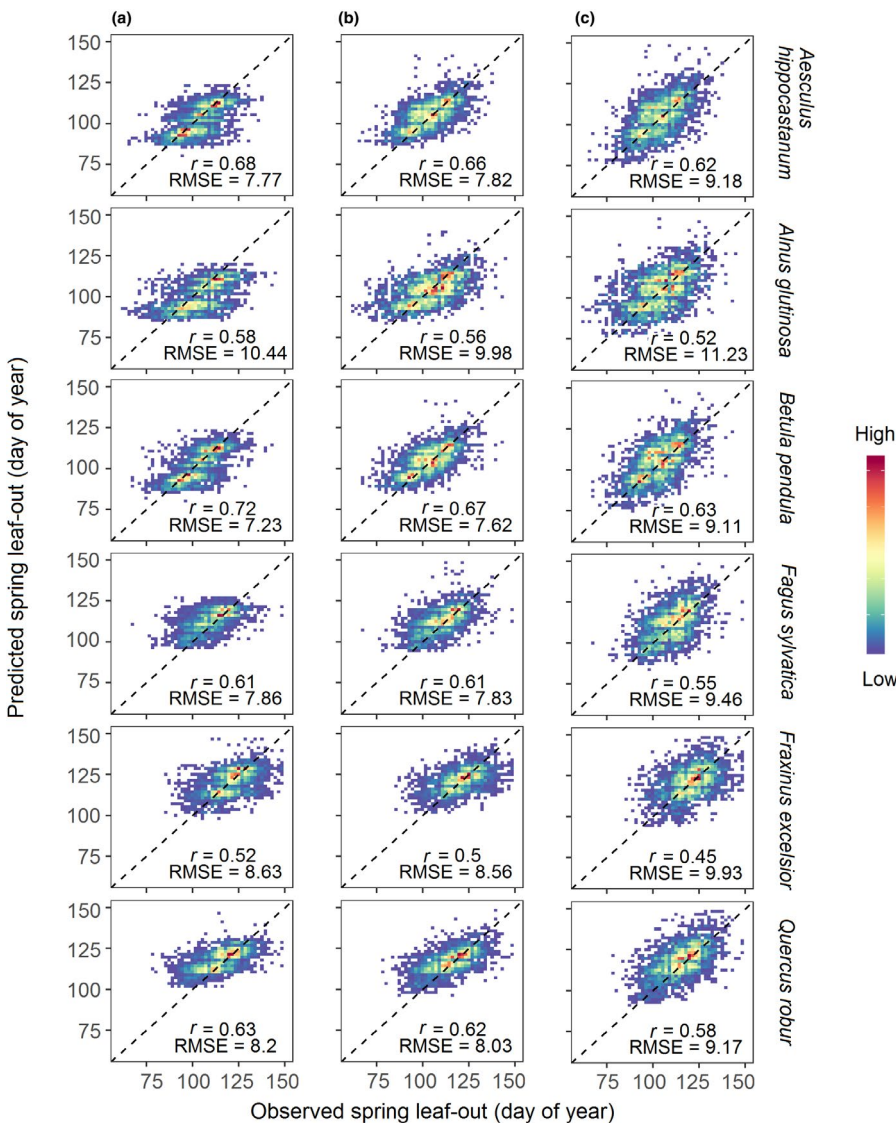
Species	Low forcing			Medium forcing			High forcing		
	Low	Medium	High	Low	Medium	High	Low	Medium	High
<i>Aesculus hippocastanum</i>	0.882***	0.853***	0.145**	1.424***	0.443***	0.276***	0.891***	0.858***	-0.197**
<i>Alnus glutinosa</i>	0.414***	1.035***	0.035	1.445***	0.281***	0.211***	0.972***	0.542***	-0.268**
<i>Betula pendula</i>	0.998***	0.905***	-0.135**	1.629***	0.509***	0.291***	0.894***	1.029***	0.1
<i>Fagus sylvatica</i>	0.588***	0.676***	0.322***	1.209***	0.416***	0.17***	1.061***	1.118***	-0.122
<i>Fraxinus excelsior</i>	0.722***	0.62***	-0.015	1.611***	0.407***	0.13	1.441***	0.912***	-0.286***
<i>Quercus robur</i>	0.769***	1.033***	0.473***	1.646***	0.574***	0.287***	1.353***	1.066***	-0.196**

\*\* $p < 0.05$ , \*\*\* $p < 0.01$ .

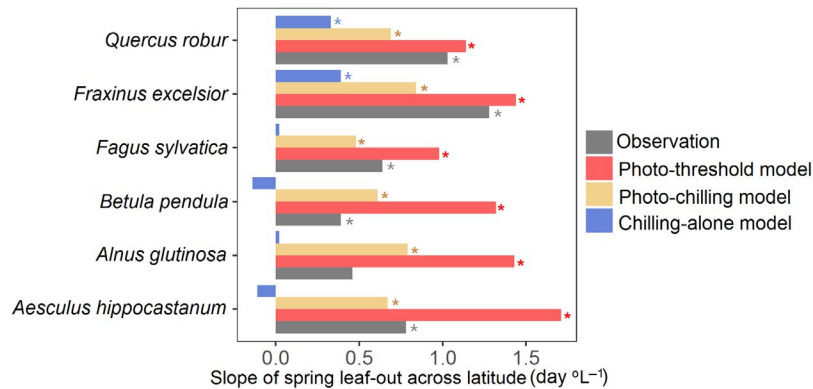




**FIGURE 3** Changes in spring leaf-out across latitudes in the medium forcing group. Points and shaded areas represent mean and uncertainty (i.e., 50% of standard deviation), respectively, of spring leaf-out at a  $0.1^\circ$  latitude. We stratified the data into nine temperature groups based on three forcing and three chilling accumulations at high, medium, and low levels for each deciduous tree species based on the 33.3% and 66.6% quantiles of forcing or chilling accumulations during the period 1980–2016. Chilling is calculated as the number of days when daily mean temperature is below  $5^\circ\text{C}$  from November 1 in the preceding year to leaf-out. Fitted linear regression lines for spring leaf-out with latitude are shown in each chilling group. Results for high and low forcing groups are shown in Figures S3 and S4



**FIGURE 4** Evaluation of the photo-threshold (a), photo-chilling (b), and chilling-alone (c) models. Color of pixels represents the number of observations. The black 1:1 line, root mean square error (RMSE), and correlation ( $r$ ) are shown



**FIGURE 5** Observed and predicted slopes of spring leaf-out across latitudes for six deciduous tree species. The slopes (derived from the linear regressions in Figure 6) represent the number of days changed in spring leaf-out per latitudinal degree increase. Positive slopes represent delayed spring leaf-out northward. Spring leaf-out data were selected from all site-year data during the period 1980–2016 based on the following two criteria: (1) forcing accumulation was within 65%–75% quantiles of all forcing accumulations and (2) chilling accumulation was within 25%–35% quantiles of all chilling accumulations. Significance is shown ( $p < 0.01$ )

### 3.2 | The underlying mechanism of the photoperiod effect

The photo-threshold model well captured the observed spatial variation in spring leaf-out for the six deciduous tree species (e.g., later leaf-out at higher latitudes, depicted by the gray curve in Figure 6), but neither the photo-chilling model nor the chilling-alone model did the same (Figure 6). Such contrast in model performances indicates that photoperiod affects the spatial variation in spring leaf-out mainly by imposing a threshold to trigger the forcing process, rather than varying with chilling conditions to influence the effectiveness of forcing accumulation. The photo-chilling and chilling-alone models predicted a similar latitudinal distribution pattern (depicted by the gray curve), but the former showed a considerably improved prediction of latitudinal trends of spring leaf-out (Figure 6c,d) by simply adding photoperiod as an additional variable. We obtained similar results using either a wider or a narrower forcing and chilling threshold to select data (Figures S6 and S7), indicating that the general patterns are robust for different selection criteria and sample sizes. These results illustrate that incorporating the photoperiod effect into phenological models greatly improves the predictability of spring leaf-out and its spatial variation.

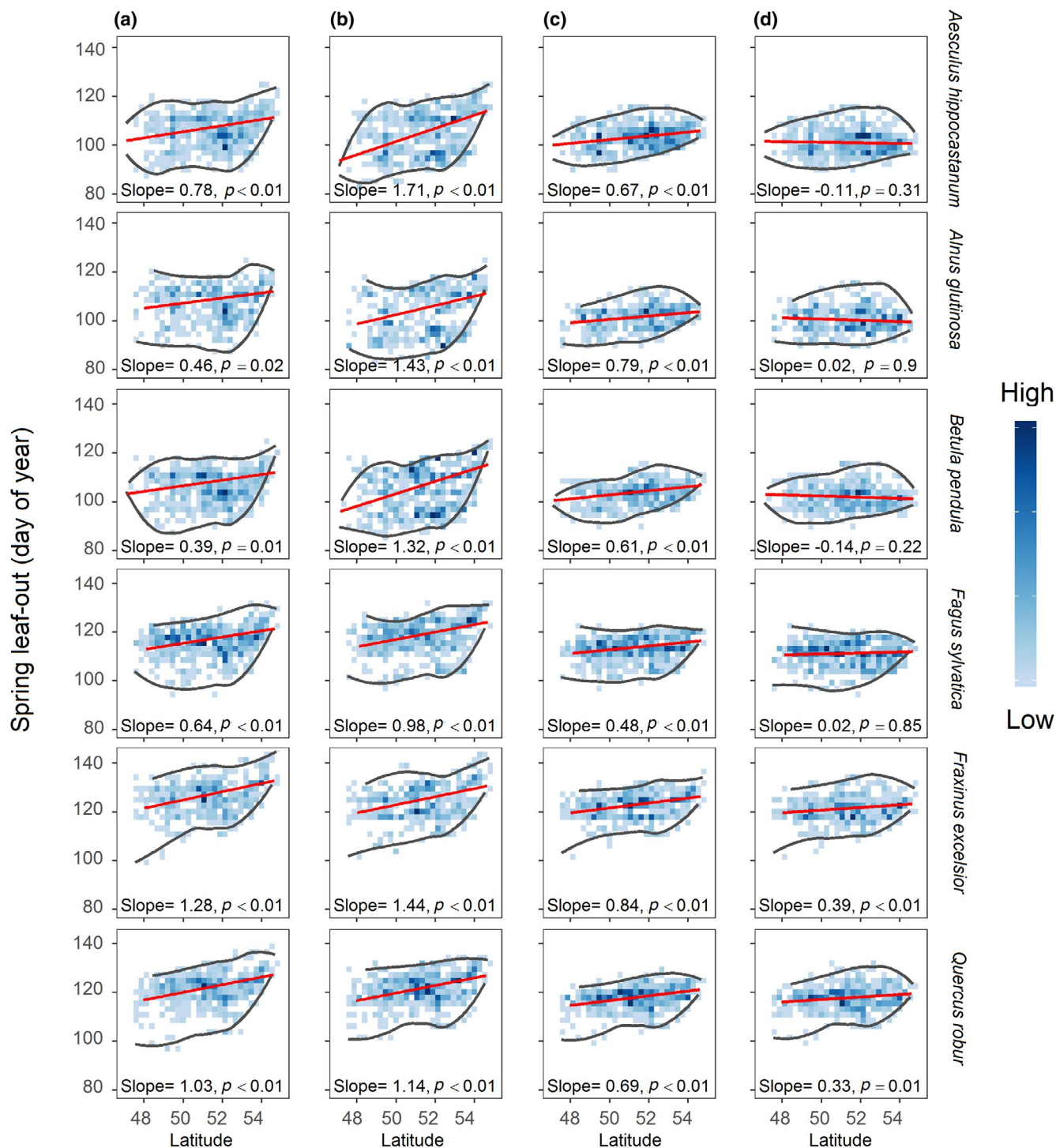
In addition, model performance in predicting latitudinal delay in spring leaf-out varied greatly across species, indicating a highly species-specific phenological dependence on the photoperiod effect. Specifically, the photo-chilling model best predicted the magnitude of delay for *A. hippocastanum*, *A. glutinosa*, *B. pendula*, and *F. sylvatica*, while the photo-threshold model best predicted the magnitude of delay for *F. excelsior* and *Q. robur* (Figure 5). The photo-threshold model overestimated the magnitudes, especially for *A. hippocastanum*, *A. glutinosa*, and *B. pendula*, whereas the photo-chilling model underestimated the magnitudes of delay for four out of six species (ranging from 65% for *F. excelsior* to 86% for *A. hippocastanum*; Figures 5 and 6).

### 3.3 | Interactions between photoperiod and temperature

The photoperiod effect on spring leaf-out showed clear interactions with temperature (Figure 7). How and to what extent photoperiod changed spring leaf-out across latitudes depended on temperature, as represented by the nine forcing and chilling accumulation groups. As shown in Figure 7, spring leaf-out either remained unchanged or significantly advanced across latitudes (negative slopes) in the high forcing and high chilling group (i.e., the upper right portion of the data point, e.g., *F. sylvatica* showed the largest advance at  $-0.3 \text{ day } ^\circ\text{L}^{-1}$ ), while leaf-out mostly showed significant delay northward in other temperature groups (positive slopes, earlier leaf-out in the southern region;  $p < 0.05$ ). There were greater delays in the low chilling group (i.e., the left portion of the data point in Figure 7,  $1.1 \pm 0.4 \text{ day } ^\circ\text{L}^{-1}$ , mean  $\pm$  standard deviation of slopes across six deciduous tree species and forcing groups) than in the medium chilling group ( $0.7 \pm 0.3 \text{ day } ^\circ\text{L}^{-1}$ ), and the delay effect gradually diminished or became nonsignificant toward high chilling and low forcing groups (i.e., the bottom right portion in Figure 7;  $0.1 \pm 0.2 \text{ day } ^\circ\text{L}^{-1}$ ). When putting together the changes in photoperiod effect with spring leaf-out, we found the advancing effect of photoperiod (negative slopes, Figure 7) occurred when spring leaf-out was relatively late (i.e., brown in the upper right portion in Figure 7 subfigures) while the delaying effect existed for the mid-to early spring leaf-out (gray and green in Figure 7 subfigures). The results are relatively consistent across all six deciduous tree species despite differences in magnitude.

### 3.4 | Mitigation of frost risks

All three models show that spring leaf-out will be significantly advanced under climate warming ( $p < 0.001$ ; Figure 8). More importantly, models show that photoperiod slows down the advancement



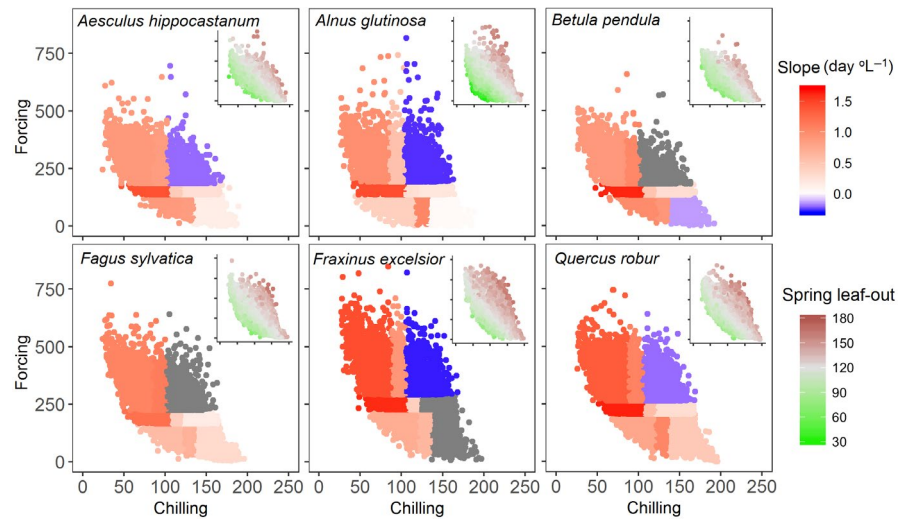
**FIGURE 6** Observed (a) and predicted spring leaf-out by the photo-threshold model (b), photo-chilling model (c), and chilling-alone model (d) across latitudes. Color of pixels represents the number of observations. Spring leaf-out (day of year) was selected from all site-year data during the period 1980–2016 based on the following criteria: (1) forcing accumulation was within the 65%–75% quantiles of all forcing accumulations and (2) chilling accumulation was within the 25%–35% quantiles of all chilling accumulations. Gray lines represent the boundary of data distribution, fitted by a Loess smooth approach using the maximum and minimum spring leaf-out at each  $0.1^\circ$  latitude. Linear regression lines, slopes, and  $p$ -values for spring leaf-out against latitudes are shown. The results based on different selection criteria and sample sizes are shown in Figures S6 and S7

of spring leaf-out and reduces the frost risk of deciduous trees under the projected warming climate. The advancing rate of spring leaf-out predicted by the chilling-alone model ( $-4.12$  to  $-3.15$  days decade $^{-1}$ )

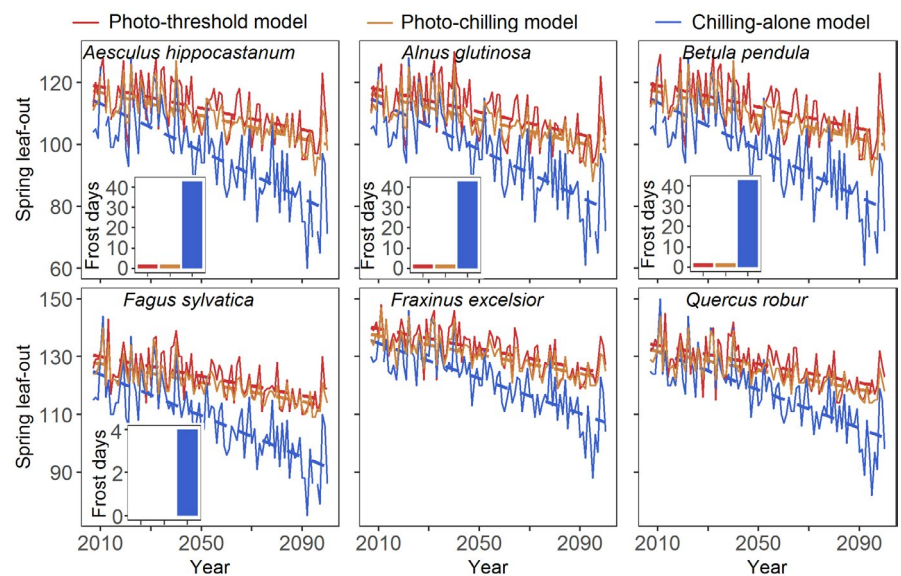
was around twice than that predicted by two photoperiod-enabled models ( $-2.00$  to  $-1.61$  days decade $^{-1}$ ;  $p < 0.001$ , Table 3). According to the chilling-alone model, spring leaf-out was predicted to advance



**FIGURE 7** Interaction between photoperiod and temperature on spring leaf-out. Colors represent slopes (number of days changed in spring leaf-out per latitudinal degree increase) derived from Table 2 ( $p < 0.01$ ). Positive slopes represent spring leaf-out was delayed northward. Gray indicates a nonsignificant trend at  $p > 0.05$ . The color of the subfigures represents spring leaf-out (day of the year) with the same axes as the main figures. Spring leaf-out and the calculated forcing and chilling accumulation are from observation data



**FIGURE 8** Model prediction of spring leaf-out and frost days during the period 2007–2100 for six deciduous tree species. Fitted linear regressions are shown for each model ( $p < 0.001$ ). The subfigures are the accumulated frost days during the period 2007–2100. All three models predict no frost days for *Fraxinus excelsior* and *Quercus robur*



**TABLE 3** Slopes of predicted spring leaf-out during 2007–2100 by three phenological models. The slopes are from fitted linear regression in Figure 8 ( $p < 0.001$ )

Slope (days/decade)	<i>Aesculus hippocastanum</i>	<i>Alnus glutinosa</i>	<i>Betula pendula</i>	<i>Fagus sylvatica</i>	<i>Fraxinus excelsior</i>	<i>Quercus robur</i>
Photo-threshold model	-1.86	-1.92	-1.87	-1.68	-1.80	-1.61
Photo-chilling model	-1.97	-2.00	-2.00	-1.63	-1.65	-1.64
Chilling-alone model	-4.12	-4.12	-4.12	-3.70	-3.15	-3.3

up to 36 days by 2100, in contrast to only 17 days predicted by the two photoperiod-enabled models across six deciduous species (Figure 8). Consequently, the chilling-alone model (mean  $\pm$  standard deviation:  $22 \pm 11$  days) predicts 21 more accumulated frost days than the photoperiod-enabled models (mean  $\pm$  standard deviation:  $1 \pm 0.5$  days) for the six deciduous tree species from 2007 to 2100 (Figure 8), demonstrating the effective mitigation of frost risk by photoperiod. The spring leaf-out of *F. sylvatica*, *F. excelsior*, and *Q. robur* showed less advance by 2100, compared to that of *A. hippocastanum*, *A. glutinosa*, and *B. pendula* (Table 3). In addition, the

accumulated frost days for *F. sylvatica*, *F. excelsior*, and *Q. robur* were significantly fewer compared to those for *A. hippocastanum*, *A. glutinosa*, and *B. pendula*, indicating highly species-specific risk of frost damage, with higher risks for earlier phenology species.

## 4 | DISCUSSION

The photoperiod effect on phenology we reported here is a two-way effect, that is, advancing excessive late spring leaf-out and delaying

excessive early spring leaf-out caused by temperature variation. The advance and delay effects of photoperiod have been proposed and discussed conceptually in previous studies (Basler & Körner, 2014; Vitasse & Basler, 2013; Way & Montgomery, 2015), and the delay effect has been reported from experimental studies (Zohner & Renner, 2015). However, this is the first study to reveal photoperiod advances excessive late spring leaf-out at the regional scale based on field observational datasets. Our findings point to the necessity of considering photoperiod together with temperature in predicting phenological changes under climate warming. Previously, it has been often assumed that temperature has a prominent effect on spring phenology at the current climate regime; as a result, the photoperiod effect and its interaction with temperature have not been as widely studied as the temperature effect itself (Basler & Körner, 2014; Meng, Mao, et al., 2020; Tang et al., 2016). As the scientific communities focus on the considerable advancement of spring phenology driven by climate warming, our study calls attention to the fact that photoperiod actually mitigates and may eventually limit such advancement in the future. As the warming trend continues, the temperature effect on phenology may decline whereas photoperiodic cues may become increasingly critical to spring phenology. Our findings also have significant implications for forecasting forest vulnerability in a warming world. Although extreme climate events may lead to increased risks of spring leaf-out (Gu et al., 2008), photoperiod may reduce the risk of frost damage associated with premature onset of tree growth by decelerating the advance in spring phenology.

This study addressed the challenge to disentangle the photoperiod and temperature effects on spring leaf-out by using the natural topography of the Alps, that is, spatially relatively homogenous temperatures caused by higher elevations at lower latitudes and a significant latitudinal gradient of daylength. We further constrained temperature variation to the minimum by dividing all site-year data into nine temperature groups according to forcing and chilling accumulation. Although there was possibly still minor temperature variation within each group, the trend of spring leaf-out in Figure 3 was mainly caused by photoperiod, not temperature, for two reasons. First, the photo-chilling model simulated the latitudinal trend of leaf-out, but the chilling-alone model did not (Figures 5 and 6). Having the same model structure, these two models only differ in whether considering photoperiod effect. Therefore, photoperiod mainly caused the difference in simulated spring leaf-out between these two models, that is, the latitudinal trend of spring leaf-out. Second, we used observational data within a very narrow temperature range (i.e., 65%–75% quantiles of forcing and 25%–35% quantiles of chilling) without latitudinal trend of forcing and chilling (Table S2), and we still see the same magnitude in the latitudinal trend of spring leaf-out (Figure 6a), as compared to in the 33% quantile group in Figure 3. This indicates temperature variation is not the main reason for the observed leaf-out trend.

The two photoperiod-enabled models proposed in our study are advantageous to correlative analyses between spring leaf-out and photoperiod to disentangle the photoperiod effect and understand

the underlying mechanisms. This is because a photoperiod model describes the photoperiod effect as a complete and continuous process over a period, while the correlative analyses only depict the photoperiod effect of a single date. The biases resulted from this single date approach are particularly pronounced if the study areas extend over wide latitudinal ranges, due to the distinct seasonal changes in daylength across latitudes (e.g., relatively longer daylength occurs before the spring equinox at lower latitudes and after the spring equinox at higher latitudes; Figure S2). In contrast, our models precisely account for the reversing of relative daylength before and after the spring equinox across latitudes. A photoperiod model also allows hypothesis testing on the underlying mechanisms of the photoperiod effect and predicting phenological changes under contrasting future scenarios so that the photoperiod effect on frost risk mitigation can be quantified.

Both the photo-threshold and photo-chilling models reproduced the observed patterns in spring leaf-out, but they represent contrasting underlying mechanisms of photoperiod effects (Basler & Körner, 2014; Caffarra & Donnelly, 2011; Vitasse & Basler, 2013; Vitasse et al., 2018). In the photo-threshold model, the observed delay and advance effects of photoperiod are represented by the minimum and maximum daylength thresholds respectively. Specifically, trees in the south of this study area reach the minimum threshold and start the forcing process earlier than trees in the north (Figure S2), resulting in an earlier spring leaf-out in the south (i.e., delay effect). In an extremely cold year when the forcing threshold cannot be reached, trees in the north reach the maximum threshold earlier than trees in the south (Figure S2), leading to an earlier spring leaf-out at higher latitudes (i.e., advance effect). In addition, the photo-threshold model assumes that the daylength does not affect phenology before the minimum threshold is reached, which is consistent with the findings from experimental studies (Zohner & Renner, 2015). In terms of the photo-chilling model, longer daylength in the south before the spring equinox contributes to a stronger photoperiod effect, which causes faster forcing accumulations and leads to an earlier spring leaf-out. On the contrary, in extreme cold years, the efficiency of forcing accumulation gradually increases as the photoperiod lengthens through spring (especially prominent at higher latitudes, e.g., 55°N in Figure S2), mitigating late spring leaf-out and causing the advancing trend across latitudes.

In general, photo-threshold and photo-chilling models show similar performance, indicating that despite the photo-chilling model has an additional chilling process than the photo-threshold model, including such a process does not always lead to the improved prediction for all species in our study area. For instance, the photo-chilling model shows better prediction on the latitudinal trend of spring leaf-out for four out of six species (e.g., *A. hippocastanum*, *A. glutinosa*, *B. pendula*, *F. sylvatica*; Figure 5) than the photo-threshold model. Moreover, previous studies also showed the model complexity did not necessarily lead to improved accuracy, partly because not all species require chilling exposure (Hänninen et al., 2019). For example, Basler (2016) reported simple models (e.g., models only consider forcing process) showed similar performance to more

complex models such as chilling-alone models in six temperate tree species across central Europe. The two photoperiod-enabled models serve as examples to incorporate photoperiod to improve phenology prediction, but they are not the only model structures and do not exclude other possible representations of the photoperiod effect in phenological models.

The underlying mechanisms and/or the strength of the photoperiod effect are highly species-specific. Such a species variation may be linked to the inherently different tolerant levels to the trade-off between late-season frost risk and productivity evolved in species' life history (Borchert et al., 2005; Hänninen et al., 2019; Vitasse & Basler, 2013), that is, opportunistic and freezing-resistant species are more temperature-dependent and "risky" while late-successional species are more photoperiod sensitive and "conservative" to follow temperature variation (Basler & Körner, 2012). The photoperiod effect may also vary among populations within one species (Vitasse & Basler, 2013), which is not considered in this study. The sensitivity of the photoperiod effect may interact with other factors such as nutrition; trees with abundant nutrition tend to follow a more risky strategy to maximize growing season length probably due to higher concentrations of proteins that resist the formation of icicles (Tateno & Takeda, 2003). These different photoperiod sensitivities may potentially lead to more divergent frost risks that different species will experience under climate warming (Basler & Körner, 2012). Plant-community structures and geographical distribution of species may even be changed in the long run due to the unevenly increased risks.

Adaptation or acclimation of trees to environments under climate change has been reported and discussed (Bennie et al., 2010). However, the capacity of deciduous trees to genetically or physiologically adapt to warmer conditions in terms of the timing of growth is unclear. Understanding the degree of adaptation of deciduous trees to photoperiod effect across the wide range of latitudes will enable further advances in phenological modeling. Experimental studies on manipulating temperature and daylength are needed to ascertain the photoperiod mechanisms controlling phenology, so that more credible model extrapolations can be undertaken. In addition, extending the findings of this regional study to the global scale would require consideration of interactions with other environmental factors, such as precipitation, soil moisture, and diurnal temperature range (Laube et al., 2014; Meng, Zhou, et al., 2020). Besides climate conditions, physical and chemical properties of soil such as the concentration of exchangeable soil potassium and soil acidity are also shown to have a significant impact on spring phenology at the scale of small forest watersheds (Lapenis et al., 2017).

This study provides observational and model-based evidence that photoperiod decelerates the advance in spring phenology and thus reduces the frost risks under climate warming. The delay effect of photoperiod limits the risk of damage from late frost events, while the advance effect allows trees to take full advantage of the growing season for carbon fixation. The advance effect suggests that the underlying mechanisms on photoperiod-temperature interaction may be more complex than the notion

that photoperiod may substitute chilling requirements as previously reported (Caffarra & Donnelly, 2011; Laube, Sparks, Estrella, Höfler, et al., 2014). As warmer climate pushes spring phenology to the edge of the interannual variation especially the early edge, the delay effect of photoperiod will become more prominent while the advance effect will be reduced. Our results reconcile contradictory hypotheses about the interaction between photoperiod and temperature in regulating spring leaf-out (Flynn & Wolkovich, 2018; Way & Montgomery, 2015; Zohner et al., 2016). Current earth system models need to accurately incorporate the photoperiod effect on spring phenology, since it may substantially change the trajectory of the land feedbacks to the earth system under future warming. Increased understanding of the photoperiod effect on phenology is also crucial to ascertain whether climate warming will increase the risk of spring frost damage to terrestrial ecosystems (Ault et al., 2013; Gu et al., 2008).

## ACKNOWLEDGMENTS

This work was supported by the NASA FINESST Program (80NSSC19K1356) and the College of Liberal Arts and Science's (LAS) Dean's Emerging Faculty Leaders award at the Iowa State University. A.D.R. acknowledges support from NSF's Macrosystems Biology program (award EF-1702697). J.P. acknowledges support from European Research Council grant ERC-SyG-2013-610028. J.M. was supported by the Terrestrial Ecosystem Science Scientific Focus Area (TES SFA) project funded by the US Department of Energy, Office of Science, Office of Biological and Environmental Research. Oak Ridge National Laboratory is managed by UT-Battelle, LLC, for the DOE under contract DE-AC05-1008 00OR22725. We acknowledge the E-OBS dataset from the EU-FP6 project UERRA (<http://www.uerra.eu>) and the Copernicus Climate Change Service, and the data providers in the ECA&D project (<https://www.ecad.eu>). We also acknowledge all members of the PEP725 project for providing the phenological data.

## DATA AVAILABILITY STATEMENT

The phenology data that support the findings of this study are openly available at <http://www.pep725.eu>. E-OBS gridded observational dataset are openly available at <https://www.ecad.eu/download/ensembles/download.php>. CMIP5 dataset are openly available at <https://cds.climate.copernicus.eu/cdsapp#!/home>. The 90 m digital elevation dataset are openly available at <https://srtm.csi.cgiar.org/>.

## ORCID

Lin Meng  <https://orcid.org/0000-0002-1603-4200>

Yuyu Zhou  <https://orcid.org/0000-0003-1765-6789>

Lianhong Gu  <https://orcid.org/0000-0001-5756-8738>

Josep Peñuelas  <https://orcid.org/0000-0002-7215-0150>

Yongshuo Fu  <https://orcid.org/0000-0002-9761-5292>

Yongguang Zhang  <https://orcid.org/0000-0001-8286-300X>



## REFERENCES

- Ault, T., Henebry, G., De Beurs, K., Schwartz, M., Betancourt, J. L., & Moore, D. (2013). The false spring of 2012, earliest in North American record. *Eos, Transactions American Geophysical Union*, 94(20), 181–182.
- Basler, D. (2016). Evaluating phenological models for the prediction of leaf-out dates in six temperate tree species across central Europe. *Agricultural and Forest Meteorology*, 217, 10–21.
- Basler, D., & Körner, C. (2012). Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology*, 165, 73–81.
- Basler, D., & Körner, C. (2014). Photoperiod and temperature responses of bud swelling and bud burst in four temperate forest tree species. *Tree Physiology*, 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 Biology*, 16(5), 1503–1514.
- Borchert, R., Robertson, K., Schwartz, M. D., & Williams-Linera, G. (2005). Phenology of temperate trees in tropical climates. *International Journal of Biometeorology*, 50(1), 57–65.
- Caffarra, A., & Donnelly, A. (2011). The ecological significance of phenology in four different tree species: Effects of light and temperature on bud burst. *International Journal of Biometeorology*, 55(5), 711–721.
- Caffarra, A., Donnelly, A., Chuine, I., & Jones, M. B. (2011). Modelling the timing of *Betula pubescens* budburst. I. Temperature and photoperiod: A conceptual model. *Climate Research*, 46(2), 147–157.
- Chuine, I., Morin, X., & Bugmann, H. (2010). Warming, photoperiods, and tree phenology. *Science*, 329(5989), 277.
- Cornes, R. C., van der Schrier, G., van den Besselaar, E. J., & Jones, P. D. (2018). An ensemble version of the E-OBS temperature and precipitation data sets. *Journal of Geophysical Research: Atmospheres*, 123(17), 9391–9409.
- Flynn, D., & Wolkovich, E. (2018). Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist*, 219(4), 1353–1362.
- Forsythe, W. C., Rykiel, E. J. Jr, Stahl, R. S., Wu, H.-I., & Schoolfield, R. M. (1995). A model comparison for daylength as a function of latitude and day of year. *Ecological Modelling*, 80(1), 87–95.
- Fu, Y. H., Piao, S., Vitis, Y., Zhao, H., De Boeck, H. J., Liu, Q., Yang, H., Weber, U., Hänninen, H., & Janssens, I. A. (2015). Increased heat requirement for leaf flushing in temperate woody species over 1980–2012: Effects of chilling, precipitation and insolation. *Global Change Biology*, 21(7), 2687–2697.
- Fu, Y. H., Zhang, X., Piao, S., Hao, F., Geng, X., Vitis, Y., & Janssens, I. A. (2019). Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global Change Biology*, 25(7), 2410–2418.
- Gu, L., Hanson, P. J., Post, W. M., Kaiser, D. P., Yang, B., Nemani, R., Pallardy, S. G., & Meyers, T. (2008). The 2007 eastern US spring freeze: Increased cold damage in a warming world? *BioScience*, 58(3), 253–262.
- Hänninen, H. (1990). Modelling bud dormancy release in trees from cool and temperate regions. *Acta Forestalia Fennica*, 0(213), <https://doi.org/10.14214/aff.7660>
- Hänninen, H., Kramer, K., Tanino, K., Zhang, R., Wu, J., & Fu, Y. H. (2019). Experiments are necessary in process-based tree phenology modelling. *Trends in Plant Science*, 24(3), 199–209. <https://doi.org/10.1016/j.tplants.2018.11.006>
- Heide, O. (1993). Dormancy release in beech buds (*Fagus sylvatica*) requires both chilling and long days. *Physiologia Plantarum*, 89(1), 187–191.
- 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(7), 2365–2377.
- Jarvis, A. (2008). Hole-field seamless SRTM data, International Centre for Tropical Agriculture (CIAT). <http://srtm.csi.cgiar.org>
- Körner, C., & Basler, D. (2010). Response—Warming, photoperiods, and tree phenology. *Science*, 329(5989), 278.
- Kramer, K. (1994). Selecting a model to predict the onset of growth of *Fagus sylvatica*. *Journal of Applied Ecology*, 172–181.
- Lapenis, A. G., Lawrence, G. B., Buyantuev, A., Jiang, S., Sullivan, T. J., McDonnell, T. C., & Bailey, S. (2017). A newly identified role of the deciduous forest floor in the timing of green-up. *Journal of Geophysical Research: Biogeosciences*, 122(11), 2876–2891.
- Larcher, W. (2003). *Physiological plant ecology: Ecophysiology and stress physiology of functional groups*. Springer Science & Business Media.
- Laube, J., Sparks, T. H., Estrella, N., Höfler, J., Ankerst, D. P., & Menzel, A. (2014). Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology*, 20(1), 170–182.
- Laube, J., Sparks, T. H., Estrella, N., & Menzel, A. (2014). Does humidity trigger tree phenology? Proposal for an air humidity based framework for bud development in spring. *New Phytologist*, 202(2), 350–355.
- Liu, Q., Piao, S., Janssens, I. A., Fu, Y., Peng, S., Lian, X. U., Ciais, P., Myneni, R. B., Peñuelas, J., & Wang, T. (2018). Extension of the growing season increases vegetation exposure to frost. *Nature Communications*, 9(1), 426.
- Melaas, E. K., Friedl, M. A., & Richardson, A. D. (2016). Multiscale modeling of spring phenology across Deciduous Forests in the Eastern United States. *Global Change Biology*, 22(2), 792–805.
- Meng, L., Mao, J., Zhou, Y., Richardson, A. D., Lee, X., Thornton, P. E., Ricciuto, D. M., Li, X., Dai, Y., Shi, X., & Jia, G. (2020). Urban warming advances spring phenology but reduces the response of phenology to temperature in the conterminous United States. *Proceedings of the National Academy of Sciences of the United States of America*, 117(8), 4228–4233.
- Meng, L., Zhou, Y., Li, X., Asrar, G. R., Mao, J., Wanamaker, A. D. Jr, & Wang, Y. (2020). Divergent responses of spring phenology to daytime and nighttime warming. *Agricultural and Forest Meteorology*, 281, 107832.
- Menzel, A., & Fabian, P. (1999). Growing season extended in Europe. *Nature*, 397(6721), 659.
- Peñuelas, J., & Filella, I. (2001). Responses to a warming world. *Science*, 294(5543), 793–795.
- Peñuelas, J., & Filella, I. (2009). Phenology feedbacks on climate change. *Science*, 324(5929), 887–888.
- Richardson, A. D., Hufkens, K., Milliman, T., Aubrecht, D. M., Furze, M. E., Seyednasrollah, B., Krassovski, M. B., Latimer, J. M., Nettles, W. R., Heiderman, R. R., Warren, J. M., & Hanson, P. J. (2018). Ecosystem warming extends vegetation activity but heightens vulnerability to cold temperatures. *Nature*, 1.
- Richardson, A. D., Keenan, T. F., Migliavacca, M., Ryu, Y., Sonnentag, O., & Toomey, M. (2013). Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology*, 169, 156–173.
- Saxe, H., Cannell, M. G., Johnsen, Ø., Ryan, M. G., & Vourlitis, G. (2001). Tree and forest functioning in response to global warming. *New Phytologist*, 149(3), 369–399.
- Tang, J., Körner, C., Muraoka, H., Piao, S., Shen, M., Thackeray, S. J., & Yang, X. (2016). Emerging opportunities and challenges in phenology: A review. *Ecosphere*, 7(8).
- Tateno, R., & Takeda, H. (2003). Forest structure and tree species distribution in relation to topography-mediated heterogeneity of soil nitrogen and light at the forest floor. *Ecological Research*, 18(5), 559–571.
- Templ, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., Rutishauser, T., Busto, M., Chmielewski, F.-M., Hájková, L., Hodzić, S., Kaspar, F., Pietragalla, B., Romero-Fresneda, R., Tolvanen, A., Vučetić, V., Zimmermann, K., & Züst, A. (2018). Pan

- European Phenological database (PEP725): A single point of access for European data. *International Journal of Biometeorology*, 62(6), 1109–1113.
- Vitasse, Y., & Basler, D. (2013). What role for photoperiod in the bud burst phenology of European beech. *European Journal of Forest Research*, 132(1), 1–8.
- Vitasse, Y., Signarbieux, C., & Fu, Y. H. (2018). Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences of the United States of America*, 115(5), 1004–1008.
- Wareing, P. (1953). Growth studies in woody species V. Photoperiodism in dormant buds of *Fagus sylvatica* L. *Physiologia Plantarum*, 6(4), 692–706.
- Way, D. A., & Montgomery, R. A. (2015). Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment*, 38(9), 1725–1736.
- Zohner, C. M., Benito, B. M., Svenning, J.-C., & Renner, S. S. (2016). Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change*, 6(12), 1120–1123.
- Zohner, C. M., & Renner, S. S. (2015). Perception of photoperiod in individual buds of mature trees regulates leaf-out. *New Phytologist*, 208(4), 1023–1030.

#### SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

**How to cite this article:** Meng L, Zhou Y, Gu L, et al.

Photoperiod decelerates the advance of spring phenology of six deciduous tree species under climate warming. *Glob Change Biol.* 2021;27:2914–2927. <https://doi.org/10.1111/gcb.15575>