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# Spring phenology at different altitudes is becoming more uniform under global warming in Europe

Lei Chen[1,2,†] | Jian-Guo Huang[1,2,†] | Qianqian Ma[1,2] | Heikki Hänninen[3] | Sergio Rossi[1,4] | Shilong Piao[5,6] | Yves Bergeron[7]

[1]Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems of the Chinese Academy of Sciences, Guangzhou, China

[2]Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden of the Chinese Academy of Sciences, Guangzhou, China

[3]State Key Laboratory of Subtropical Silviculture, Zhejiang A&F University, Hangzhou, China

[4]Département des Sciences Fondamentales, Université du Québec à Chicoutimi, Chicoutimi, QC, Canada

[5]Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing, China

[6]Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China

[7]Université du Québec en Abitibi-Temiscamingue, Rouyn-Noranda, QC, Canada

**Correspondence**
Jian-Guo Huang, Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems of the Chinese Academy of Sciences, Guangzhou, China.
Email: huangjg@scbg.ac.cn

## Abstract

Under current global warming, high-elevation regions are expected to experience faster warming than low-elevation regions. However, due to the lack of studies based on long-term large-scale data, the relationship between tree spring phenology and the elevation-dependent warming is unclear. Using 652k records of leaf unfolding of five temperate tree species monitored during 1951–2013 in situ in Europe, we discovered a nonlinear trend in the altitudinal sensitivity ($S_A$, shifted days per 100 m in altitude) in spring phenology. A delayed leaf unfolding (2.7 ± 0.6 days per decade) was observed at high elevations possibly due to decreased spring forcing between 1951 and 1980. The delayed leaf unfolding at high-elevation regions was companied by a simultaneous advancing of leaf unfolding at low elevations. These divergent trends contributed to a significant increase in the $S_A$ (0.36 ± 0.07 days 100/m per decade) during 1951–1980. Since 1980, the $S_A$ started to decline with a rate of −0.32 ± 0.07 days 100/m per decade, possibly due to reduced chilling at low elevations and improved efficiency of spring forcing in advancing the leaf unfolding at high elevations, the latter being caused by increased chilling. Our results suggest that due to both different temperature changes at the different altitudes, and the different tree responses to these changes, the tree phenology has shifted at different rates leading to a more uniform phenology at different altitudes during recent decades.

**KEYWORDS**
climate change, elevation-dependent warming, leaf unfolding, phenology

## 1 | INTRODUCTION

Plant phenology, the timing of periodic biological events in the seasonal cycle, has significant influences on various aspects of

ecosystem functioning, such as cycling of carbon, water and nutrients, tree fitness and distribution of species, and trophic interactions and structures (Chuine, 2010; Edwards & Richardson, 2004; Richardson et al., 2013). Due to the high sensitivity of phenological processes to climate change, their monitoring is an important approach to study the influence of global warming on terrestrial ecosystems (Richardson et al., 2013). In the northern hemisphere, advanced spring leaf phenology due to rising temperature has been reported in many studies in the context of global warming (Fu et al., 2015; Richardson et al., 2013). However, many temperate tree species have been shown to require a sufficient exposure to chilling temperatures to release dormancy before visible bud burst is initiated by long-term exposure to forcing temperatures (Hänninen, 2016). Because plants can experience a reduction in chilling in a warmer climate and this may postpone leaf unfolding, the response of spring leaf phenology to the temperature rise might be modified due to responses to the variation in forcing and chilling under climate warming (Hänninen & Tanino, 2011).

In the last century, the global mean temperature increased by 0.7°C (IPCC, 2014). To date, there is growing evidence that warming is amplified at high altitudes (Pepin et al., 2015), that is, high-elevation regions experience faster warming than low-elevation areas. Short-term altitudinal variation in spring phenology has been studied in several regions (Cory, Wood, & Neufeld, 2017; Guyon et al., 2011). Based on long-term phenological records at 128 sites, Vitasse, Signarbieux, and Fu (2018) reported that global warming has led to a more uniform spring phenology across elevations in the European Alps since 1960. However, the long-term relationship between spring phenology and the elevation-dependent warming in other regions still remains unknown. In some species leaf unfolding is also known to be under photoperiodic control (Körner & Basler, 2010). However, because photoperiod has not changed as a result of climatic change, then the observed changes in phenological timing at different altitudes are probably caused by tree responses to changes in air temperature.

Here, we used 652k phenological records of leaf unfolding of five temperate tree species monitored in situ during 1951–2013 in Europe (Table S1) and aimed to quantitate the long-term changes of the altitudinal sensitivity of spring phenology ($S_A$, shifted days per 100 m in altitude). By analyzing the phenological records together with long-term temperature data, we further attempted to elucidate the mechanisms causing the shifts observed in the phenological timing at different altitudes.

## 2 | MATERIALS AND METHODS

### 2.1 | Phenological and climate data

Phenological data for the five temperate tree species (Table S1) were obtained from the Pan European Phenology (PEP) network which provides an open access to in situ phenology records across Europe (www.pep725.eu; Templ et al., 2018). The leaf unfolding dates were defined according to the BBCH code (Biologische Bundesanstalt,

Bundessortenamt und CHemische Industrie) (Meier, 1997), where the timing of spring leaf unfolding is expressed as the day of year (DOY). Because the records were not always observed at the same sites for each species, the number of sites where the timing of leaf unfolding was recorded through the years of 1951–2013 was limited. To enlarge the dataset and simultaneously yield reliable results, we excluded some deviating observations using the following criteria. First, using the interquartile ranges method (IQRs), we excluded the records with latitudinal outliers that are more than 1.5 × IQR above the third quartile or below the first quartile. Second, using the Median Absolute Deviation (MAD) method we further excluded the outlier sites deviating more than 3.0 times the MAD (very conservative criterion) in all combinations of year and species (Leys, Ley, Klein, Bernard, & Licata, 2013). After these exclusions, the records of different years were distributed similarly for each species from 46.8°N to 54.8°N (Figure S1). The mean elevation of the observation sites was 256 m, with the standard deviation of 210 m and range from 0 to 1,000 m. In total, we used 652,069 records of leaf unfolding from 1951 to 2013 for the five temperate tree species (Table S1). The total number of records in each year for any given species was 2,070 ± 523 (mean ± SD).

To investigate the relationship between temperature and leaf phenology measured daily temperature data from meteorological stations were collected from the database E-OBS (http://ensembles-eu.metoffice.com). In the E-OBS climate database, the quality of the observations is classified into valid, suspect or missing. The observations classified as suspect or missing were excluded from our study.

### 2.2 | Statistical analysis

For the calculation of the $S_A$ of leaf unfolding, the sites were first divided into eight groups based on their latitudes and elevations (Table S2). Stratified sampling without replacement method based on the eight groups was used to split the heterogeneous sites in each year into fairly homogeneous groups. In each year, a total of 160 sites (20 sites per group × 8 groups) were sampled. The sites with elevation above 1,000 m are mainly located between 47 and 48° and because they for this reason may affect the power of the stratified sampling method, they were excluded from the data analysis.

After stratified sampling, linear mixed model (LMM) include random intercepts and slopes among groups was used to calculate the altitudinal sensitivity ($S_A$) of each tree species in each year, that is, the shift in phenological timing per 100 m change in altitude:

$$y_{ij} = \beta_0 + \beta_1 x_{ij} + \gamma_{0j} + \gamma_{1j} x_{ij} \qquad (1)$$

where $y_{ij}$ is the phenological timing (DOY) of site $i$ in group $j$; $x_{ij}$ is elevation of site $i$ in group $j$; $\beta_0$ and $\beta_1$ are the coefficients of the fixed effects; $\gamma_0$ and $\gamma_1$ are the random intercept and slope of group $j$. The estimated value of $\beta_1$ was used to represent the mean altitudinal sensitivity $S_A$ across groups. In addition, the $S_A$ in Switzerland, a mountainous region, was also calculated using Equatio 1 to validate the patterns observed across large spatial scales.

We used a data-driven generalized additive mixed model (GAMM) for estimating the overall time course of $S_A$ in the entire data set for all five species. The method was also used to detect the culmination points marking the boundaries of potential nonlinear trends of $S_A$. Then, the LMMs was used to determine the time course of $S_A$ within each period marked by the boundaries determined with GAMM. The general form of the LMMs is as follows:

$$y_{ij} = \alpha + \beta x_{ij} + \varepsilon_i \qquad (2)$$

where $y_{ij}$ is the $S_A$ of species $i$ at year $j$; $x_{ij}$ is calendar year $j$ of species $i$; $\alpha$ and $\beta$ are the coefficients of the fixed effects; $\varepsilon_i$ is the random intercept across species.

In addition, we examined the temporal variability in the timing of leaf unfolding in the five species during 1951–2013 separately at low and high altitudes. To that end, the data was divided into groups corresponding to 100 m range in altitude (Figures S2 and S3). It appeared that at low elevations the timing of leaf unfolding started to be delayed since 2000, especially in the regions below 10 m elevation (Figure S2). A delayed leaf unfolding was also observed in high-elevation regions during 1951–1980 with the highest rate of delay at elevations above 800 m (Figure S3). The detected temporal patterns were generally similar in different altitudinal ranges within both low (Figure S2) and high elevations (Figure S3). For this reason, due to their high sensitivities the regions below 10 m (Figure S2) and between 800 and 1,000 m (Figure S3) were selected to represent the low- and high-elevation regions, respectively.

Measured daily maximum and minimum temperature data from 28 stations in high-elevation regions (800–1,000 m, Table S3) and from 118 stations in low-elevation regions (less than 10 m, Table S4), all stations located between 46.8°N and 54.8°N, were used in the study. The mean distance between the phenological sites and the closest climate stations was ca. 15 km. Using an idealized daily temperature curve, the daily maximum and minimum temperatures were averaged and converted into hourly temperature records for the calculation of chilling and forcing units (Linvill, 1990). Based on earlier studies, the temperature range from 0 to 5°C was taken as effective in chilling (Hänninen, 2016). In the northern hemisphere, 1 November has been often used in earlier studies as the starting day for chilling accumulation (Fu et al., 2015; Zohner & Renner, 2014); and in our study, the averaged DOY of leaf unfolding of the examined five temperate tree species was approximately 120. Accordingly, the index for chilling accumulation was calculated as the number of hours from 1 November to 30 April with temperature in the range from 0 to 5°C. The accumulation of spring forcing units was calculated as the number of hours with hourly temperature above 5°C from 1 February to 30 April.

Local regression analysis was used to investigate potential nonlinear trends of accumulation of chilling and forcing units during 1951–2013. The relative influence of winter chilling and spring forcing on the timing of leaf unfolding was calculated to assess their relative contributions, or importance, to the timing of leaf unfolding (Grömping, 2006). In addition, t-statistic followed by the use of the bootstrapping method was used to compare the difference between the calculated relative influence of chilling and forcing during different periods.

The LMMs were achieved using lme4 (Bates, Maechler, Bolker, & Walker, 2014) package of R (R Core Team, 2015), and mgcv (Wood, 2017) and gamm4 (Wood & Scheipl, 2013) packages of R (R Core Team, 2015) were used to perform GAMs and GAMMs, respectively. The "chillR" package (Luedeling, Kunz, & Blanke, 2013) of R (R Core Team, 2015) was used to perform the calculation of the chilling and forcing units. The "relaimpo" (Grömping, 2006) package of R (R Core Team, 2015) was used to calculate the relative influence of winter chilling and spring forcing on the timing of leaf unfolding.

## 3 | RESULTS

### 3.1 | Altitudinal sensitivity and timing of leaf unfolding

In Europe, we found a significant increase in the $S_A$ (0.36 ± 0.07 day 100/m per decade; $p < .001$; Figure 1) during 1951–1980. Since 1980, it started to decrease with a rate of −0.32 ± 0.07 day 100/m per decade ($p < .001$; Figure 1). In particular, between 1990 and 2013, the $S_A$ showed a more drastically decrease compared to that during 1980–2013, −0.61 ± 0.10 day 100/m per decade ($p < .001$).

In Switzerland, we also observed a significant increase in the $S_A$ (0.46 ± 0.11 day 10/m per decade; $p < .001$) between 1951 and 1980 (Figure S4); the $S_A$ also started to decrease since 1980
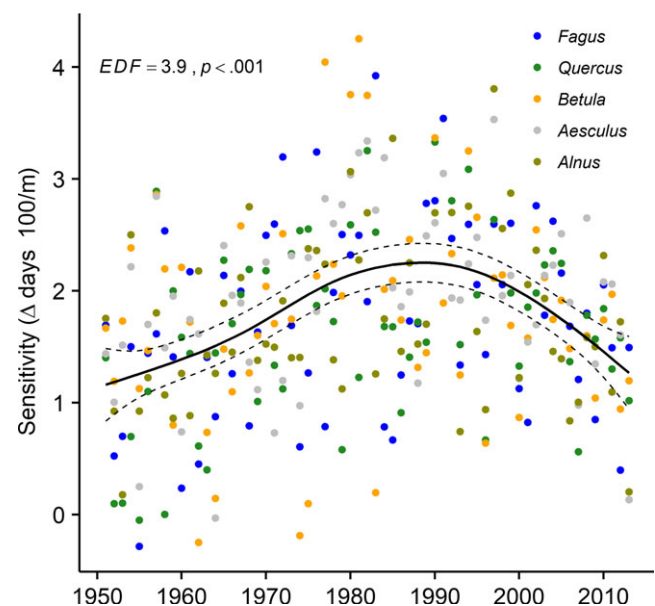


**FIGURE 1** Altitudinal sensitivity $S_A$ (the shift in phenological timing per 100 m change in altitude) of leaf unfolding of five temperate tree species in Europe during 1951–2013. The tree species indicated by the different colors are *Fagus sylvatica*, *Quercus robur*, *Betula pendula*, *Aesculus hippocastanum*, and *Alnus glutinosa*. EDF indicates the estimated degrees of freedom in the generalized additive mixed model [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure S4). Similarly, the $S_A$ also shifted a greater rate during 1990–2013 than that during 1980–2013 (0.71 ± 0.10 day 100/m per decade during 1980–2013 and −1.38 ± 0.16 day 100/m per decade during 1990–2013, $p$ < .001; Figure S4).

In addition, contrasting trends in the leaf unfolding were found in low- and high-elevation regions before 1980, as the timing of leaf unfolding remained unchanged at low elevations (Figure 2a) while it was delayed at high elevations (Figure 2b). Since 1980 leaf unfolding has been advancing at high elevations until today (Figure 2b) but at low elevations it had advanced until 2005, followed by a delay after that (Figure 2a).

## 3.2 | Changes in winter chilling and spring forcing

At low elevations, the winter chilling remained constant between 1951 and 1986 and decreased significantly after that during 1987–2013 (−12.8 ± 4.9 hours per year, $p$ = .014) (Figure 3a). At high elevations winter chilling increased through the whole period of 1951–2013 (0.70 ± 0.26 hours per year, $p$ = .008) (Figure 3b).

The spring forcing increased through the whole period of 1951–2013 (6.41 ± 1.34 hours per year, $p$ < .001) at low elevations (Figure 3c). On the contrary, a slight decrease in spring forcing was observed during 1951–1980 at high elevations (−3.30 ± 1.86 hours per year, $p$ = .086) before it started to increase (3.65 ± 1.40 hours per year, $p$ = .013) (Figure 3d).

## 3.3 | Relative influence of winter chilling and forcing

In low-elevation regions, spring forcing had much stronger influence on the timing of leaf unfolding than winter chilling during the entire
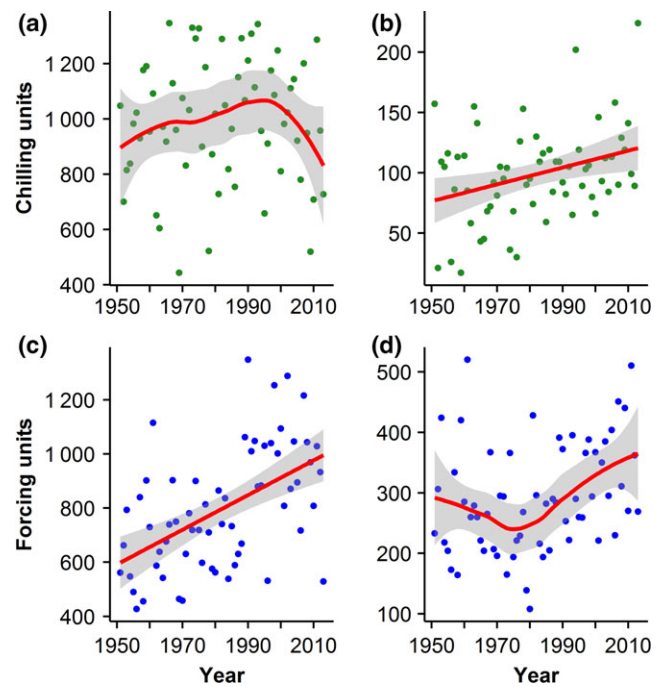
**FIGURE 3** Accumulation of chilling units in winter (from 1 November to 30 April) and forcing units in Spring (from 1 February to 30 April) in the stations at low elevations (a, c) (less than 10 m) and at high elevations (b, d) (800 to 1,000 m) between 46.8°N and 54.8°N in Europe during 1951–2013. The shaded area indicates the 95% confidence intervals [Colour figure can be viewed at wileyonlinelibrary.com]

period of 1951–2013 (Table 1a). However, the relative influence of spring forcing decreased during latter part of the period significantly at low elevations by approximately 10% (96.1% during 1951–1980
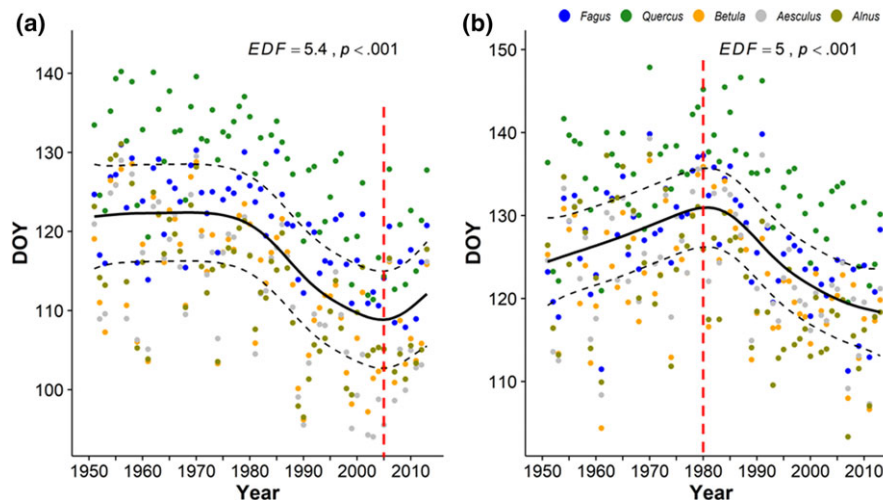
**FIGURE 2** Timing of leaf unfolding of five temperate tree species in Europe (a) at low elevations (less than 10 m) and (b) at high elevations (800 to 1,000 m) during 1951–2013. The solid and dashed black lines indicate the mean predicted values and the 95% confidence intervals, respectively. The vertical red lines indicate boundaries for periods based on the culmination points of the two respective fitted curves. EDF indicates the estimated degrees of freedom in the generalized additive mixed models. The tree species indicated by the different colors are *Fagus sylvatica*, *Quercus robur*, *Betula pendula*, *Aesculus hippocastanum* and *Alnus glutinosa* [Colour figure can be viewed at wileyonlinelibrary.com]

**TABLE 1** Relative influence of accumulation of chilling units in winter (from 1 November to 30 April) (CH) and accumulation of forcing units in spring (from 1 February to 30 April) (FO) on the timing of leaf unfolding in five tree species (a) at low elevations (<10 m) and (b) at high elevations (800 to 1,000 m) in Europe during five different periods. "CH × FO" represents the interaction term

|  | 1951–1980 | 1981–2013 | 1990–2013 |
|---|---|---|---|
| (a) Low elevation | | | |
| CH | 3.84% | 4.63% | 12.37% |
| FO | 96.12% | 95.34% | 86.53% |
| CH × FO | 0.04% | 0.03% | 1.10% |
| (b) High elevation | | | |
| CH | 3.16% | 5.96% | 3.74% |
| FO | 96.45% | 90.25% | 84.99% |
| CH × FO | 0.39% | 3.79% | 11.27% |

and 86.5% during 1990–2013; $p < .001$; Table 1a). On the contrary, the relative influence of winter chilling increased significantly at low elevations by 8.6% (3.8% during 1951–1980 and 12.4% during 1990–2013; $p < .001$; Table 1a).

The relative influence of spring forcing on the timing of leaf unfolding was also in the high-elevation regions stronger than that of winter chilling during the entire period of 1951–2013 (Table 1b). The relative influence of spring forcing decreased significantly at high elevations during the latter part of the period by approximately 11% (96.0% during 1951–1980 and 85.0% during 1990–2013; $p < .001$) (Table 1b). In contrast, the influence of the interaction between spring forcing and winter chilling increased significantly at high elevations to 11.3% since 1990 (0.4% during 1951–1980 and 11.3% during 1990–2013; $p < .001$) (Table 1b).

## 4 | DISCUSSION

The altitudinal sensitivity ($S_A$) first increased between 1951 and 1980, before it started to decrease since 1980 (Figure 1). To clarify the mechanisms underlying the increased and decreased $S_A$, we detected and quantified the trends of winter chilling and spring forcing at low- and high-elevation regions during 1951–2013. At low elevations, spring forcing increased from 1951 to 2013 (Figure 3c). However, we observed a slight decrease in the spring forcing at high-elevation regions during 1951–1980 (Figure 3d). We further calculated the relative influence of the winter chilling and spring forcing on the timing of leaf unfolding to assess their relative importance. Spring forcing had much stronger influence on the timing of leaf unfolding than winter chilling at both low- and high-elevation regions (Table 1). This suggests that chilling requirements were fulfilled in most of the years, and thus variation in leaf unfolding dates was mainly explained by variation in spring forcing. In response to the contrasting changes of spring forcing in low- and high-elevation regions, leaf unfolding was therefore correspondingly advanced, or delayed, at the two respective elevations between

1951 and 1980. This in turn led to the increased altitudinal sensitivity ($S_A$) (Figure 1).

Our finding of delayed spring phenology at high elevations between 1951 and 1980 contrasts with spring phenology advancement at high-altitude ecosystems widely reported (Hänninen, 2016; Zhang, Zhang, Dong, & Xiao, 2013), but is consistent with Yu, Luedeling, and Xu (2010) who reported delayed spring phenology in meadow and steppe vegetation on the Tibetan Plateau since 1996. However, Yu et al. (2010) attributed this delayed spring phenology to the reduced winter chilling as a result of winter warming, rather than to decreased spring forcing.

Since 1980, the relative influence of spring forcing on the timing of leaf unfolding was at low elevations still greater than that of winter chilling, as was also previously (Table 1a). However, with the decrease in winter chilling at low elevations (Figure 3a), after 1990 the relative influence of spring forcing has decreased and that of winter chilling increased by approximately 10% and 8.6% respectively (Table 1a). Therefore, although the overall role of the spring forcing was greater than winter chilling during the whole period of 1951–2013, winter chilling may have taken over spring forcing after 2005. According to this reasoning, the leaf unfolding advanced until 2005 because of increased spring forcing (Figure 3c) but after that it was delayed, possibly due to reduced winter chilling (Figure 3a).

In contrast to low-elevation regions, in high-elevation regions both winter chilling (Figure 3b) and spring forcing (Figure 3d) increased significantly since 1980. Therefore, leaf unfolding was advanced since 1980 (Figure 2b). Furthermore, the influence of the interaction between spring forcing and winter chilling increased significantly to 11.3% since 1990 (Table 1b). This finding suggests that since 1990 spring forcing at high elevations might play a more efficient role in initiating the leaf unfolding due to increased winter chilling. In other words, less spring forcing is required to initiate the leaf unfolding when more winter chilling is perceived by the trees. As a consequence, temperature sensitivity can be greater at high than at low elevations, that is, a greater shift of phenology is induced at high than at low elevations by even a slight climate warming. Therefore, during 1990–2013, the shifting rate of leaf unfolding was also higher at high-elevation regions ($-0.38 \pm 0.07$ days per year, $p < .001$; Figure 2b) than at low-elevation regions ($-0.13 \pm 0.08$ days per year, $p = .09$; Figure 2a). In all, then, the altitudinal sensitivity $S_A$ was reduced during 1990–2013 (Figure 1).

Vitasse et al. (2018) reported a reduced $S_A$ of spring leaf unfolding of four different temperate tree species in 128 sites in the European Alps. Contrary to our results, the $S_A$ started to decrease since 1960, with a rate of $-0.23 \pm 0.03$ day 100/m per decade, and did not show an increase before it started to decrease (Vitasse et al., 2018). When only analyzing the $S_A$ based on the phenological sites located in Switzerland, we also found a significant increase in the $S_A$ ($0.46 \pm 0.11$ day 100/m per decade; $p < .001$) between 1951 and 1980, followed by a declining trend after 1980 ($-0.71 \pm 0.10$ day 100/m per decade; $p < .001$) (Figure S4). If we considered the period between 1960 and 2013, a similar period to Vitasse et al. (2018), the $S_A$ decreased with a rate of $-0.18 \pm 0.05$ day 100/m per

decade (Figure S4), a bit lower than the reported result ($-0.23 \pm 0.03$ day 100/m per decade) in Vitasse et al. (2018). The contrasting findings of our study and those of Vitasse et al. (2018) suggest that the responses of spring phenology to climate change at different altitudes may vary among species and regions. It is therefore important to conduct further research to comprehensively elucidate the elevational shifts of spring phenology under global warming.

Understanding the long-term changes in spring phenology along the altitudinal gradient is critical for clarifying and predicting the impacts of climate warming on terrestrial ecosystems. On the basis of long-term and large-scale ground observations, we discovered a divergence in the timing of leaf unfolding between low-elevation and high-elevation regions, which in turn led to a nonlinear trend in the altitudinal sensitivity $S_A$ in spring leaf unfolding. The nonlinear response of spring phenology of temperate trees to climate change depends in a complicated way on the changes of chilling and forcing temperatures at the various altitudes. It is therefore important to incorporate the elevation-dependent spring phenology into current dynamic vegetation models for a precise prediction of the impacts of climate change on the structure and functioning of temperate forest ecosystems under future warming scenarios.

## ORCID

*Lei Chen* ORCID http://orcid.org/0000-0001-7011-8782
*Jian-Guo Huang* ORCID http://orcid.org/0000-0003-3830-0415
*Qianqian Ma* ORCID http://orcid.org/0000-0001-9399-9375
*Heikki Hänninen* ORCID http://orcid.org/0000-0003-3555-2297
*Shilong Piao* ORCID http://orcid.org/0000-0001-8057-2292

## REFERENCES

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). *lme4: Linear mixed-effects models using Eigen and S4. R package version1*, 1-23.

Chuine, I. (2010). Why does phenology drive species distribution? *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *365*, 3149–3160. https://doi.org/10.1098/rstb.2010.0142

Cory, S. T., Wood, L. K., & Neufeld, H. S. (2017). Phenology and growth responses of Fraser fir (Abies fraseri) Christmas trees along an elevational gradient, southern Appalachian Mountains, USA. *Agricultural and Forest Meteorology*, *243*, 25–32. https://doi.org/10.1016/j.agrformet.2017.05.003

Edwards, M., & Richardson, A. J. (2004). Impact of climate change on marine pelagic phenology and trophic mismatch. *Nature*, *430*, 881–884. https://doi.org/10.1038/nature02808

Fu, Y. H., Zhao, H., Piao, S., Peaucelle, M., Peng, S., Zhou, G., . . . Janssens, I. A. (2015). Declining global warming effects on the phenology of spring leaf unfolding. *Nature*, *526*, 104–107. https://doi.org/10.1038/nature15402

Grömping, U. (2006). Relative importance for linear regression in R: The package relaimpo. *Journal of Statistical Software*, *17*, 1–27.

Guyon, D., Guillot, M., Vitasse, Y., Cardot, H., Hagolle, O., Delzon, S., & Wigneron, J.-P. (2011). Monitoring elevation variations in leaf phenology of deciduous broadleaf forests from SPOT/VEGETATION time-series. *Remote Sensing of Environment*, *115*, 615–627. https://doi.org/10.1016/j.rse.2010.10.006

Hänninen, H. (2016). *Boreal and temperate trees in a changing climate*. Dordrecht, the Netherlands: Springer. https://doi.org/10.1007/978-94-017-7549-6

Hänninen, H., & Tanino, K. (2011). Tree seasonality in a warming climate. *Trends in Plant Science*, *16*, 412–416. https://doi.org/10.1016/j.tplants.2011.05.001

IPCC (2014). *Climate change 2014: Mitigation of Climate Change: Working Group III Contribution to the IPCC Fifth Assessment Report*, Cambridge University Press.

Körner, C., & Basler, D. (2010). Phenology under global warming. *Science*, *327*, 1461–1462. https://doi.org/10.1126/science.1186473

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. *Journal of Experimental Social Psychology*, *49*, 764–766. https://doi.org/10.1016/j.jesp.2013.03.013

Linvill, D. E. (1990). Calculating chilling hours and chill units from daily maximum and minimum temperature observations. *HortScience*, *25*, 14–16.

Luedeling, E., Kunz, A., & Blanke, M. M. (2013). Identification of chilling and heat requirements of cherry trees—a statistical approach. *International Journal of Biometeorology*, *57*, 679–689. https://doi.org/10.1007/s00484-012-0594-y

Meier, U. (1997). *Growth stages of mono-and dicotyledonous plants*. Berlin, Germany: Blackwell Wissenschafts-Verlag.

Pepin, N., Bradley, R. S., Diaz, H. F., Baraer, M., Caceres, E. B., Forsythe, N., . . . Yang, D. Q. (2015). Elevation-dependent warming in mountain regions of the world. *Nature Climate Change*, *5*, 424–430.

R Core Team (2015). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

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. https://doi.org/10.1016/j.agrformet.2012.09.012

Templ, B., Koch, E., Bolmgren, K., Ungersböck, M., Paul, A., Scheifinger, H., . . . Zust, A. (2018). Pan European Phenological database (PEP725): A single point of access for European data. *International Journal of Biometeorology*, https://doi.org/10.1007/s00484-018-1512-8

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*, *115*, 1004–1008. https://doi.org/10.1073/pnas.1717342115

Wood, S. N. (2017). *Generalized additive models: An introduction with R*. Boca Raton, FL: CRC Press.

Wood, S., & Scheipl, F. (2013). *gamm4: Generalized additive mixed models using mgcv and lme4. R package version 0.2-2*. Retrieved from http://CRAN. R-project. org/package= gamm4.

Yu, H., Luedeling, E., & Xu, J. (2010). Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proceedings of the National Academy of Sciences*, 107, 22151–22156. https://doi.org/10.1073/pnas.1012490107

Zhang, G., Zhang, Y., Dong, J., & Xiao, X. (2013). Green-up dates in the Tibetan Plateau have continuously advanced from 1982 to 2011. *Proceedings of the National Academy of Sciences*, 110, 4309–4314. https://doi.org/10.1073/pnas.1210423110

Zohner, C. M., & Renner, S. S. (2014). Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecology Letters*, 17, 1016–1025. https://doi.org/10.1111/ele.12308

## SUPPORTING INFORMATION

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