





Climate warming increases spring phenological differences among temperate trees

Xiaojun Geng¹  | Yongshuo H. Fu^{1,2}  | Fanghua Hao¹ | Xuancheng Zhou¹ | Xuan Zhang¹ | Guodong Yin¹ | Yann Vitasse³ | Shilong Piao^{4,5,6}  | Kechang Niu⁷ | Hans J. De Boeck² | Annette Menzel⁸ | Josep Peñuelas^{9,10} 

¹College of Water Sciences, Beijing Normal University, Beijing, China

²Plants and Ecosystems, Department of Biology, University of Antwerp, Antwerp, Belgium

³Swiss Federal Institute for Forest, Snow and Landscape Research (WSL), Birmensdorf, Switzerland

⁴College of Urban and Environmental Sciences, Sino-French Institute for Earth System Science, Peking University, Beijing, China

⁵Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing, China

⁶Center for Excellence in Tibetan Earth Science, Chinese Academy of Sciences, Beijing, China

⁷School of Life Science, Nanjing University, Nanjing, China

⁸TUM School of Life Sciences, Ecoclimatology, Technical University of Munich, Freising, Germany

⁹CREAF, Barcelona, Spain

¹⁰CSIC, Global Ecology Unit CREAF-CSIC-UAB, Barcelona, Spain

Correspondence

Yongshuo H. Fu, College of Water Sciences, Beijing Normal University, Beijing 100875, China.

Email: yfu@bnu.edu.cn

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Abstract

Climate warming has substantially advanced spring leaf flushing, but winter chilling and photoperiod co-determine the leaf flushing process in ways that vary among species. As a result, the interspecific differences in spring phenology (IDSP) are expected to change with climate warming, which may, in turn, induce negative or positive ecological consequences. However, the temporal change of IDSP at large spatiotemporal scales remains unclear. In this study, we analyzed long-term in-situ observations (1951–2016) of six, coexisting temperate tree species from 305 sites across Central Europe and found that phenological ranking did not change when comparing the rapidly warming period 1984–2016 to the marginally warming period 1951–1983. However, the advance of leaf flushing was significantly larger in early-flushing species EFS (6.7 ± 0.3 days) than in late-flushing species LFS (5.9 ± 0.2 days) between the two periods, indicating extended IDSP. This IDSP extension could not be explained by differences in temperature sensitivity between EFS and LFS; however, climatic warming-induced heat accumulation effects on leaf flushing, which were linked to a greater heat requirement and higher photoperiod sensitivity in LFS, drove the shifts in IDSP. Continued climate warming is expected to further extend IDSP across temperate trees, with associated implications for ecosystem function.

KEYWORDS

climate change, interspecific differences in spring phenology, phenological shift, photoperiod, temperature sensitivity

1 | INTRODUCTION

Climate warming impacts terrestrial ecosystem carbon and water cycles (Bradley, Leopold, Ross, & Huffaker, 1999; Cannell & Smith, 1986; Chuine, 2010; Snyder & Spano, 2013) over the long term, partly due to earlier spring leaf flushing in temperate and boreal deciduous forests (Basler & Körner, 2014; Chuine, 2010; Fu, Piao, et al., 2019; Fu, Zhang, et al., 2019; Laube et al., 2014; Menzel et al., 2020). The timing of spring leaf flushing is one of the most sensitive and visible bio-indicators of ongoing climate change (Kharouba et al., 2018; Van Asch & Visser, 2007; Zohner, Benito, Svenning, & Renner, 2016) because it is principally controlled by temperature (Peñuelas, Rutishauser, & Filella, 2009; Zohner, Mo, & Renner, 2018). However, other factors, such as winter low temperature (or chilling accumulation; Keenan et al., 2014; Piao et al., 2019), and photoperiod (day length; Chuine, 2010; Körner & Basler, 2010), also affect the timing of leaf flushing and their importance may increase under further warming (Menzel, Sparks, Estrella, Koch, et al., 2006; Menzel et al., 2020). Species differences in forcing, chilling, and photoperiodic requirements (Chuine et al., 2016; Fu et al., 2014; Keenan et al., 2014) may result in altered interspecific time differences in leaf flushing phenology (IDSP), which may ultimately alter the sequence in time of leaf flushing ("ranking," previously also known as interception; Peñuelas et al., 2009) among the different species. There are three theoretical shifts in IDSP between early and late flushing species (Vitasse, Lenz, Hoch, & Körner, 2014; called hereafter EFS and LFS, respectively, ranking based on the timing of leaf-out) from current to future climatic conditions (Figure S1a): stable IDSP, where leaf flushing advance is similar between EFS and LFS (Figure S1b); reduced IDSP between EFS and LFS, due to greater leaf flushing advance for LFS than EFS (Figure S1c); and extended IDSP between EFS and LFS, due to greater leaf flushing advance for EFS than LFS (Figure S1d).

Changes in IDSP may elicit ecological perturbations. For example, plant competition may change, as species with greater advance in leaf flushing may profit from a longer growing season, shade competitors with later flushing and thus gain a competitive advantage providing that they can still avoid damaging late spring frost events. Changes in competitive relationships or trophic mismatches could further influence resource allocation and structural adjustment of the ecosystem, eventually altering terrestrial carbon and water cycling. For example, leaf phenology directly affects the light and water requirements in the forest canopy and understory, which further determines the photosynthetic efficiency and carbon uptake and metabolism (Cleland, Chuine, Menzel, Mooney, & Schwartz, 2007; Peñuelas et al., 2009; Schwartz, 1998). Reductions in spatial variation of leaf flushing have been reported across Central Europe within species both across elevations (Vitasse, Signarbieux, & Fu, 2018) and latitudes (Ma, Huang, Hänninen, & Berninger, 2018), which was also confirmed by remote sensing analyses associated with climatic warming across the Northern hemisphere (Liu et al., 2019). However, temporal changes in IDSP among species have been little studied (but see Peñuelas & Filella, 2001; Roberts, Tansey, Smithers, &

Phillimore, 2015) despite their importance in understanding ecosystem responses to ongoing climate change.

Therefore, we investigated the IDSP among six common, coexisting tree species, three of them EFS and three LFS, across 305 Central European sites with temperate forest tree species (Figure S2). The aim of our study was to determine and quantify temporal changes and associated physiological and climatic drivers in leaf flushing IDSP among the six species during the period 1951–2016.

2 | MATERIALS AND METHODS

2.1 | Datasets

Leaf flushing data for EFS *Betula pendula* (BP, European silver birch), *Aesculus hippocastanum* (AH, horse chestnut), and *Alnus glutinosa* (AG, European alder), and LFS *Fagus sylvatica* (FS, European beech), *Quercus robur* (QR, Pedunculate oak), and *Fraxinus excelsior* (FE, European ash) co-occurring in Central European sites during the period 1951–2016 were obtained from the open access Pan European Phenology network (www.pep725.eu). The recorded date mostly represents the phenological development of a group of two to three individuals per site; however, only one (flushing) date per species and site is recorded (DWD, 1991). Datasets comprised a minimum of 30 years over the period 1951–2016, representing 15 years in each of two 33-year periods (mild warming period of 1951–1983 and pronounced warming period of 1984–2016, Figure S3), for all six species at each site. Data $> 2 \times SD$ (standard deviation of the mean leaf flushing date) were excluded to discard possible errors, which account for 3.8% in EFS and 4.0% in LFS during 1951–2016, distributed randomly. Similar results without data reduction were found (Figure S4). In total, we selected data for 305 sites (Figure S2), to which a gridded climatic dataset was applied, with a spatial resolution of 0.25° (approximately 25 km; Beer et al., 2014), comprising daily mean air temperature, precipitation, and radiation measurements (Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015). We further tested the reliability of the results using the well-known Princeton climatic dataset, at 0.25° spatial resolution (<http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>), and very similar results were found (Figure S5).

2.2 | Analysis

We analyzed spring warming as the mean value and the corresponding *SD* of the air temperature during the temperature-relevant period (TRP). TRP was calculated as the period before leaf flushing with the highest absolute partial correlation between leaf flushing date and mean air temperature. Considering the differences among species and sites in responding to climate change, different TRPs were used for each species and site (Figure S6), like in earlier analyses (Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015), ranging from 15 to 120 days, with 15 day steps. We investigated the TRP variation with latitudes (Figure S6). The mean length of TRP was 59 days prior to the day of

leaf flushing, but a large variation was found among sites and species, with TRP decreasing with increasing latitudes (Figure S6), thus showing the robustness of the location-specific application of the TRP in the present study.

Apparent temperature sensitivity (S_T) was defined as the number of advanced days per 1°C of warming, which has been widely used to evaluate the long-term implications of temperature changes for plant phenology. The S_T was determined by reduced major-axis regression between leaf flushing date and mean air temperature during the TRP (Keenan, Richardson, & Hufkens, 2019). To validate the results, we also used daily maximum temperatures to analyze TRP and apparent sensitivities of leaf flushing to maximum temperature during TRP ($S_{T_{max}}$). Similar results were found (Figure S7).

Chilling accumulation breaks dormancy in deciduous tree species and heat accumulation leads to leaf flushing, so their metrics have been widely used to estimate the physiological requirement of spring leaf flushing in temperate woody species. Chilling requirement (CD_{req}) was defined as the number of days with non-freezing mean air temperature (generally between 0 and 5°C) during the period 1 November to the mean leaf flushing date:

$$CD_{req}(t) = \sum_{t_0}^{LO} 1 \quad \text{if } 0 \leq T_t \leq T_{high},$$

where t_0 is the start date of chilling accumulation (fixed at 1 November before the year of leaf flushing), LO is the mean leaf flushing date, T_t is the mean daily air temperature, and T_{high} is the upper limit of the temperature threshold (generally 5°C or 8°C). We tested the same calculation by setting the temperature threshold within 0°C–8°C and tested 1 September as start date (Figure S8); In addition, because the correlation between chilling and forcing is still unclear, to test the robustness of the chilling estimation, we also calculated the chilling accumulation by fixing the time period from 1 November to 31 December (Figure S8d). This led to very similar results, so we reported the results using the threshold of 5°C and 1 November until the start date of leaf flushing.

The heat requirement for leaf flushing was defined as the growing degree days (GDD), calculated as the sum of mean air temperature above a temperature threshold from 1 January to leaf flushing date. We used three common methods as follows:

1. Linear function, using a base temperature of 5°C:

$$GDD = \sum_{t_0}^{LO} (T_t - 5) \quad \text{if } T_t \geq 5.$$

2. Piecewise function, using a temperature threshold of 5°C and 15°C, and fixed units when temperature was above 15°C:

$$GDD = \sum_{t_0}^{LO} \begin{cases} 0 & \text{if } T_t < 5 \\ T_t - 5 & \text{if } 5 \leq T_t \leq 15 \\ 10 & \text{if } T_t > 15. \end{cases}$$

3. Sigmoidal function, using a base temperature of 0°C:

$$GDD = \sum_{t_0}^{LO} \begin{cases} 0 & \text{if } T_t < 0 \\ \frac{28.4}{1 + e^{-0.185(T_t - 18.4)}} & \text{if } T_t \geq 0, \end{cases}$$

where t_0 is the start date of GDD calculation, fixed at 1 January, LO is the leaf flushing date, and T_t is daily mean air temperature. The three methods produced similar results, so we only reported the results of the linear function in the main text and reported the results of the other two functions in the appendix (Figure S9).

2.3 | Statistical analysis

We then determined the frequency distributions of main variables (difference in leaf flushing dates/temperature sensitivity/chilling accumulation/GDD requirements between EFS and LFS or between 1951–1983 and 1984–2016), and plotted in histograms. For each species, we applied paired t tests to detect whether the average flushing date and its variance changed significantly between time periods. To adequately model the structure in the data (e.g., site locations, species, years), we adopted the mixed-effect models using lmerTest package in R3.5.2 (Phillimore, Leech, Pearce-Higgins, & Hadfield, 2016), by setting leaf flushing dates, temperature sensitivity, chilling accumulation, and GDD requirements as response variables, setting time period (1951–1983 vs. 1984–2016) and grouping of species (EFS vs. LFS) as fixed effects, and setting sites (including latitude, longitude, and elevation), species, and years as random effects (Table S1). We also analyzed the number of sites in which species phenological shift occurred and the direction of change, and presented the results through CIRCOS figures (Figure 1c) by <http://mkweb.bcgsc.ca/tableviewer/>.

3 | RESULTS

The mean leaf flushing date over the period 1951–2016 was 21 April (day of year: 111 ± 6 , mean \pm SD across sites and species) for the EFS BP, AH, and AG, and 4 May (day of year: 124 ± 5) for the LFS FS, QR, and FE (Figure 1a). Thus, there was a difference of 13 days in mean leaf flushing dates between EFS and LFS. Variation in mean leaf flushing date (measured as the standard deviation of leaf flushing date over the study period, $1 \times$ SD) tended to be greater for EFS (9.4 ± 2.5 days) than for LFS (7.8 ± 2.0 days; $p < .05$, Figure 1a). We found that the advance in leaf flushing date across the six temperate tree species increased from 0.9 ± 0.7 days (mean \pm SE) during the period 1951–1983 to 13.5 ± 0.7 days during the period 1984–2016, when climate warming accelerated (the species-specific temporal changes in leaf flushing dates across all sites between the two time periods which are shown in Table S2 and Figure S10), supporting previous reports (Fu, Zhang, et al., 2019; Menzel, 2013). Trends of vegetative spring development over 30-year moving periods

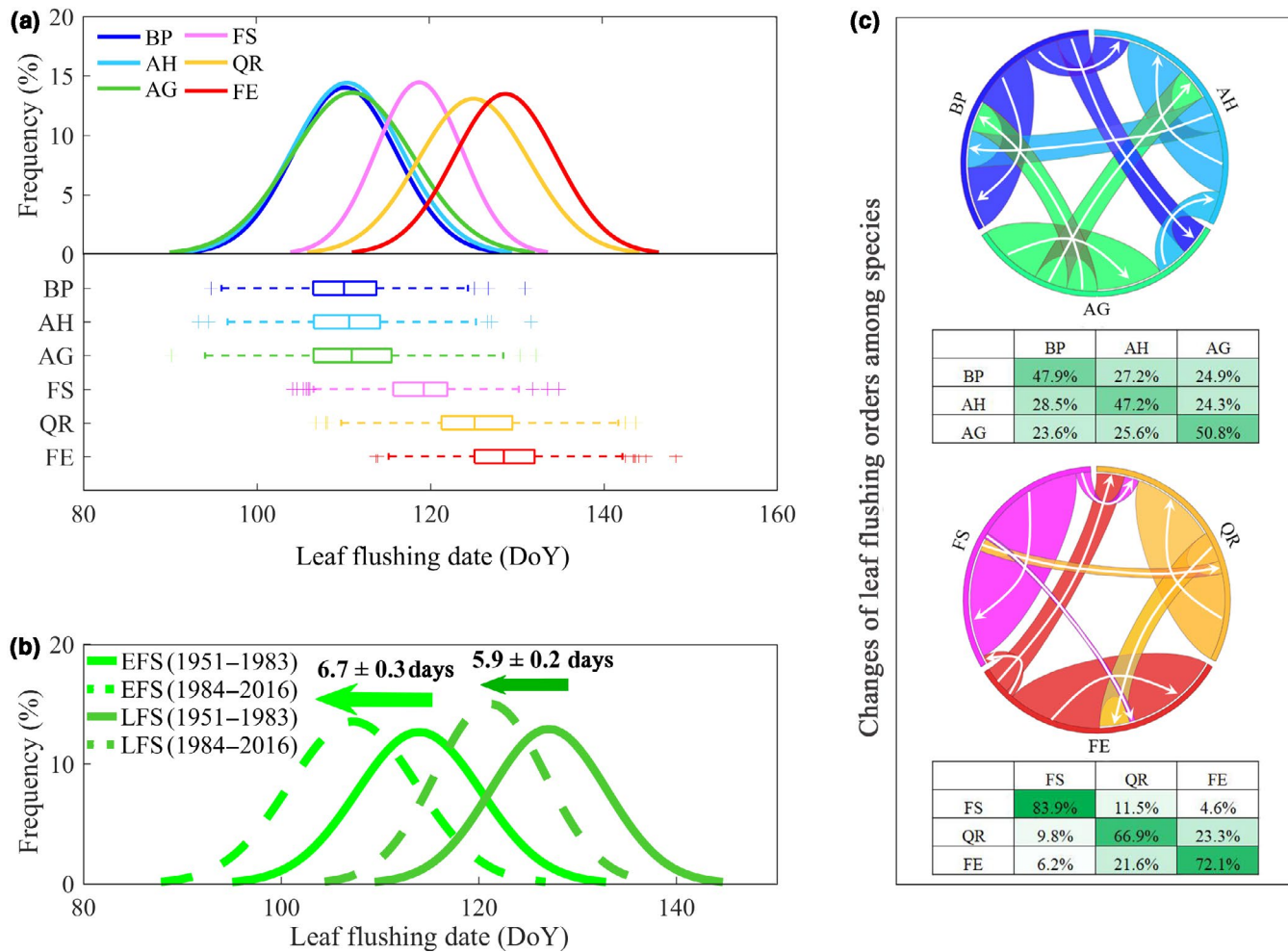


FIGURE 1 Distribution of mean leaf flushing dates in early and late flushing species (early flushing species [EFS] and late flushing species [LFS], respectively) and changes in leaf flushing orders. (a) Distribution of leaf flushing for each species during the period 1951–2016. (b) Direction and magnitude of phenological shift (indicated by arrow direction and length) in leaf flushing dates of EFS and LFS. (c) Direction and proportion of changes in leaf flushing orders across 305 sites within EFS and LFS. The arrow indicates the direction of changes in leaf flushing orders among species within group. Each value in the tables indicate the percentage of sites where the leaf flushing order of the two species in the corresponding row and column is interchanged. AG, *Alnus glutinosa*; AH, *Aesculus hippocastanum*; BP, *Betula pendula*; FE, *Fraxinus excelsior*; FS, *Fagus sylvatica*; QR, *Quercus robur*

suggest that the maximum delays ($\sim +0.15$ days/year) were recorded for 1951–1986 and the strongest advances for 1975–2004 (~ -0.5 days/year) followed by 1982–2011 (Menzel et al., 2020); thus, these numbers for all fruit trees and wild plant species support the findings of the six temperate tree species. Although the magnitudes of advance differed among the six species, the overall phenological ranking remained stable over the period 1951–2016 (Figure S10) while site-specific shifts in ranking occurred at 49.2%–52.8% of sites for EFS and 16.1%–33.1% of sites for LFS (Figure 1c). When compared the leaf flushing dates between 1951–1983 and 1984–2016, we found a greater magnitude of advancement in the EFS (mean \pm SE: 6.7 ± 0.3 days) than in the LFS (5.9 ± 0.2 days; Figure 1b, mixed-effect model was applied including sites and species as random effects: $p < .001$), confirming an enlarged IDSP between 1951–1983 and 1984–2016. This finding is largely consistent with Menzel et al. (2020) who reported more strongly advancing trends of vegetative spring development prior to week 12 of the

year but comparable advances of the weeks 16–18 matching mean EFS and LFS dates.

4 | DISCUSSION

To explain our finding of an extended IDSP, but a general stable rank order of leaf flushing among the six species, we propose four mutually non-exclusive hypotheses: (a) difference in seasonal warming, since warming may be stronger during earlier spring than in later spring; (b) difference in temperature sensitivity, where temperature sensitivity to leaf flushing may be greater in EFS than LFS (Menzel, Estrella, & Fabian, 2001; Menzel, Sparks, Estrella, & Roy, 2006); (c) interaction between chilling effects and heat requirements among species, where chilling effects are similar due to identical winter conditions, but LFS may have greater heat requirement than EFS (Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015); and (d) differences in

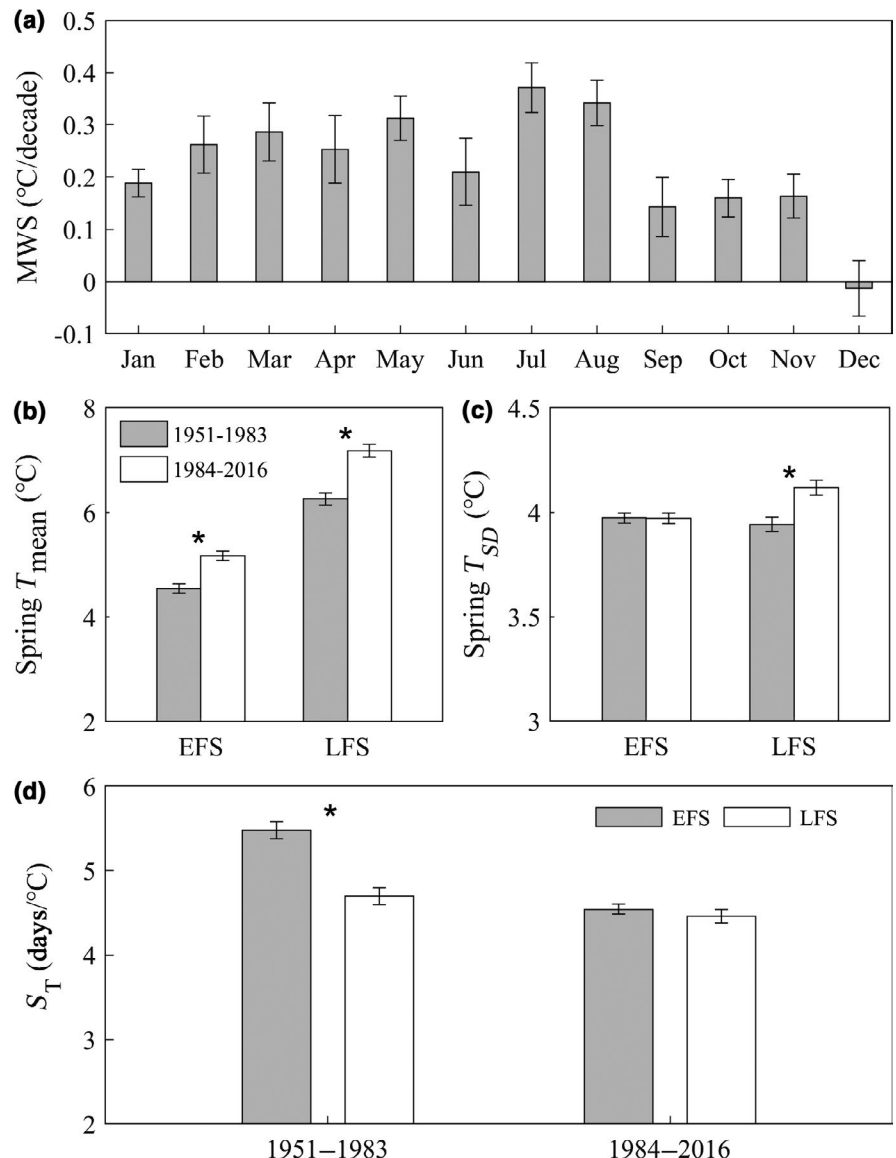
photoperiod and water limitation among species, where sensitivity to photoperiod and water shortage may be greater in LFS than EFS (Chuine, 2010; Cleland et al., 2007), leading to a smaller advance in LFS under climate warming.

To test the first hypothesis, we analyzed monthly warming trends over the study period, but did not find early spring (February and March) significantly more strongly warming ($p > .05$) than later spring (April and May); in contrast, climate warming in May was greater than in February and March (Figure 2a). Next, we estimated mean temperature and its variability ($1 \times SD$) during the most TRP (see Section 2) for leaf flushing during the periods 1984–2016 and 1951–1983, and found increased temperatures during the TRP for both groups of tree species (EFS and LFS), but in contrast to the hypothesis, because the increase was greater in LFS (mean increase: 0.9°C) than in EFS (mean increase: 0.7°C ; Figure 2b). Variation in temperature during the most relevant period remained stable for EFS, but increased for LFS (Figure 2c). A higher fluctuated temperature may constrain advances of leaf flushing of LFS to avoid frost

damages (Zohner, Benito, Fridley, Svenning, & Renner, 2017). These results indicate that the climate variation, more than warming, may drive the extended time difference in leaf flushing between EFS and LFS, assuming that the temperature sensitivity of EFS and LFS was identical.

It is more likely that sensitivity to temperature changes is greater in EFS than in LFS to enable competitive advantages, although earlier leaf flushing may also increase the risk of late frost damage (Inouye, 2008; Richardson et al., 2018). Therefore, a greater advancement in leaf flushing may be expected in EFS, given stable warming trends. Indeed, we found significantly larger S_T (apparent temperature sensitivity) of leaf flushing in EFS than in LFS (3.8 ± 0.1 and 2.9 ± 0.1 days/ $^\circ\text{C}$, respectively) during the period 1951–1983 ($p < .05$, mixed-effect model was applied including sites and species as random effects); however, S_T was significantly reduced to 2.9 ± 0.1 days/ $^\circ\text{C}$ in EFS during the period 1984–2016, but remained stable in LFS. As a result, there was no overall difference in S_T between EFS and LFS during the recent period 1984–2016

FIGURE 2 Temporal changes of temperature and leaf flushing sensitivity to temperature (S_T). (a) Mean monthly warming rates across all sites during the period 1951–2016. Mean monthly warming rate was calculated using linear regression between mean monthly temperature and year. (b) Mean spring temperature during the temperature-relevant period (TRP; Spring T_{mean}) over the periods 1951–1983 and 1984–2016 for early and late flushing species (early flushing species [EFS] and late flushing species [LFS], respectively). (c) Changes of spring temperature variance (T_{SD}) during the TRP over the periods 1951–1983 and 1984–2016 for EFS and LFS. (d) Temperature sensitivity of leaf flushing (S_T) for EFS and LFS between 1951–1983 and 1984–2016, determined by reduced major-axis regression. Asterisks indicate differences at $p < .05$



(Figure 3d, mixed-effect model: $p = .14$). Reduced S_T in EFS and a trend toward higher temperatures at leaf flushing in LFS rather than in EFS (Figure 2b) did not explain the extended time difference in leaf flushing between the two groups, because a warmer late spring and similar S_T for EFS and LFS during the period 1984–2016 should have led to the greater advancement in leaf flushing for LFS.

The third hypothesis relates to physiological processes associated with chilling and subsequent heat requirements for spring leaf flushing. Climate warming may reduce the plants' ability to fulfill the amount of chilling that is required to break dormancy in many temperate tree species (Hänninen, 2016; Piao et al., 2019), with the consequence that greater heat is required to trigger leaf flushing (Cannell & Smith, 1983; Fu, Piao, et al., 2015; Fu, Zhao, et al., 2015). EFS and LFS experience the same length of chilling days during the winter, but EFS and LFS experience different amounts of chilling accumulation

during the spring. Our data support this hypothesis, because the difference in chill days between EFS and LFS during the period 1951–1983 (2.0 ± 0.1 days) was not significantly different from the period 1984–2016 (1.8 ± 0.1 days; Figure 3a, $p = .62$, mixed-effect model was applied including sites and species as random effects), but species' heat requirements, defined as GDD (see Section 2), were negatively related to chilling accumulation and significantly increased in both EFS (1951–1983: $113.1 \pm 1.9^\circ\text{C}$; 1984–2016: $118.2 \pm 2.0^\circ\text{C}$) and LFS (1951–1983: $173.2 \pm 2.5^\circ\text{C}$; 1984–2016: $183.4 \pm 2.7^\circ\text{C}$; Figure 3b). This larger increase in GDD in LFS led to increased differences in GDD requirements between the two groups (1951–1983: $60.1 \pm 1.0^\circ\text{C}$; 1984–2016: $65.3 \pm 1.1^\circ\text{C}$; Figure 3b, $p < .01$). The time required to accumulate an increased GDD in LFS may subsequently result in a smaller advance in leaf flushing in LFS and extend the time difference in leaf flushing between the two groups. Thus, the extended IDSP is likely to occur due to the asymmetric increase in heat requirements between EFS and LFS.

Our fourth hypothesis relates to effects of photoperiod on the leaf flushing process that may vary with species due to genotype and ontogeny (Chuine et al., 2016; Flynn & Wolkovich, 2018; Richardson, Hufkens, Li, & Ault, 2019; Yang & Rudolf, 2010); for example, it has been suggested that LFS rely on photoperiod to a greater extent than EFS (Van Asch & Visser, 2007). We found that climate warming advanced leaf flushing, so the effects of a resulting shorter photoperiod on the leaf flushing process may have increased in both EFS and LFS, but larger in LFS, and thus led to a relatively shorter advancement in leaf flushing date. Since it was not possible to assess direct effects of photoperiod in this study, we estimated changes in variation of leaf flushing dates for both EFS and LFS between the two study periods as a surrogate measure, because a higher photoperiod effect is likely to be associated with a lower variation in flushing dates (the variation of flushing dates was defined as one standard deviation: $1 \times \text{SD}$, LO_{SD}). We found that the LO_{SD} tended to be lower during the period 1984–2016 (EFS: 7.4 ± 1.8 days; LFS: 5.9 ± 1.6 days) than during 1951–1983 (EFS: 8.1 ± 1.7 days; LFS: 6.1 ± 1.5 days; Figure 3c) for both EFS and LFS, but the reduction was significantly lower in LFS (0.2 ± 0.1 days) than in EFS (0.7 ± 0.1 days), suggesting a larger photoperiod effect in LFS. To further test the photoperiod limitation hypothesis, we investigated the correlation between latitude and IDSP comparing EFS and LFS, as well as the species-specific variation of advanced leaf flushing date along latitude. Interestingly, we found the IDSP was significantly reduced at lower latitudes across all species (Figure 4), and the flushing dates advanced more at higher latitudes for each species ($p < .05$, Figure S11). The significant reduction in advancement at low latitudes suggested that photoperiod likely limits the advancement at the low latitudes, rather than at high latitudes, to constrain too early leaf flushing, similarly also shown for spring vegetative development in general (see Menzel et al., 2020). Furthermore, a relatively smaller advancement in leaf flushing was found at higher latitudes for LFS than EFS, which may be because LFS is more sensitive to photoperiod than EFS at higher latitudes. These results

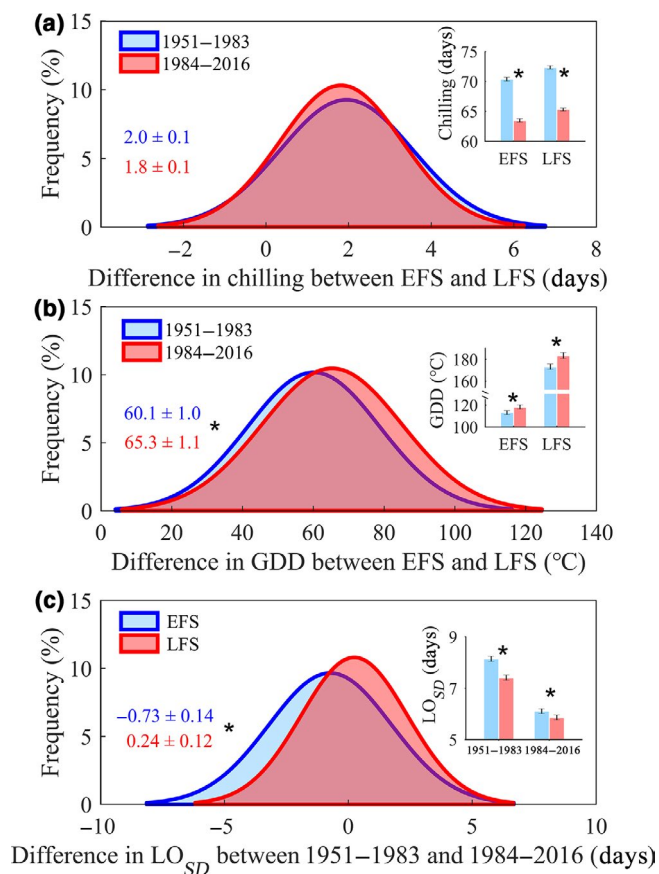


FIGURE 3 Changes in chilling and heat accumulation, as well as standard deviation of leaf flushing dates (LO_{SD}) between 1951–1983 and 1984–2016 in early and late flushing species (early flushing species [EFS] and late flushing species [LFS]). (a) Difference in chilling accumulation between EFS and LFS, which was calculated as the number of days when mean air temperature was $<5^\circ\text{C}$ from 1 November until leaf flushing date. (b) Difference in growing degree days (GDD) between EFS and LFS, which was calculated as the sum of mean air temperatures $>5^\circ\text{C}$ from 1 January until leaf flushing date. Numbers in blue and red font are means \pm SE for 1951–1983 and 1984–2016, respectively. (c) Difference in LO_{SD} between 1951–1983 and 1984–2016 for EFS and LFS. Asterisks indicate differences at $p < .05$

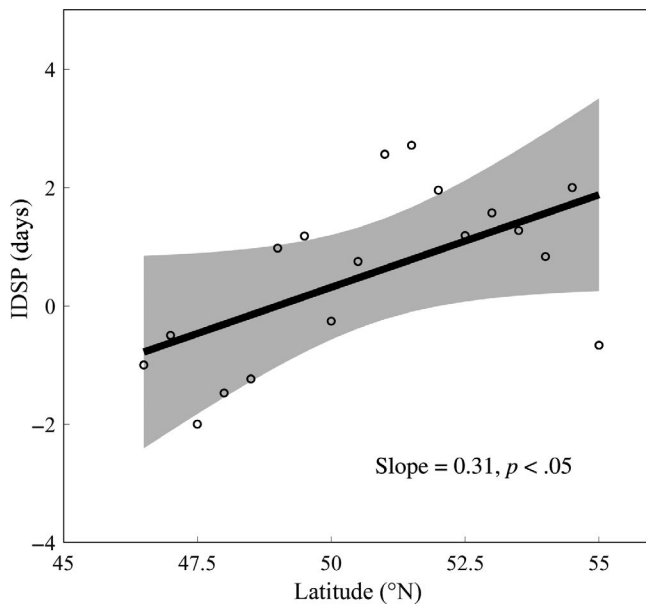


FIGURE 4 The interspecific differences in leaf flushing date (IDSP) between early and late flushing species (early flushing species and late flushing species) varied along latitudes. All the sites were averaged every 0.5 degree along the latitude gradient

suggest that the extended IDSP difference between EFS and LFS may partially explained by the photoperiod. In addition, within forests, earlier flushing of EFS may increase the water stress for LFS (Bradley et al., 1999; Spano, Snyder, & Cesaraccio, 2013), and thus postpone the date of leaf flushing of LFS (Spano et al., 2013). However, annual precipitation over the study area is larger than 700 mm (EEA, 2012), and the difference in precipitation sum over the TRP between EFS and LFS was insignificant (Figure S12). This suggests that effects of water shortage on spring leaf-out for LFS were unlikely, rendering a contribution to the extended IDSP between EFS and LFS improbable.

Phenological sensitivity to environmental changes is a strategy of temperate trees to optimize growth in regard to climatic fluctuations. Our results provide empirical evidence for an overall stability in phenological ranking among temperate tree species in Central Europe over the past six decades. Interestingly, we found that differences in phenological responses between EFS and LFS under rapid warming resulted in a significantly extended IDSP. Plant phenology plays a key role in ecosystem structure and function, and changes in IDSP are likely to elicit ecological consequences (Cleland et al., 2007; Van Asch & Visser, 2007; Vitasse et al., 2018). The advancement in leaf flushing in EFS may be exacerbated under future climate warming conditions to a greater extent than in LFS so that EFS may benefit from a longer growing season and gain a competitive advantage over LFS in light and water accessibility. Shifts in IDSP may also affect trophic interactions because of the reliance of many vertebrates on leaf-feeding insects for food. However, great variation exists in the speed of phenological adjustments of insects, possibly leading to trophic synchrony disruption (Gaudry et al., 2015; Renner & Zohner, 2018). Further studies are warranted to confirm these results for

different tree species and in different climate zones, especially in regions with larger climatic ranges, such as North America and Alpine ecosystems.

Under future climate warming conditions, differences in timing of spring leaf flushing among species may continue to increase, and may result in a change in the order of spring phenology in temperate forests, especially due to species-specific chilling requirement, as argued by Roberts et al. (2015) using modeling approaches. Furthermore, as extreme weather events become more frequent, it is also worth noting that chilling and GDD requirements for some tree species would also be altered, which will further complicate the model development. However, accurate prediction of the development of phenological difference under future climate change remains a challenge and requires additional investigation, because chilling and GDD requirements, and the temperature thresholds in chilling and GDD estimation, differed at species- and site-scales, and their correlations with photoperiod effects are still uncertain. Ecosystem-scale impacts of enlarged IDSP, for example, effects of extended phenological differences on the carbon and water balance and on nutrient losses, are largely unknown. In LFS-dominated forests, like in our study area (EEA, 2017), the extended IDSP would likely hamper increases in the forests' carbon sink strength because the LFS would not be able to extend their leaf season to the same extent than EFS. In addition, the extended IDSP may increase uncertainty in spring phenology estimation from satellite images, as remote sensing approaches mainly trace the phenology of EFS (Fu, Piao, et al., 2019), and are subsequently prone to overestimation of ecosystem carbon uptake (Piao, Friedlingstein, Ciais, Viovy, & Demarty, 2007). In addition, previous studies have estimated that an earlier start of growing season will increase the vegetation productivity (Zohner, Mo, Pugh, Bastin, & Crowther, 2020). However, when considering the spatial variability of phenology shifts and the possible mutual constraints caused by interspecific differences in leaf flushing, the prediction of ecosystem productivity becomes more uncertain. Therefore, we encourage further research that focuses on potential implications of shifted IDSP for ecosystem carbon and water balance, as well as for plant-animal interactions, where experimental studies would be particularly insightful to improve our understanding of shifted IDSP consequences for ecosystems.

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CONFLICT OF INTEREST

The authors declare no competing interests.

AUTHOR CONTRIBUTION

Y.H.F. designed the research and drafted the paper, X.G. performed the analyses and all authors contributed to the interpretation of the results and to the text.

DATA AVAILABILITY STATEMENT

Phenology data are available at <http://www.pep725.eu/>. The Princeton climatic datasets can be downloaded from <http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/>. Other data used in this study are also available from the corresponding author upon request.

ORCID

Xiaojun Geng  <https://orcid.org/0000-0002-1064-1739>

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

Shilong Piao  <https://orcid.org/0000-0001-8057-2292>

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

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SUPPORTING INFORMATION

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

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