

## RESEARCH ARTICLE

# Atmospheric brightening counteracts warming-induced delays in autumn phenology of temperate trees in Europe

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## Abstract

**Aim:** Ongoing climate warming has been widely reported to delay autumn phenology, which in turn impacts carbon, water, energy and nutrient balances at regional and global scales. However, the underlying mechanisms of autumn phenology responses to climate change have not been fully elucidated. The aims of this study were to determine whether brightening that was defined as the increase of surface solar radiation and warming during recent decades affect autumn phenology in opposite directions and explore the underlying mechanisms.

**Location:** Central Europe.

**Time period:** 1950–2016.

**Major taxa studied:** Four dominant European tree species in central Europe: *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur*.

**Methods:** We investigated the temporal trends of leaf senescence, pre-season temperature and radiation by separating the period of 1950–2016 into two sub-periods (1950–1982 and 1983–2016) and determined the relationship between temperature, radiation and leaf senescence using partial correlation analysis.

**Results:** We found a significant warming and brightening trend after the 1980s in central Europe, yet this led to only slight delays in leaf senescence that cannot be explained by the well-known positive correlation between leaf senescence and autumn warming. Interestingly, we found opposite effects between warming (partial correlation coefficient,  $r = .37$ ) and brightening ( $r = -.23$ ) on leaf senescence. In addition, the temperature sensitivity of leaf senescence decreased with increasing radiation ( $-5.08$  days/°C/10<sup>8</sup> J/m<sup>2</sup>).

**Main conclusions:** The results suggested that brightening accelerated the leaf senescence dates, counteracting the warming-induced delays in leaf senescence, which may be attributed to photooxidative stress and/or sink limitation. This emphasizes the need to consider radiation to improve the performance of autumn phenology models.

## KEYWORDS

autumn phenology, brightening, climate warming, leaf senescence, radiation, temperature sensitivity

## 1 | INTRODUCTION

Global climate change causes substantial shifts in vegetation phenology, thereby affecting plant fitness as well as the functioning of terrestrial ecosystems and services they provide (Cannell & Smith, 1986; Geng, Fu, et al., 2020; Lieth, 1974; Menzel & Fabian, 1999; Peñuelas & Filella, 2001; Piao et al., 2017). Previous studies have reported that global warming has advanced the onset of vegetation growth in spring (Fu et al., 2015; Menzel et al., 2020) and, to a lesser extent, delayed the timing of autumn leaf senescence (Fu, Piao, et al., 2019; Ge et al., 2015). Spring phenology has been fairly well investigated (Fu, Piao, et al., 2014; Menzel et al., 2020; Piao et al., 2019), whereas the environmental drivers of autumn phenology are less understood (Gallinat et al., 2015), likely because many factors, such as drought, nutrient availability, light conditions and temperature, interactively influence autumn phenology (Buermann et al., 2013; G. Liu et al., 2019; Vitasse et al., 2021). Nevertheless, autumn phenology plays a fundamental role in the carbon cycle and the relationship between climate and the biosphere (Garonna et al., 2014; Q. Liu et al., 2016; Piao et al., 2008; Zhang et al., 2020; Zhu et al., 2012). Investigating autumn phenology is therefore integral to improving our understanding of the responses of terrestrial ecosystems to ongoing climate change.

Recent autumn phenology models predict that, in spite of the ongoing autumn warming trends, leaf senescence might slightly advance rather than delay over the rest of the century (Zani et al., 2020). Gunderson et al. (2012) found a significant delaying effect of warming on autumn senescence of *Liquidambar styraciflua*, *Quercus rubra*, *Populus grandidentata* and *Betula alleghaniensis* by conducting a temperature-controlled experiment in Oak Ridge National Environmental Research Park, USA. Fu et al. (2018) investigated the spring and autumn phenology by using saplings of *Fagus sylvatica* in Belgium and found a significantly larger temperature response of autumn leaf senescence than of spring leaf-out. These seemingly inconsistent findings between natural and experimental conditions are likely due to the fact that autumn phenology is greatly affected by environmental cues besides temperature, such as photoperiod, solar radiation and early-season productivity, which cannot be controlled in natural conditions (Chen et al., 2020; Estiarte & Peñuelas, 2015; Fu, Campioli, et al., 2014; Way & Montgomery, 2015). For example, the senescence dates of European aspen vary very little between years, suggesting photoperiod as the primary driver of autumn leaf senescence (Fracheboud et al., 2009). In addition, previous research also demonstrated that the leaf senescence dates of oak and beech significantly advanced with elevation, but leaf senescence in ash and sycamore remained stable along elevational gradients, which might be explained by photoperiod limitation (Vitasse et al., 2009). Overall, environmental cues are likely to interactively regulate leaf senescence (Fu et al., 2015; Hänninen, 2016; G. Liu et al., 2019; Maes et al., 2019; Zani et al., 2020), and exploring how different environmental cues interact is thus critical to better understand the timing of autumn phenology.

In recent years, reductions in atmospheric pollution and cloud cover have led to significant atmospheric brightening in several regions (Sanchez-Lorenzo et al., 2015; Wild et al., 2007), with the increased radiation likely affecting the physiological processes of plants (Pfeifroth et al., 2018; Stanhill, 2007). For example, Nemani et al. (2003) found that forest net primary production in Amazon rain forests significantly increased over recent decades, which was largely driven by increased solar radiation. Similar results were also reported in Europe, Panama, Thailand and Malaysia (Dong et al., 2012; Graham et al., 2003; Trigo et al., 2002). Recently, increased vegetation growth during the growing season was reported to advance autumn phenology, which can likely be explained by the carbon sink limitation hypothesis (Zani et al., 2020). This suggests that solar radiation might affect autumn phenology processes through regulating plant productivity. A delay in leaf senescence dates under reduced light availability has recently also been shown in a manipulative experiment on four European trees (Vitasse et al., 2021). Yet, to our knowledge, the direct effects of atmospheric brightening on autumn phenology and the relationship between atmospheric brightening and the temperature sensitivity of leaf senescence ( $S_T$ , the change in days in leaf senescence per degree warming) under natural conditions have not yet been studied. Testing these effects will contribute to deciphering the physiological mechanisms of autumn leaf senescence of temperate trees in response to ongoing environmental changes.

Based on in situ phenological records during the period 1950–2016 in central Europe, we here investigate the effects of temperature and radiation on autumn phenology by applying partial correlation analysis. We propose and test the hypothesis that atmospheric radiation controls autumn phenology through increasing leaf-level photooxidative stress. In addition, increased light availability might lead to elevated photosynthetic rates, which in turn should increase leaf-level carbon to nitrogen ratios, leading to an earlier initiation of leaf senescence (Paul & Foyer, 2001; Zani et al., 2020). This hypothesis thus predicts that: (a) increased atmospheric brightening and warming during recent decades affects autumn phenology in opposite directions, advancing and delaying the leaf senescence process, respectively; and (b) increasing solar radiation reduces the apparent temperature sensitivity of autumn phenology.

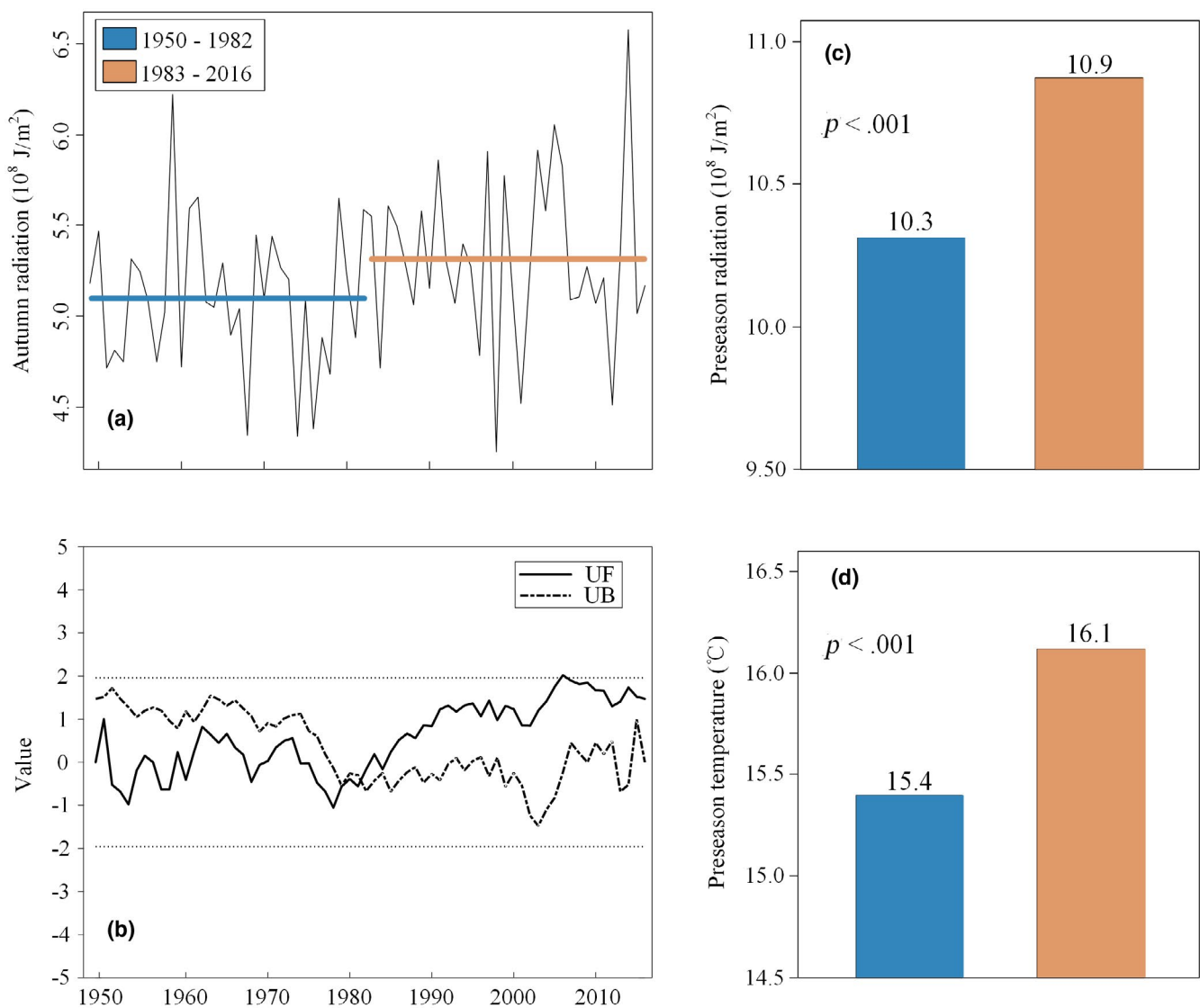
## 2 | MATERIAL AND METHODS

### 2.1 | Datasets

Site-level daily air temperature and shortwave downward radiation of all phenological sites were derived from a gridded climate dataset with a spatial resolution of 0.25° (E-OBS gridded dataset, <http://www.ecad.eu/download/ensembles/download.php>). The Mann-Kendall (MK) test was used to evaluate the monotonic temporal trend of the average autumn (from September to November) radiation across all sites (Kendall, 1948). UF and UB are statistical variables

of the MK test.  $UF > 0$  indicates an upward trend,  $UF < 0$  indicates a downward trend. If  $UF$  and  $UB$  intersect between the critical straight lines, this indicates a significant trend shift (mutation) for the year corresponding to the intersection point (Kendall, 1948; Yue et al., 2002). According to the MK test, there was a turning point in autumn radiation in 1982, with, on average, significantly higher radiation in 1983–2016 compared to the 1950–1982 period (Figure 1a,b). We then calculated the average temperature and radiation sums throughout the whole year and the growing season (from June to November) across all sites for the 1950–1982 and the 1983–2016 periods (Figure S1.1). In addition, we analysed the changes in seasonal radiation over the two periods and found that radiation increased across all seasons, but the amplitudes were different among seasons (Table S1.1).

In situ leaf phenology records were obtained from the Pan European Phenology (PEP) network (<http://www.pep725.eu/>), which provides phenological observations of autumn leaf senescence dates across central Europe (Templ et al., 2018). The dates of leaf senescence were defined according to the Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie (BBCH) code 94, which refers to the date when 50% of a tree's leaves show autumnal colouring. The date of autumn leaf senescence of each tree was represented by day of the year (DOY). Records were excluded from the analysis when autumn senescence occurred before DOY 181 (end of June) to avoid abnormal dates resulting from measurement error, extreme summer drought-induced leaf senescence, or diseases. Based on the turning point year of autumn radiation (1982), we only selected time series that had more than 15 years of leaf



**FIGURE 1** Autumn radiation changes (a) and turning point test [Mann-Kendall (MK) test] (b) over the period 1950–2016. The two horizontal dotted lines in (b) are 95% confidence intervals, and the intersection of  $UF$  and  $UB$  inside these two lines indicates a significant mutation point. Panels (c) and (d) show the mean pre-season radiation sums and mean pre-season daily air temperatures, respectively, during the period 1950–1982 (blue) and 1983–2016 (orange).  $p$  is the significance level using ANOVA

senescence records in both the periods 1950–1982 and 1983–2016. In total, we selected 1,161 phenological sites and 169,771 phenological observations of four dominant deciduous tree species: *Aesculus hippocastanum* (horse chestnut), *Fagus sylvatica* (European beech), *Betula pendula* (European silver birch) and *Quercus robur* (pedunculate oak), which are widely distributed trees and have autumnal phenology dates across central Europe available since 1950. The distribution of these sites is shown in Figure S1.2.

## 2.2 | Analysis of temporal changes in leaf senescence dates

For each species and time series (species  $\times$  site combination), we calculated the average leaf senescence date (LSD) of the 1950–1982 and 1983–2016 periods as well as the difference in LSD between the two periods ( $\Delta$ LSD). ANOVA was conducted to test for significant shifts in LSD between the two time periods.

## 2.3 | Partial correlation analysis

The timing of leaf senescence is affected by the environmental conditions during the period before the phenological event, defined as the pre-season (Fu et al., 2015; Geng, Zhou, et al., 2020). In this study, we defined the pre-season as the 3 months (90 days) prior to the mean date of leaf senescence for each time series. For each time series and year, we obtained the radiation sums and mean temperature during the pre-season. We then conducted a partial correlation analysis to investigate the relationships between the timing of leaf senescence and one of the climate variables (radiation or temperature) while controlling the other over the whole study period, as well as within the two sub-periods, for each time series. As leaf senescence is affected by both daily maximum and minimum temperature, we further tested the effect of either minimum ( $T_{\min}$ ) or maximum ( $T_{\max}$ ) temperature on leaf senescence using the same method. In addition, ANOVA was also used to determine the interactive effects of solar radiation and temperature on leaf senescence.

## 2.4 | Temperature sensitivity of leaf senescence

To further explore the effect of radiation on the temperature sensitivity of leaf senescence, we investigated the correlation between the date of leaf senescence and temperature under different radiation conditions. We first divided the data into six radiation subsets (R1–R6) for each species at each site according to the radiation sums (RAD) following the method used in Fu, Zhang, et al. (2019). Then, for each radiation subset, we divided the data into six temperature subsets (T1–T6) according to the mean temperature of the pre-season (TEM), see details in Table S1.2. We thus ended up with 36 radiation–temperature combinations, for which we determined the mean leaf senescence dates, the mean temperature and radiation sums of the

pre-season. This allowed us to estimate the temperature sensitivity of leaf senescence ( $S_T$ ), defined as the change in days in leaf senescence per degree warming, for each radiation subset using the linear regression analysis. In addition, to test the robustness of the results, we further divided the radiation and temperature into three or eight subgroups. The RAD and TEM were divided into three subgroups by using the mean  $\pm$  SD of RAD/TEM as breakpoints and into eight subgroups using the mean  $\pm$  1/3 SD and the mean  $\pm$  2/3 SD.

## 3 | RESULTS

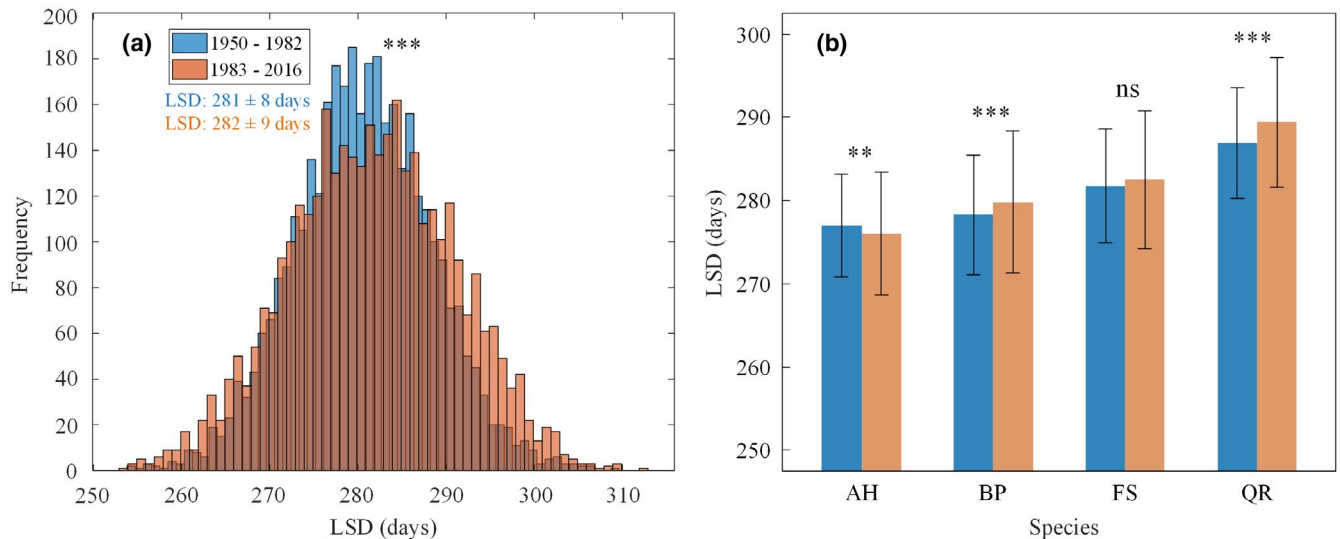
### 3.1 | Temporal changes in climate and leaf senescence dates

According to the MK test, the year 1982 was a turning point regarding autumn radiation over the period 1950–2016 (Figure 1a,b). Separated by the year 1982, the pre-season radiation significantly increased ( $p < .001$ ) from an average of  $10.3 \times 10^8$  J/m<sup>2</sup> during 1950–1982 to  $10.9 \times 10^8$  J/m<sup>2</sup> during 1983–2016 (Figure 1c). We obtained similar results when summing radiation over the whole growing season (from June to November), that is, significantly brighter growing seasons were found for the 1983–2016 period compared to the 1950–1982 period (Figure S1.1), which is consistent with a previous study (Wild et al., 2005). Pre-season temperatures were, on average, 0.7 °C warmer in 1983–2016 compared to 1950–1982 ( $p < .001$ , Figure 1d); similar results were also detected for the whole year and growing season (Figure S1.1).

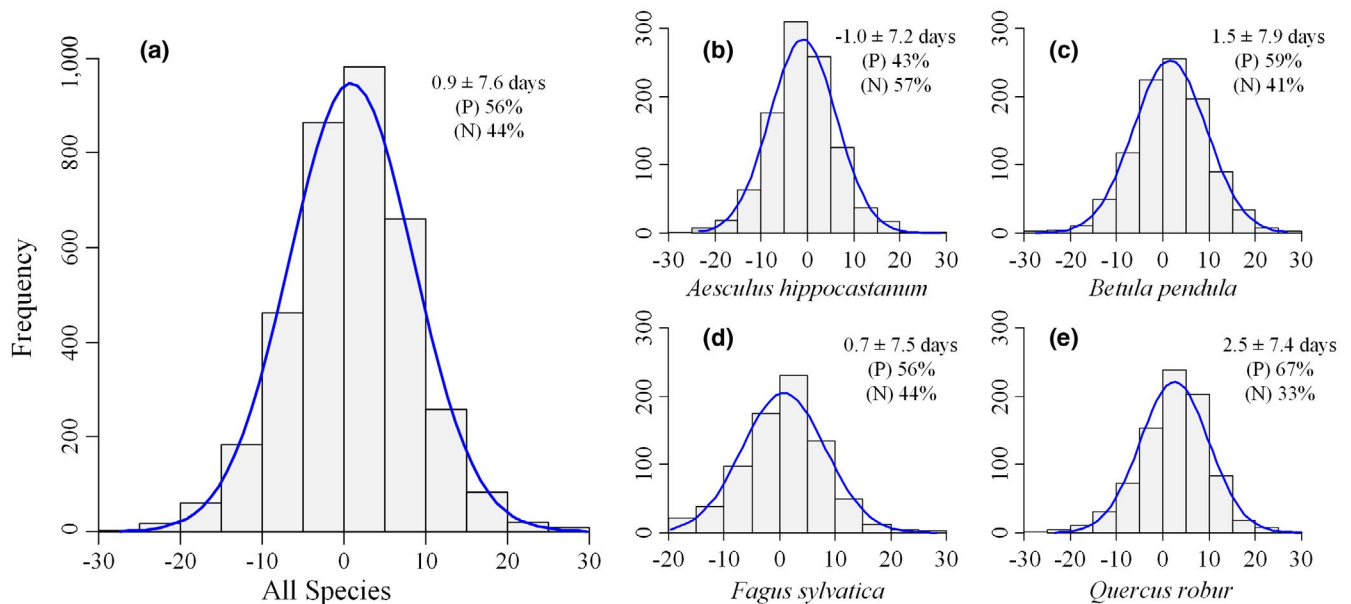
Across the four studied species, the average LSD occurred slightly later (1 day on average) during the period 1983–2016 (LSD = 282) than during the period 1950–1982 (LSD = 281;  $p < .001$ , Figure 2a). Within species, the average LSDs of *Betula pendula* (BP) and *Quercus robur* (QR) were significantly delayed but with very small amplitudes, that is, from 1 to 3 days only, while the LSDs of *Aesculus hippocastanum* (AH) significantly advanced by 1 day (Figure 2b). We also calculated the difference in LSD between the two sub-periods for each species at each site ( $\Delta$ LSD, Figure 3) and found similar results, that is, across all species,  $\Delta$ LSD did not significantly deviate from zero ( $\Delta$ LSD =  $0.9 \pm 7.6$  days). Within species,  $\Delta$ LSD was delayed by  $1.5 \pm 7.9$ ,  $0.7 \pm 7.5$  and  $2.5 \pm 7.4$  days, respectively, for *Betula pendula*, *Fagus sylvatica* and *Quercus robur*; for *Aesculus hippocastanum*,  $\Delta$ LSD was advanced by  $1.0 \pm 7.2$  days (Figure 3). Overall, LSD did not significantly change over the period 1950–2016, with a delay of only 1 day in the period 1983–2016 compared to the period 1950–1982.

### 3.2 | Correlations between leaf senescence dates and climatic factors

Both temperature and radiation affected the leaf senescence process at the significance level of  $p < .10$ , and interestingly these effects were opposite. In line with previous studies, we found a positive



**FIGURE 2** Distribution of leaf senescence dates (LSDs) across all species and sites over the two periods, 1950–1982 (blue) and 1983–2016 (orange) (a) and the mean leaf senescence date (mean  $\pm$  SD) of each species for the two periods (b). AH, BP, FS and QR are species acronyms referring to *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur* respectively. 'ns' indicates that no significant differences in the LSD exist between the two periods, \*\* and \*\*\* indicate  $p < .01$  and  $p < .001$ , respectively

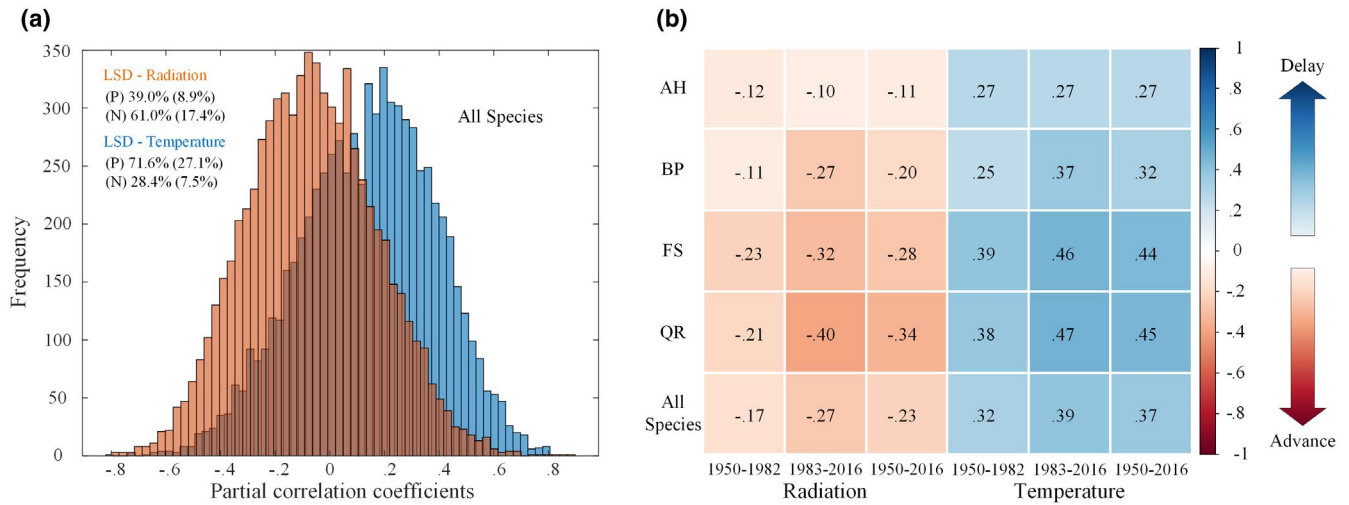


**FIGURE 3** The distribution of  $\Delta$ LSD for all species (a), *Aesculus hippocastanum* (b), *Betula pendula* (c), *Fagus sylvatica* (d) and *Quercus robur* (e).  $\Delta$ LSD is the difference between the mean site-level leaf senescence date (LSD) in 1983–2016 and the mean site-level LSD in 1950–1982. Percentages of positive (P) and negative (N) cases are provided

partial correlation between temperature and LSD of  $r = .37$  across all species, and  $r = .27$ ,  $.32$ ,  $.44$  and  $.45$  for *Aesculus hippocastanum*, *Betula pendula*, *Fagus sylvatica* and *Quercus robur*, respectively, over the whole study period 1950–2016 (Figure 4). Compared to the period 1950–1982, the partial correlation coefficient during the period 1983–2016 increased by  $.07$  (from  $.32$  to  $.39$ ) across all species, with similar patterns observed within species. The distributions of partial correlation coefficients between leaf senescence and temperature

or radiation are shown in Figure 4a (all species) and Figure S1.3 (each species separately).

Radiation was negatively correlated with LSD, suggesting that atmospheric brightening was likely associated with an earlier leaf senescence. The partial correlation between radiation and LSD was  $-.23$  across all species. Similar patterns were found within species, with partial correlation coefficients of  $-.11$ ,  $-.20$ ,  $-.28$  and  $-.34$  for *Aesculus hippocastanum*, *Betula pendula*, *Fagus*



**FIGURE 4** (a) Distributions of partial correlation coefficients across all species. The orange and blue bars represent the partial correlation coefficients between leaf senescence dates (LSDs) and radiation or temperature, respectively. Percentages of positive (P) and negative (N) correlations and corresponding marginally significant correlations ( $p < .1$ , in parentheses) are also provided. (b) The partial correlation coefficients between leaf senescence dates and radiation or temperature, for *Aesculus hippocastanum* (AH), *Fagus sylvatica* (FS), *Betula pendula* (BP), *Quercus robur* (QR) and across all species (All). The colour scale indicates the magnitude of the partial correlation coefficients, with positive values indicating senescence delays with increases in the climate variable and negative values indicating advances

*sylvatica* and *Quercus robur*, respectively, over the whole study period 1950–2016 (Figure 4b). Interestingly, the partial correlation coefficients between LSD and radiation became more negative during the period 1983–2016 ( $r = -0.27$ ) compared to the period 1950–1982 ( $r = -0.17$ ). We further tested the interactive effects of temperature and radiation using ANOVA and found these were significant over the two separate periods ( $p < .01$  for the period 1950–1982 and  $p < .001$  for the period 1983–2016) and the whole period ( $p < .001$ ). Similar results were also observed by considering the interactive effects of minimum/maximum temperature and radiation (Figure S1.4), as well as using the radiation and temperature across the growing season (June–November, Figure S1.5).

### 3.3 | Temperature sensitivity of leaf senescence

Based on the temperature and radiation combination subsets (see details in Table S1.3), we found that the temperature sensitivity of LSD was significantly reduced under elevated radiation (Figure 5). Based on the temperature and radiation combination subsets (Table S1.3), we found that warming significantly delayed the LSD dates by 21, 12, 7 and 3 days for R1 through R4 ( $p < .05$ , Figure 5a) and the temperature sensitivity of LSD was significantly reduced with radiation increases (Figure 5). Under strong radiation conditions, that is, R5 and R6, the leaf senescence date was constant or even advanced by 9 days with warming. Overall, we found that the temperature sensitivity of leaf senescence was significantly reduced with increased radiation at an average rate of  $-5.08 \text{ days}/^{\circ}\text{C}/10^8 \text{ J}/\text{m}^2$  (Figure 5b). Similar results were obtained by dividing the radiation

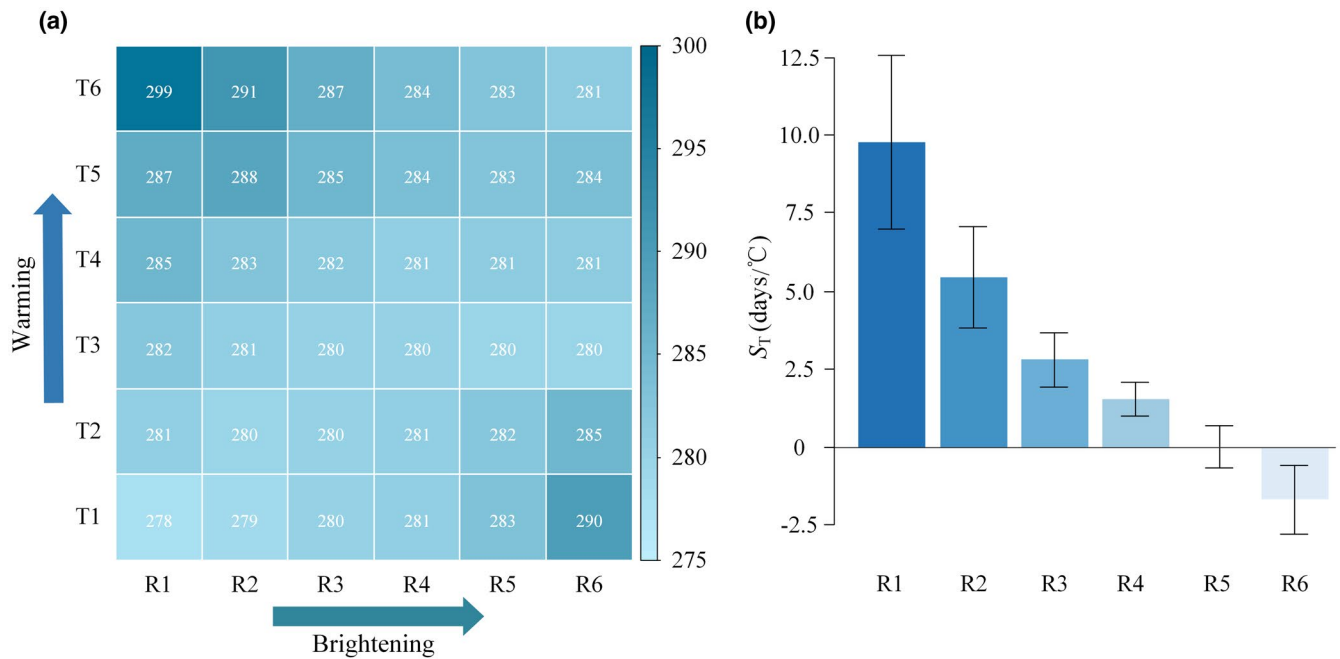
and temperature into either three or eight subgroups (Figures S1.6 and S1.7).

## 4 | DISCUSSION

### 4.1 | The effects of warming and brightening on leaf senescence

Climate warming is expected to shift the autumn phenology of temperate and boreal plants, yet inconsistent results have been obtained so far (Chen et al., 2020; Q. Liu et al., 2016; Piao et al., 2019). Here we show that the autumn leaf senescence dates of dominant European tree species became slightly later during the warmer and brighter period 1983–2016 except for *Aesculus hippocastanum*, which is in line with previous findings (Fu, Campioli, et al., 2014; Meier et al., 2021; Menzel et al., 2020). Accordingly, we found a predominantly positive correlation between pre-season temperature and leaf senescence, likely explaining the slight delays in leaf senescence over recent years. Potential mechanisms proposed to explain the positive effect of temperature on leaf senescence dates involve enhanced activity of photosynthetic enzymes (Shi et al., 2014) and other physiological processes (Yang et al., 2015), slowing down the degradation of chlorophyll (Fracheboud et al., 2009) and postponing the onset of leaf senescence.

However, we found that the delays in leaf senescence dates were minor, only shifting by 1 day among the two sub-periods, which contradicted previous experimental studies, in which significant delays were found in response to autumn warming (8 days per  $^{\circ}\text{C}$  warming, as reported in Fu et al., 2018). Our study suggests that the



**FIGURE 5** (a) The average dates of leaf senescence under six temperature (T1–T6) and six radiation (R1–R6) gradients. The number in each box refers to the average leaf senescence date under the 36 combinations of radiation and temperature. (b) The temperature sensitivity of leaf senescence under different radiation regimes (R1–R6)

atmospheric brightening trend since the 1980s (Sanchez-Lorenzo et al., 2015; Wild et al., 2005) may have slowed down the expected delay due to warming. This opposing effect has been largely ignored in studies so far. As reported in previous studies, a change of 4–6% in radiation may profoundly influence the temperature and hydrological cycles of terrestrial ecosystems (Liepert et al., 2004; Ramanathan et al., 2001). We found that, although pre-season temperature plays an important role in the autumn phenology process, radiation affects leaf senescence in the opposite direction, advancing leaf senescence dates in Europe. This was consistent with a recent study conducted on saplings that showed that shade conditions largely delayed leaf senescence of three temperate tree species (Vitasse et al., 2021). Similar results were also obtained using large scale spatial datasets on 396 Northern Hemisphere woody species that included species that we used, and they found that the time of leaf senescence in eastern North America, which receives higher solar irradiation during autumn than Europe, was  $11 \pm 4$  days earlier than in Europe in 2014 (Renner & Zohner, 2019; Zohner & Renner, 2017). In our study, we further demonstrated that the temperature sensitivity of leaf senescence was significantly reduced with brightening. Our results thus suggest that temperature and radiation counteract each other and interactively regulate the autumn leaf senescence process.

#### 4.2 | A mechanistic explanation for the brightening effect on leaf senescence

To explain how climate warming and brightening can interact to affect leaf senescence, and why brightening advance leaf senescence,

we propose two mutually non-exclusive mechanisms: photoprotection and sink limitation. The photoprotection hypothesis predicts that once the light energy absorption of a leaf exceeds the capacity for light utilization, reactive oxygen species accumulate (Müller et al., 2001), increasing the risk of photo-oxidative damage (Juvany et al., 2013) and reducing the nutrient reabsorption capacity (Renner & Zohner, 2019). Pigments in autumnal leaves play critical roles in dissipating excess light energy (Ruban et al., 2002) and reactive oxygen species (Close & Beadle, 2003; Xu & Rothstein, 2018). Therefore, strong solar radiation may increase a plant's investment in anthocyanins and xanthophylls, and thus promote leaf colouring (Renner & Zohner, 2019).

The second potential mechanism is based on the sink-limitation hypothesis (Dox et al., 2020; Zani et al., 2020). Climate warming has led to increased tree productivity as a result of advances in growing season onset and enhanced photosynthesis during the growing season under elevated temperatures and increased light availability (Graham et al., 2003; Nemani et al., 2003; Trigo et al., 2002). The photosynthetically active radiation (PAR) increases under elevated solar radiation (Meek et al., 1984). This enhancement of photosynthesis may alter plants' source/sink balance, accelerating sink saturation and speeding up the senescence process (Zani et al., 2020). In other words, once the plant's carbon sink is saturated, leaf senescence will be induced, governed by interactions between photosynthate supply, phytohormones and nutrient supply (Fu, Piao, et al., 2019; Zani et al., 2020). Using experiments and long-term observations, Zani et al. (2020) demonstrated that increases in spring and summer productivity drive earlier autumn leaf senescence because of elevated light levels, temperature and

carbon dioxide, supporting the critical role of sink limitation in governing autumn leaf senescence. In addition, previous studies found that autumn senescence tends to be positively associated with the onset of spring budburst (Fu, Campioli, et al., 2014; Keenan & Richardson, 2015). Specifically, per day of earlier spring budburst, c. 0.6 days earlier autumn leaf senescence was reported on average, additionally offsetting the delaying effects of warming (Fu, Campioli, et al., 2014). However, how spring phenology interacts with autumn temperature and brightening to affect the autumn leaf senescence process is still unclear and more experimental studies are needed. Overall, the photoprotection and sink-limitation hypotheses provide plausible explanations for the negative effect of radiation on autumn senescence dates as well as for the declining temperature sensitivity of leaf senescence in response to brightening. Further experiments will be necessary to test the validity of these two hypotheses addressing the role of light conditions in regulating leaf senescence timing.

### 4.3 | Future implications of the relationship between autumn phenology and atmospheric brightening

At regional scale, brightening largely depends on synoptic meteorological conditions as well as anthropogenic air pollution, such as the emissions of aerosols and aerosol precursors (Wild et al., 2007). Atmospheric brightening due to the reduction of anthropogenic aerosols may continue in the future (Haywood et al., 2011). Our findings suggest that the interactive effects of warming and brightening on the leaf senescence process will continue to cause reductions in autumn temperature sensitivity under the ongoing atmospheric brightening trends. However, the leaf senescence of understorey trees may be delayed by the shade of overstorey trees, and the growing season will be correspondingly extended (Gressler et al., 2015; Vitasse et al., 2021). So far, temperature and photoperiod have been widely used as the sole environmental variables coupled to autumn phenology models. However, autumn phenology models consistently fail to accurately simulate autumn phenology dates (G. Liu et al., 2019), likely because of missing interactive effects with other important environmental factors, such as solar radiation. We therefore propose that solar radiation should be considered in phenology models to better simulate the autumn phenology processes. However, our study only used four tree species; further evidence, especially from manipulative experiments on more woody species, is needed. Furthermore, the underlying physiological processes of leaf senescence are still unclear; the onset of physiological activity in spring (Fu, Campioli, et al., 2014; Keenan & Richardson, 2015; Zohner & Renner, 2019), the mean daily maximum and minimum temperature (Chen et al., 2020), and drought stress (Buermann et al., 2013) have all been associated with leaf senescence. Therefore, comprehensive experiments focusing on the interactive effects among these environmental cues are needed to better understand the underlying autumn phenology processes and to improve predictions of the global

carbon and water balance of terrestrial ecosystems under future climate change.

## 5 | CONCLUSIONS

To our knowledge, this study is the first to reveal the antagonistic effect of warming and brightening on leaf senescence for the dominant tree species in central Europe. Brightening accelerates the leaf senescence process and reduces the temperature sensitivity of leaf senescence, counteracting the expected warming-induced delays in leaf senescence. The photoprotection and sink-limitation hypotheses provide plausible explanations for the negative effect of radiation on autumn senescence dates as well as for the declining temperature sensitivity of leaf senescence in response to brightening. Our study emphasizes the need to consider radiation to improve the performance of phenology models.

### ACKNOWLEDGMENTS

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### CONFLICT OF INTEREST

The authors declare that there is no conflict of interest that could be perceived as prejudicing the impartiality of the research reported.

### AUTHOR CONTRIBUTIONS

Yongshuo H. Fu designed the study. Zhaofei Wu and Yongshuo H. Fu analysed the data and led the writing of the manuscript, which received significant input from all authors.

### DATA AVAILABILITY STATEMENT

European phenology data are available at <http://www.pep725.eu/>; The climate data were derived from the E-OBS gridded dataset of the ECA, <https://eca.knmi.nl/dailydata/index.php>.

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## BIOSKETCH

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