

# Effect of climate warming on the timing of autumn leaf senescence reverses at the summer solstice

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9       Constantin M. Zohner<sup>1\*</sup>, Leila Mirzagholi<sup>1</sup>, Susanne S. Renner<sup>2</sup>, Lidong Mo<sup>1</sup>, Raymo Bucher<sup>1</sup>, Daniel  
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25 **Abstract**  
26 Climate change is causing shifts in the growing seasons of plants<sup>1,2</sup>, affecting species performance and  
27 interactions<sup>3,4</sup> as well as global carbon, water and nutrient cycles<sup>5,6</sup>. How the timing of autumn leaf  
28 senescence in extra-tropical forests will change remains unclear because of the complex seasonal  
29 interaction of climate warming, earlier and enhanced vegetation activity, and the annual day-length cycle<sup>7–</sup>  
30 <sup>10</sup>. Here we use experiments, long-term ground observations, and satellite-based vegetation monitoring to  
31 show that early-season and late-season warming have opposite effects on the onset and progression of  
32 leaf senescence, with a reversal occurring at the year's longest day (summer solstice). Across ~84% of the  
33 northern forest area, increased temperature and vegetation activity before the solstice led to an earlier  
34 senescence onset (10% greenness loss) of, on average,  $-1.6 \pm 0.1$  days-per-°C, while warmer post-solstice  
35 temperatures did not affect senescence onset but reduced its speed (progression to 50% greenness loss)  
36 by  $0.8 \pm 0.1$  days-per-°C. Due to the earlier senescence onset, the day at which autumn temperature starts  
37 driving senescence progression has been shifting to ever earlier dates, between 1951–2015 at a rate of  
38  $-0.20 \pm 0.07$  days per year. These developmental constraints suggest that senescence will start earlier but  
39 progress more slowly in the future, revealing Northern Hemisphere-wide compensation effects on trends in  
40 growing-season length, caused by enhanced pre-solstice vegetation activity. This new mechanistic insight  
41 improves our ability to model carbon uptake by extra-tropical forests under climate change.

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45 **Main text**  
46 The phenological cycles of trees exert a strong control on the structure and functioning of ecosystems<sup>4,11</sup>  
47 and global carbon, water and nutrient cycles<sup>2,5,6</sup>. Anthropogenic climate change has resulted in shifts in the  
48 growing seasons of temperate and boreal trees, with the start of the season today occurring, on average,  
49 two weeks earlier than it did during the 19<sup>th</sup> and 20<sup>th</sup> century<sup>12</sup> and the end of the season (EOS) being  
50 delayed<sup>1,6,13</sup>. Each day of a longer growing season may increase net ecosystem carbon uptake by 3.0–9.8  
51 gC m<sup>-2</sup> (ref<sup>6</sup>). Yet, due to the complex and interactive effects of growing-season climate and the annual day-  
52 length cycle the direction of EOS changes in response to climate change has remained highly  
53 uncertain<sup>8,9,14,15</sup>.

54 Characterizing the interplay among the environmental drivers of EOS is integral to improving our  
55 understanding of vegetation development and tree growth. A key outstanding question is how day length  
56 and climate effects interact and vary throughout the growing season. Local observations and experiments  
57 have shown that early-season warming, causing earlier spring leaf-out and faster development, tends to  
58 advance EOS dates<sup>8–10,16</sup>, whereas late-season warming has the opposite effect, delaying the EOS<sup>17,18</sup>.  
59 Accelerated development and increased vegetation activity in the beginning of the season might drive earlier  
60 autumn senescence through a variety of possible mechanisms, such as developmental and nutrient  
61 constraints<sup>9,19</sup>, seasonal built-up of water stress<sup>20,21</sup>, or radiation-induced leaf ageing<sup>22</sup>. In contrast, later on  
62 in the season, a direct effect of temperature (cooling) is likely to dominate phenological responses<sup>14,23,24</sup>. If  
63 these trends are correct, then climate warming has opposing effects at the start and end of the growing  
64 season, with a reversal of effects somewhere in between. Yet, we lack a global understanding of the  
65 seasonal effects of plant growth and climate on autumn phenology, limiting our ability to forecast future  
66 growing seasons and carbon uptake in extra-tropical forests.

67 Here we test whether early-season vegetation activity and development drive an earlier EOS across  
68 northern forests, with day length providing the linkage between seasonal activity, air temperature warming,  
69 and autumn phenology (Fig. 1). Cell division, tissue formation, and growth in northern trees are highest at  
70 the beginning of the season and decline with shortening days<sup>25–28</sup>, the adaptive reason being the limited  
71 time remaining for tissue maturation and bud set before the first frost<sup>29</sup>. We thus expected that inter-annual  
72 variation in EOS timing is a function of early-season growth, with an earlier onset of senescence in warm,  
73 high-activity years than in cold, low-activity years (Fig. 1 scenario 1 versus 2). Once EOS has begun, its  
74 progression (towards full dormancy) should be modulated by autumn temperature, with faster chlorophyll  
75 breakdown in colder autumns than in warmer autumns<sup>24</sup> (Fig. 1 scenario A versus B). If early-season  
76 development continues to accelerate due to advances in leaf-out timing and higher air temperature<sup>2,6,30,31</sup>,  
77 this might cause an ever earlier EOS onset, eventually outweighing the delay in the progression of  
78 senescence due to warmer autumns.

To test these hypotheses, we combined phenology data from i) satellite observations across Northern Hemisphere temperate and boreal forests, ii) ground-sourced European observations from widespread deciduous trees<sup>32</sup>, and iii) controlled experiments on European beech. As a proxy for vegetation activity, we used three photosynthesis models (satellite-derived gross-primary productivity [GPP]<sup>33</sup>, LPJ<sup>9</sup> and p model<sup>34</sup>). We then ran linear models to test for the monthly and seasonal effects of photosynthesis, temperature, short-wave radiation and water availability on EOS dates. The satellite data allowed us to differentiate between the onset of senescence and its progression, by analysing the dates when greenness had dropped by 10% ( $EOS_{10}$ ) or 50% ( $EOS_{50}$ ) relative to the seasonal maximum. The experiments allowed us to directly test for seasonal variation in the effects of day length, air temperature, radiation, water, and nutrient availability. Finally, we mapped the relative effects of early-season vegetation activity and late-season climate across Northern Hemisphere temperate and boreal forests to test for possible historic-biogeographic patterns in the drivers of autumn senescence.

Satellite-based phenology data (Fig. 2), European plot data (Fig. 3), and experiments (Fig. 4) all revealed a consistent advancing effect of pre-solstice (i.e., pre-21 June) vegetation activity on EOS dates, which declined after the June solstice. Thus, across ~84% of the northern forest area (32% or 22% with  $p < 0.1$  or  $< 0.05$ ), increased pre-solstice photosynthesis and temperature led to an earlier onset of senescence (Fig. 2a,c and Extended Data Fig. 1a,c), with each 10% increase in photosynthesis and each 1°C increase in temperature on average resulting in  $-2.8 \pm 0.1$  and  $-1.6 \pm 0.1$  days earlier  $EOS_{10}$ , respectively (Fig. 2i and Extended Data Fig. 1i). The advancing effect of pre-solstice vegetation activity was most pronounced at mid-latitudes (45–60°N) and decreased toward lower latitudes (Fig. 2b). A significant delaying effect of pre-solstice activity was found for fewer than 1% of pixels (Fig. 2d,e). Increased post-solstice photosynthesis and temperature, by contrast, had a much smaller effect on the onset of senescence ( $EOS_{10}$  dates; Figs. 2f-h and 5a and Extended Data Fig. 1f-h) but slowed down its progression ( $EOS_{50}$  dates) by, on average,  $0.8 \pm 0.1$  days per °C (see Figs. 5b and Extended Data Fig. 2 for satellite observations and Figs. 3 and 5c for European plots). Precipitation and CO<sub>2</sub> levels had comparatively small effects (Fig. 2f).

The reversal at the summer solstice of the effects that air temperature and vegetation activity have on EOS dates was consistent across i) both EOS metrics used here, i.e., the onset of senescence ( $EOS_{10}$ ; Extended Data Fig. 1) and its progression ( $EOS_{50}$ ; Extended Data Fig. 2), ii) forest types (Fig. 2a and Extended Data Fig. 3), and iii) a set of alternative variables linked to growing-season activity and development, namely climate-derived productivity (Figs. S1 and S2), day-time temperature ( $T_{day}$ ; Extended Data Figs. 1 and 2), and short-wave radiation (Figs. S3 and S4). The effect reversal at the June solstice was further supported by an analysis that used 10-day moving steps around the solstice (Fig. 2h). Furthermore, along the full latitudinal gradient (30°N–65°N) studied here, the early-season period during which vegetation activity exhibited an advancing effect on  $EOS_{10}$  dates consistently ended right after the solstice at June ~26 (Extended Data Fig. 4).

Our finding that the onset of senescence is driven by pre-solstice activity and development, while its rapid or slow progression depends on autumn temperature (Fig. 5b,c and Extended Data Fig. 2) suggests that, under global warming, senescence will start earlier but progress more slowly (scenario 2B in Fig. 1). Indeed, analysis of the temporal trends in remotely-sensed EOS dates and pre-solstice vegetation activity showed that across all analysed northern forest pixels, the onset of senescence ( $EOS_{10}$  date) has advanced by an average of  $-0.4 \pm 0.1$  days per decade between 2001–2018 (Fig. 2j), in parallel with increased pre-solstice vegetation activity (Extended Data Fig. 5a-b), with the strongest advances in  $EOS_{10}$  dates found for regions with the largest increase in pre-solstice GPP (Extended Data Fig. 5k). By contrast, senescence progression ( $EOS_{50}$  date) has slowed by an average of  $1.5 \pm 0.1$  days per decade (Extended Data Fig. 2l), in parallel with warmer autumns (Extended Data Fig. 5i,j), with the largest extension of the overall senescence duration found for regions with the largest increases in autumn temperature (Extended Data Fig. 5m). When removing the effect of pre-solstice photosynthesis (Fig. 2i) by including it as a fixed effect in addition to year, the model predicted delays in  $EOS_{10}$  and  $EOS_{50}$  dates of  $+1.3 \pm 0.1$  and  $+2.0 \pm 0.1$  days per decade, respectively (Figs. 2k and S2m), underscoring the strong advancing effect of the ongoing acceleration in pre-solstice vegetation activity on temporal trends in leaf senescence.

In line with the satellite observations, high pre-solstice vegetation activity also correlated with advanced EOS<sub>50</sub> dates in the European plot data, across all four species (Fig. 3b) and across a set of alternative variables (LPJ model-derived photosynthesis [Fig. 3], P-model-derived photosynthesis [Fig. S5], day-time temperature [ $T_{day}$ ; Fig. S6], and cumulative short-wave radiation [Fig. S7]. Based on these findings,

133 we ran multivariate mixed models, including or excluding the effects of pre-solstice or post-solstice (solstice  
134 to mean EOS<sub>50</sub>) activity and precipitation to determine the relative importance of seasonal activity,  
135 precipitation, CO<sub>2</sub> levels, and autumn night-time temperature (Autumn T<sub>night</sub>). Pre-solstice activity and  
136 autumn T<sub>night</sub> had the strongest effects on EOS<sub>50</sub> dates, with the effect of pre-solstice photosynthesis being  
137 ~3 times greater than that of precipitation and atmospheric CO<sub>2</sub> (Fig. 3h). EOS predictions from these  
138 models show that the model representing both pre- and post-solstice effects adequately captures within-  
139 site EOS<sub>50</sub> trends in response to mean annual temperature (advance of -0.4 days per each °C increase in  
140 mean annual temperature, Fig. 3g). In contrast, the post-solstice model representing only post-solstice  
141 activity and precipitation, predicts delays of +0.8 days per °C, while the pre-solstice model predicts advances  
142 of -1.0 days per °C, demonstrating that information on both pre- and post-solstice climate is necessary to  
143 reproduce the observed EOS<sub>50</sub> responses to rising temperature.

144 The offsetting effect of pre-solstice development on autumn-warming-induced delays in EOS<sub>50</sub> also  
145 is apparent when quantifying either regional trends over the past 70 years (time series and species as  
146 random effects; Fig. S8) or spatial patterns in EOS<sub>50</sub> (year and species as random effects; Fig. S9). On  
147 average, European EOS<sub>50</sub> dates have been delayed by only +0.35 ± 0.02 days per decade (Fig. S8b). Yet,  
148 when keeping pre-solstice productivity constant by including it as a fixed effect in addition to year, the model  
149 predicts a delay of +0.81 ± 0.03 days per decade (Fig. S8d), showing that the increase in pre-solstice  
150 vegetation activity has offset up to ~60% of the delay in EOS<sub>50</sub> that would have occurred if pre-solstice  
151 productivity had not increased. This explains why EOS<sub>50</sub> delays have contributed only ~15% (2.4 ± 0.2 days)  
152 to the 16.7 ± 0.4 day-long extension of the growing season that has occurred over the past 70 years (Fig.  
153 S8a, b). The advancing effect of pre-solstice productivity on EOS dates is also evident across spatial  
154 gradients (Fig. S9 a,c), such that EOS<sub>50</sub> dates occur only +0.85 ± 0.03 days later for each 1°C increase in  
155 that region's autumn temperature, while they occur +1.40 ± 0.04 days °C<sup>-1</sup> later if the advancing effect of  
156 pre-solstice productivity is removed (39% reduction of the geographic autumn temperature response; Fig.  
157 S9 b,d).

158 The progression of senescence is modulated by autumn air temperature, as is evident from the  
159 delaying effect of warm autumns on EOS<sub>50</sub> dates (Figs. 2, 3 and 5 and Extended Data Fig. 6b,c). However,  
160 if increased pre-solstice vegetation activity and development (Extended Data Fig. 5a–b) indeed is the main  
161 driver of an earlier onset of EOS, one should find an ever earlier susceptibility of trees to autumn cooling.  
162 To test this, we conducted temporal moving-window analyses on the European long-term observations  
163 showing whether the reversal date – at which increased productivity and temperature start to be associated  
164 with delayed EOS<sub>50</sub> dates – has shifted over recent decades. The results reveal that this is the case, with  
165 reversal dates shifting to earlier dates by an average of -0.6 to -1.0 days per year (Fig. 3f and Figs. S5f–  
166 S7f or Fig. S10b for a shorter moving window). It is also reflected in the moving windows of monthly effect  
167 sizes, which show that July photosynthesis, temperature and radiation have been more strongly associated  
168 with delayed EOS<sub>50</sub> dates over recent decades (Fig. 3c and Figs. S5c–S7c). As an alternative method of  
169 determining when autumn cooling starts driving senescence progression, we modelled the autumn period  
170 best explaining EOS<sub>50</sub> dates and found that it has advanced by -0.20 ± 0.07 days per year for the 1966–  
171 2015 period (Extended Data Fig. 7a) or by -0.43 ± 0.09 days per year for the 1981–2015 period (Extended  
172 Data Fig. 7b). This earlier start of the period when trees react to autumn cooling provides further evidence  
173 for an earlier onset of senescence in response to increased early-season development.

174 Previous research has suggested a negative feedback between growing-season activity and  
175 autumn phenology, with increased activity driving earlier EOS<sup>9</sup>. These findings came from monitoring of  
176 European deciduous trees and neglected possible mediating effects of the annual day length cycle. The  
177 satellite data analysed here now reveal such negative feedback across the entire Northern Hemisphere  
178 temperate and boreal forest biome, implying a widespread constraint on future growing-season extensions  
179 in response to global warming. To disentangle the environmental drivers of this negative feedback, we ran  
180 univariate (Extended Data Fig. 8) and multiple linear regression models that included air temperature, solar  
181 radiation, and water availability in addition to spring budburst dates as predictor variables, all of which factors  
182 have been shown to affect leaf senescence dates<sup>8–10,21,35–37</sup> (Fig. 5 and Extended Data Fig. 9 or Fig. S11  
183 using soil moisture instead of precipitation to represent water availability). The results showed that leaf-out  
184 timing, cumulative radiation, and water availability had small effects on EOS<sub>10</sub> and EOS<sub>50</sub> dates (Fig. 5),  
185 suggesting that temperature-driven development and growth, rather than a constrained leaf lifespan,

186 radiation-induced leaf ageing, or drought effects, is driving the advancing effect of early-season vegetation  
187 activity on autumn phenology.

188 To further isolate the mechanisms driving the discovered reversal of the effects of global warming  
189 around the June solstice, we designed two experiments using a dominant European tree (*Fagus sylvatica*).  
190 In a first experiment, we cooled (day- / night-time temperature = 10°C / 5°C) and shaded (~84% light  
191 reduction) saplings during different times of the season. Pre-solstice temperature again had a strong  
192 advancing effect on autumn phenology, with cooling of trees in June causing a delay in EOS<sub>10</sub> and EOS<sub>50</sub>  
193 dates of  $+16.5 \pm 6.6$  days and  $+10.2 \pm 2.5$  days (mean  $\pm$  standard error), respectively, whereas cooling in  
194 July had no effect and August cooling tended to advance EOS dates (Fig. 4a and S12a), in full agreement  
195 with the global-scale remote sensing data and the European ground observations. The effect of shading  
196 was small before the June solstice and most pronounced during July – the month with the highest mean  
197 daily radiation and temperature – with  $+6.5 \pm 2.8$  days later EOS<sub>50</sub> under shade conditions. Radiation effects  
198 thus followed a different seasonal pattern than temperature, supporting a direct effect of radiation on leaf  
199 ageing<sup>22,36</sup>. Summer photosynthesis was equally reduced in both the shade and the temperature treatments  
200 by 52–72% compared to the control (Fig. S13). That pre-solstice temperature, but not pre-solstice light  
201 availability, affected EOS dates provides further support for the idea that accelerated growth and  
202 development under warmer temperatures, rather than photosynthesis- or UV-induced leaf ageing, are the  
203 main drivers of the pre-solstice effects on senescence dates.

204 In a second experiment, we tested the effects of elevated sink strength (nutrient addition) and soil  
205 moisture. In agreement with the idea that nitrogen supply governs the sink control of leaf development and  
206 senescence<sup>19</sup>, there was a strong delaying effect of extra nutrients on EOS dates, with  $+22 \pm 6$ -day (mean  
207  $\pm$  standard error) later EOS<sub>10</sub> and  $+14 \pm 5$ -day later EOS<sub>50</sub> in trees grown in nutrient-rich soils compared to  
208 trees grown in NPK-poor soils (Extended Data Fig. 10 and Fig. S14). Reduced soil moisture slightly delayed  
209 EOS dates (by ~2 days) up to a threshold at which complete soil dehydration led to premature leaf die-off  
210 (Extended Data Fig. 10 and Fig. S15). These experimental findings match our findings from European  
211 phenological gardens and satellite-derived *in situ* observations, in which direct precipitation or soil moisture  
212 had smaller effects than air temperature and early-season growth.

213 In conclusion, our Northern-Hemisphere-wide investigation of the seasonal drivers of autumn  
214 phenology shows a consistent reversal in the effects of global warming on leaf senescence timing after the  
215 summer solstice, present i) across large biogeographic ranges with varying pre-solstice growth (satellite  
216 data), ii) in four tree species with different spring phenologies (ground data), and iii) under controlled  
217 experimental conditions. These findings lend strong support to the idea that the annual day-length cycle  
218 mediates the seasonal control on EOS by vegetation activity and air temperature (Solstice-as-Phenology-  
219 Switch [SPS] hypothesis; Fig. 1). Hence, EOS variations emerge as the result of a complex synchronization  
220 between a trees' developmental state, seasonal variation in the circadian rhythm and climate fluctuations.  
221 This mediation provides a unifying framework to explain previous results on the seasonal effects of  
222 temperature on autumn phenology, in which the magnitude and direction of the temperature effect varied  
223 depending on the season<sup>15,17,18,31,38,39</sup>. Across the whole temperate and boreal forest area, warmer pre-  
224 solstice temperatures drive an earlier onset of senescence, while warmer post-solstice temperatures slow  
225 down the progression of senescence, suggesting that senescence will start earlier but progress more slowly  
226 in the future.

227 The reversal in how trees respond to temperature during the summer likely evolved as an adaptation  
228 to seasonal climates with harsh winters because it allows plants to reliably predict the progression of the  
229 seasons and prepare for winter dormancy long before the temperature actually starts dropping<sup>29</sup>. A response  
230 shift around the June solstice enables trees to initiate tissue maturation and the physiological processes of  
231 leaf senescence and nutrient resorption<sup>26</sup> in a fine-tuned balance between source and sink dynamics. Trees'  
232 physiological response to the annual day length cycle essentially calibrates their seasonal rhythms and  
233 mediates how they react to warm or cool temperatures, now and in the future. Improved models of plant  
234 development and growth under climate change will need to incorporate the reversal of warming effects  
235 around the summer solstice.

236

237   **Methods**  
238239   **Analysis of ground-sourced European phenology observations**  
240241   **Phenology data.** Direct observations of spring leaf-out and autumn leaf senescence dates for four dominant  
242   tree species from 1951–2015 were collected from the Pan European Phenology Project ([www.pep725.eu](http://www.pep725.eu))<sup>32</sup>,  
243   which provides open-access phenological data for Europe (mainly Germany, Switzerland, and Austria; Fig.  
244   S16). The start-of-season (SOS) was defined as the date when the first leaf stalks are visible (BBCH11).  
245   For a few time series, BBCH11 data was not available, and we used the date when 50% of leaf stalks are  
246   visible (BBCH13) instead. The end-of-season (EOS<sub>50</sub>) corresponded to the date when 50% of leaves had  
247   lost their green color (BBCH94). Alternatively, for time series for which BBCH94 data was not available, we  
248   used the date when 50% of leaves had fallen (BBCH95).  
249250   **Data cleaning.** Following ref<sup>40</sup>, we removed (i) individual time series with fewer than 15 years of leaf-out  
251   and leaf senescence observations, (ii) dates deviating from an individual's median more than 4 times the  
252   median absolute deviation, and (iii) time series for which the standard deviation of phenological observations  
253   across years was higher than 20 for leaf-out and 25 for leaf senescence. The thresholds differed because  
254   the mean absolute deviation for leaf-out time series was lower than that for leaf senescence. In total, we  
255   kept records of the four most abundant tree species in the database (*Aesculus hippocastanum*, *Betula*  
256   *pendula*, *Fagus sylvatica*, and *Quercus robur*) at 3,851 sites across Central Europe, resulting in a total of  
257   396,411 phenological observations (individuals x year) and 12,759 individual time series (with a median  
258   length of 33 years; minimally 15 years, maximally 65 years) during the period 1951–2015 (Fig. S16). The  
259   number of time series per species was 3,477 for *Aesculus hippocastanum*, 3,375 for *Betula pendula*, 3,050  
260   for *Fagus sylvatica*, and 2,857 for *Quercus robur*.  
261262   **Climate data.** For each site, information on air temperature, precipitation, air humidity, net and downward  
263   short-wave radiation, net long-wave radiation, and soil moisture (at 0–10 cm and 10–40 cm depth) at a  
264   spatial resolution of 0.25 arc degrees (approximately 25 km at the equator) and a cadence of 3 hours were  
265   derived from the Global Land Data Assimilation System (GLDAS)<sup>41</sup> for the period 1951–2015. We then  
266   calculated daily means for each of the climate variables and the day-time ( $T_{\text{day}}$ ) or night-time ( $T_{\text{night}}$ )  
267   temperature. To obtain  $T_{\text{day}}$  and  $T_{\text{night}}$ , we approximated hourly temperatures using the “stack\_hourly\_temps”  
268   R function from the chillR package<sup>42</sup>, and then calculated the means of all temperatures from sunrise to  
269   sunset or sunset to sunrise, respectively, whereby sunset and sunrise were calculated with the “daylength”  
270   function (chillR package) based on latitude and day-of-year information. Means of monthly atmospheric CO<sub>2</sub>  
271   concentrations for each degree of latitude were taken from the CMIP6 concentration dataset<sup>43</sup>. To represent  
272   soil water availability in the photosynthesis model (see next section), for each site, we extracted physical  
273   soil properties (clay and coarse fragment content) from world maps at 250 m spatial resolution through  
274   SoilGrids<sup>44</sup>. Soil texture was computed based on the texture-to-parameter conversion by ref<sup>45</sup>, using the  
275   Database of Hydraulic Properties of European Soils (HYPRES) implemented in the R package soiltexture<sup>46</sup>.  
276277   **Photosynthesis calculation.** We derived daily net daytime photosynthesis estimates (excluding night-time  
278   respiration) [ $\text{Anet}_{\text{day}}$ ] from two photosynthesis models, hereafter referred to as LPJ model and P model.  
279280   *LPJ model:*  $\text{Anet}_{\text{day}}$  was computed using empirical information on  $T_{\text{day}}$ , minimum and maximum daily  
281   temperature, air humidity, atmospheric CO<sub>2</sub>, short- and long-wave radiation, and soil moisture, following the  
282   coupled photosynthesis and stomatal conductance sub-model of LPJ-GUESS<sup>47</sup>. The temperature response  
283   of photosynthesis followed ref<sup>48</sup>, with the minimum temperature limit at 1°C, the maximum at 45°C, and the  
284   temperature optimum between 18°C and 25°C (see Fig. S17). To account for the effect of water availability  
285   on photosynthesis<sup>49</sup>, we included a daily water stress factor in our seasonal photosynthesis estimates, which  
286   was calculated following the water balance module of LPJ-GUESS<sup>50</sup>. The fraction of absorbed  
287   photosynthetically active radiation (fAPAR) was set to 0 before SOS and to 0.5 after the SOS date, since  
288   nearly half of the short-wave radiation is intercepted by the canopy<sup>45</sup>. See Supplementary Materials in Zani  
289   et al.<sup>9</sup> for a detailed description of the model and [Github](#) for the annotated R code.  
290290   *P model* (developed by Stocker et al.<sup>34</sup> and following the theory of refs<sup>51,52</sup>): Photosynthesis was computed  
as a function of  $T_{\text{day}}$ , vapor pressure deficit, atmospheric CO<sub>2</sub>, short-wave radiation, and relative soil

moisture (actual moisture relative to field capacity). In addition, information on elevation and the site-level ratio of actual over potential annual mean evapotranspiration was included to represent atmospheric pressure and average local aridity, respectively. Apparent quantum yield efficiency was set to 0.087, optimal leaf-internal/ambient CO<sub>2</sub> ratios (ci/ca) were calculated based on the method developed in ref<sup>51</sup>, and limitations in the photosynthetic capacity for electron transport (Jmax) were accounted for based on the method developed in ref<sup>52</sup>. As for the LPJ model, fAPAR was set to 0 before SOS. The P model was run via the rmodel function in the R package rmodel<sup>34</sup>.

**Analysis.** In total, we included seven variables in our analyses: LPJ-model photosynthesis, P-model photosynthesis, T<sub>day</sub> and T<sub>night</sub>, short-wave radiation, CO<sub>2</sub> levels, and precipitation.

Seasonal and monthly photosynthesis/climate: To obtain monthly photosynthesis, T<sub>day</sub>, and short-wave radiation values, we took the sums of daily photosynthesis and radiation values and the means of daily T<sub>day</sub> values for each month (January to October) [see e.g., Fig. 3a, b]. Similarly, we aggregated values of these variables for six 30-day intervals before, during, and after the June solstice (with 10-day steps), i.e., from May 13 to June 11, May 23 to June 21, June 2 to July 1, June 12 to July 11, June 22 to July 21, and July 2 to July 31 (see e.g., Fig. 3d). In addition, we summed the daily photosynthesis values for eight periods (SOS to May 22, SOS to June 21 [solstice], SOS to July 21, SOS to August 20, SOS to mean EOS<sub>50</sub>, May 22 to mean EOS<sub>50</sub>, June 21 [solstice] to mean EOS<sub>50</sub>, and July 21 to mean EOS<sub>50</sub>) [see e.g., Fig. 3e]. For T<sub>day</sub> and short-wave radiation we calculated the means for eight periods starting on 21 March instead of the variable SOS date.

*Autumn temperature intervals:* It is well known that cold temperatures at the end of the season accelerate the senescence process<sup>9,17,18</sup>, and, for each time series, we therefore determined the optimal autumn interval for which temperature explains most of the variation in EOS<sub>50</sub> dates. To do so, we ran linear regressions between EOS<sub>50</sub> dates and the temperature interval (T<sub>day</sub> or T<sub>night</sub>) 10 to 120 days before the average EOS<sub>50</sub> date of each time series (with 10-day steps). Relationships were evaluated using both the coefficient of determination (R<sup>2</sup>) values and the standardized coefficients (Extended Data Fig. 6c). These analyses showed slightly higher R<sup>2</sup>s and standardized coefficients for T<sub>night</sub> than for T<sub>day</sub>, and, for each time series, we therefore included the respective T<sub>night</sub> interval with the highest R<sup>2</sup> in the analyses (hereafter referred to as Autumn T<sub>night</sub>, see e.g., Fig. 3h).

*Models:* To test for the effects of photosynthesis and climate parameters during different times of the year on EOS<sub>50</sub> dates, we ran linear mixed models, implemented in the R package lme4<sup>53</sup>. All models included either both time series and species random effects, or only a time series random effect in case the model was run separately for each species. Both predictor and dependent variables were standardized – by subtracting the mean and dividing by the standard deviation – to obtain relative effect sizes. For the monthly models of photosynthesis, March to October values were included as predictors in the model, with March values representing the sum of January to March (Figs. 3 and S5). This aggregation was done because no or only very little photosynthesis occurred during the January-to-March period (average leaf-out date across all observations: 26 April). For the monthly T<sub>day</sub> model, January to October values were included as predictors (Fig. S6a,b). To characterize the effects of photosynthesis, T<sub>day</sub>, and short-wave radiation within 30-day-long intervals around the June solstice, we included the variable value within the respective interval and Autumn T<sub>night</sub> (to control for autumn temperature) as fixed effects (Figs. 3d and S5d–S7d). To characterize the seasonal effects of photosynthesis, T<sub>day</sub>, and short-wave radiation, we included the variable value within the respective interval as single fixed effect (Figs. 3e and S5e–S7e).

Finally, we ran mixed models based on the seasonal periods that emerged as the strongest drivers of leaf senescence, i.e., pre-solstice (leaf-out or March 21 to June 21) and post-solstice climate (June 22 to mean senescence date). Models were run separately for photosynthesis, T<sub>day</sub> and short-wave radiation, and we accounted for possible effects of water availability, atmospheric CO<sub>2</sub> concentration, and autumn temperature by additionally including the sums of pre-solstice (March 20 to June 21) and post-solstice (June 21 to mean time series senescence date) precipitation, annual CO<sub>2</sub> concentration, and Autumn T<sub>night</sub> as fixed effects (full model; Fig. 3g). To test for the individual effects of pre-solstice and post-solstice variables on model performance and predictions, we additionally ran models that only included either pre-solstice

photosynthesis,  $T_{\text{day}}$ , or radiation and pre-solstice precipitation (pre-solstice model) or post-solstice photosynthesis,  $T_{\text{day}}$ , or radiation and post-solstice precipitation (post-solstice model; Figs. 3g and S5g–S7g). To test for multicollinearity among covariates, we calculated variance-inflation factors – using the vif function implemented in the R package car<sup>54</sup>, for all models that contained multiple variables, i.e., the monthly and the full models. All VIFs were < 2, indicating sufficient independence among predictors.

*Moving-window analysis:* To test whether the relative effects of variables have been changing over the past decades, we additionally ran all above-mentioned mixed models separately for each 20-year time period from 1966–2015. To ensure that the long-term average climate of sites did not differ across the moving-window periods as a result of site-level differences, we excluded high-elevation sites > 600 m a.s.l. as they were underrepresented in earlier years. We then tested whether the average long-term (1948–2015) climate of sites included in each moving-window period differed between years and found no trend (Fig. S18), demonstrating that there is no systematic bias in the average site-level climate conditions among moving windows. Within each 20-year moving-window, time series with fewer than 15 years of observations were excluded. To ensure that all sites were equally represented in each moving-window period, we ran a reduced analysis with 15-year moving-window intervals for the 1980–2015 period, including only time series for which at least 30 years of observations were available in total during 1980–2015 and for which at least 12 years were available during each 15-year moving window (Fig. S10).

To estimate the reversal date of the climate-autumn phenology relationship at which increased temperature and productivity start to be associated with delayed EOS<sub>50</sub> dates, we conducted moving-window analyses of the monthly photosynthesis/climate effects. To do so, for each 20-year (Fig. 3f) or 15-year (Fig. S10b) moving-window, we interpolated the date at which the effect of monthly photosynthesis/climate crosses the zero line during summer (see e.g., Fig. 3a). The dates were inferred both across species (based on models including time series and species random effects) and separately for each species (based on models including only time series random effects; see e.g., Fig. 3f). To estimate the overall trend in the reversal dates over time, we ran a linear regression between the reversal date obtained for each moving window and year.

As an alternative to estimating the day at which autumn temperature starts driving senescence progression, for each moving window, we estimated the autumn temperature-sensitive period, based on the autumn period for which temperature best explained variation in EOS<sub>50</sub> dates (see above paragraph on *Autumn temperature intervals*) [Extended Data Fig. 7].

## Analysis of satellite-derived phenology observations

**Phenology data.** Spring leaf-out and autumn leaf senescence dates for the period 2001–2018 were collected from the MODIS Global Vegetation Phenology product (MCD12Q2 V6)<sup>55</sup>, which provides phenological metrics at 500 m spatial resolution for every vegetated pixel on land derived from time series of the 2-band Enhanced Vegetation Index (EVI2) calculated from MODIS Nadir Bidirectional Reflectance Distribution Function (BRDF)-Adjusted Reflectance (NBAR). SOS was defined as the date when EVI2 first crossed 15% of the segment EVI2 amplitude greenness. EOS was defined as the date when EVI2 last dropped by 10% (EOS<sub>10</sub>) or 50% (EOS<sub>50</sub>) of the segment EVI2 amplitude, representing the start of senescence and mid-greendown, respectively.

**Data cleaning.** We extracted phenology information for all Northern Hemisphere pixels classified as mixed, broadleaf deciduous, evergreen needleleaf, or deciduous needleleaf forest (tree cover >60%) by the MODIS land cover type map (MCD12Q1 V6)<sup>56</sup>. We removed pixels (i) for which phenology information for fewer than 15 years was available and (ii) for which the mean SOS occurred before March 1 or after May 31 and for which the mean EOS<sub>50</sub> occurred before July 18 and after November 30. We then aggregated the data to 0.25 arc-degree (27.8 km at the Equator) spatial resolution to match with the resolution of the climate data. This resulted in a total of 15,459 pixels of which 60% (9,240) are classified as mixed forest, 19% (2,958) as broadleaf deciduous forest, 19% (3,004) as evergreen needleleaf forest, and 2% (257) as deciduous needleleaf forest.

398     **Analysis.** As for the ground-sourced phenology data, climate and soil moisture information at a spatial  
399 resolution of 0.25 arc degrees were derived from the Global Land Data Assimilation System (GLDAS)<sup>41</sup>.  
400 Information on gross primary production (GPP) was extracted from the MODIS Gross Primary Productivity  
401 product (MOD17A2H V6)<sup>33</sup>, which provides an 8-day composite dataset at 500 m spatial resolution. In total,  
402 we included eight variables in our analyses: GPP, LPJ model-derived  $A_{net_{day}}$ ,  $T_{day}$  and  $T_{night}$ , short-wave  
403 radiation,  $CO_2$  levels, precipitation, and soil moisture (at 0–40 cm depth).

404  
405     *Seasonal and monthly photosynthesis/climate:* To obtain monthly photosynthesis,  $T_{day}$ , and short-wave  
406 radiation values, we took the sums (GPP, LPJ model  $A_{net_{day}}$ , and P model  $A_{net_{day}}$ ) or means ( $T_{day}$ , short-  
407 wave radiation) of daily values for each month. Similarly, we aggregated values of these variables for six  
408 30-day intervals with 10-day moving steps around the June solstice (see 1.5.1 for details).

409  
410     Autumn temperature intervals: The optimal autumn intervals at which temperature has the strongest effect  
411 on senescence dates were calculated as described in the above section *Analysis of ground-sourced*  
412 *European phenology observations – Autumn temperature intervals.* For EOS<sub>50</sub> dates, these analyses  
413 showed slightly higher R<sup>2</sup>s and standardized coefficients for  $T_{day}$  than for  $T_{night}$  (Extended Data Fig. 6b), and,  
414 for each time series, we therefore included the respective  $T_{day}$  interval with the highest R<sup>2</sup> in the analyses  
415 (hereafter referred to as Autumn  $T_{day}$ , Extended Data Fig. 2h,j and Figs. S2h and S4h). For EOS<sub>10</sub> dates,  
416 we found no delaying effect of any autumn temperature interval (Extended Data Fig. 6a) and we therefore  
417 did not control for autumn temperature in the analyses.

418  
419     *Models:* To test for the effects of photosynthesis and climate parameters during different times of the year  
420 on autumn senescence dates, we ran pixel-level linear models. Both predictor and dependent variables  
421 were standardized to obtain relative effect sizes. To run the monthly models, we included the relative  
422 photosynthesis/climate value of each month (January to October) in a multivariate model. For the monthly  
423 effects of photosynthesis and short-wave radiation on EOS<sub>10</sub> dates, only April to September values were  
424 included as predictors in the model, with April values representing the sums of January to April (Fig. 2g). To  
425 characterize the effects of photosynthesis,  $T_{day}$ , and short-wave radiation within 30-day-long intervals  
426 around the June solstice on EOS<sub>10</sub> dates, we included the variable value within the respective interval as  
427 single fixed effect (see e.g., Fig. 2h), whereas we additionally included Autumn  $T_{day}$  (to control for autumn  
428 temperature) as fixed effect when testing for the effects on EOS<sub>50</sub> dates (see e.g., Extended Data Fig. 2).  
429 We then ran models including information on pre-solstice (sum of photosynthesis from leaf-out to June 21  
430 or mean of  $T_{day}$  and radiation from March 20 to June 21) and post-solstice vegetation activity / climate (sum  
431 or mean from June 22 to mean senescence date). Models were run separately for photosynthesis,  $T_{day}$  and  
432 short-wave radiation, and we accounted for possible effects of water availability, atmospheric  $CO_2$   
433 concentration, and autumn temperature by additionally including the sums of pre-solstice (March 20 to June  
434 21) and post-solstice (June 22 to mean time series senescence date) precipitation, annual  $CO_2$   
435 concentration, and Autumn  $T_{day}$  (only for EOS<sub>50</sub> dates) as fixed effects (full model; Fig. 2f). To test for the  
436 explanatory power of pre-solstice variables on inter-annual variation in the timing of EOS, we ran univariate  
437 models that included either pre-solstice GPP,  $T_{day}$ , radiation, soil moisture or leaf-out date as single effect  
438 (Extended Dta Fig. 8).

439     To approximate the end of the period during which early-season vegetation activity exhibited an  
440 advancing effect on the onset of senescence, we ran pixel-level linear regression models between gross  
441 primary productivity (GPP) and EOS<sub>10</sub> dates. GPP summation always started at the day of leaf-out and  
442 ended at different dates, using 30-day steps. For each pixel, we then kept the period with the most negative  
443 (advancing) effect on EOS<sub>10</sub> dates. Extended Data Fig. 4 shows the estimated end date (red line) and  
444 starting date (leaf-out date; green line) of this period along latitude, whereby pixel-level estimates were  
445 averaged for each degree latitude.

446     To test for decadal-scale temporal trends in EOS dates, we additionally ran mixed effects models  
447 where pixels are treated as grouping variables of random intercepts, (including only year or year and pre-  
448 solstice photosynthesis, temperature or radiation as fixed effects (Fig. 2i-k). )

452      **Experiments**

453  
454      **Experiment 1 – Seasonal temperature and light manipulation.** The experiment was conducted in Zurich,  
455      Switzerland, between March and December 2021. Three-year old *Fagus sylvatica* trees were used to  
456      observe the seasonal effects of cooling and shading (9 treatments: 1 control, 4 temperature and 4 shade  
457      treatments) on autumn phenology. Plants were obtained from a local nursery in February 2021, transferred  
458      to 20 l plastic pots containing a 1:1:1 sand / peat / organic soil mixture with a Nitrogen (N) concentration of  
459      ~65 g m<sup>-3</sup>, a Phosphate (P<sub>2</sub>O<sub>5</sub>) concentration of ~140 g m<sup>-3</sup>, and a Potassium (K<sub>2</sub>O) concentration of ~400  
460      g m<sup>-3</sup>.

461      We exposed trees to cooling or shading conditions during four 1 month-long periods (30 April – 30  
462      May [hereafter referred to as May treatment], 26 May – 25 June [June treatment], 26 June – 26 July [July  
463      treatment], and 27 July – 26 August [August treatment]). The experimental and observational unit was a pot  
464      with a single individual. The control consisted of 38 trees growing outside under full sun conditions. The  
465      treatments consisted of 14 trees each. In the cooling treatments, trees were kept in a climate chamber with  
466      a night-time temperature of 5°C and a day-time temperature of 10°C, and simulating ambient day length  
467      and light intensities. In the shading treatments, trees were exposed to shade conditions using a shading net  
468      that intercepted c. 84% ( $\pm$  10%; mean  $\pm$  SD) of the PAR experienced by the control treatment. All trees were  
469      watered regularly to keep soil moisture constant.

470      To quantify seasonal changes in leaf chlorophyll content, we measured the relative chlorophyll  
471      content at, on average, 4 wk intervals during summer and 1 wk intervals from mid-September until  
472      December with a SPAD-502 Plus (Soil Plant Analysis Development, Minolta Camera Co., Ltd, Tokyo,  
473      Japan). Per individual, SPAD readings from nine leaves were averaged, whereby we randomly selected  
474      three leaves from the top, middle and lower parts of the tree crown. SPAD readings were then transferred  
475      to total chlorophyll content (*Chl* in  $\mu\text{g/g}$  fresh weight) using an empirically established equation for *Fagus*  
476      *sylvatica* leaves<sup>57</sup>:

$$Chl = -0.0029 \times SPAD^2 + 1.175 \times SPAD + 3.8506$$

477      To calculate individual-level leaf chlorophyll content, we additionally included the percentage of leaf  
478      abscission in autumn for each individual, that is, the already-dropped leaves in autumn have a chlorophyll  
479      content of 0. For example, an individual that lost already 50% of leaves with a chlorophyll content of 30 for  
480      the remaining leaves has a total chlorophyll content of 15 (30  $\times$  0.5). The chlorophyll content between two  
481      consecutive measurement dates was estimated using linear interpolation. Finally, we calculated individual  
482      leaf senescence dates as the day-of-year when chlorophyll content last fell below 90% (EOS<sub>10</sub>) or 50%  
483      (EOS<sub>50</sub>) of the maximum chlorophyll content in summer. Because the shading treatment caused short-term  
484      changes in chlorophyll content that do not reflect autumn phenological responses, chlorophyll  
485      measurements during the treatment until two weeks after the respective treatment period were excluded for  
486      the determination of autumn phenology.

487      Leaf net photosynthesis (CO<sub>2</sub> uptake per leaf area) was monitored on a monthly basis from May to  
488      July on one leaf of 3–13 individuals per treatment using a portable infrared gas analyzer (LI-6800, Li-  
489      Cor, Lincoln, NE) with a 3 x 3 cm leaf chamber. Leaf chamber temperature during the measurements reflected  
490      the mean day-time (8.00 – 15.00) temperature experienced by each treatment in the respective month, leaf  
491      chamber light intensities reflected the mean light intensities experienced by each treatment in the respective  
492      month. Humidity was set to 65%, leaf chamber CO<sub>2</sub> to 400 ppm. Measurements were taken between 2 to  
493      6 hours after sunrise with replicate individuals of each treatment done on four consecutive days.

494      To test for differences in leaf senescence dates among treatments, we ran multivariate linear  
495      models including temperature and shade treatments as categorical variables.

496      **Experiment 2 – Nutrient and soil moisture manipulation.** The experiment was conducted in Zurich,  
497      Switzerland (450 m a.s.l.) between June and December 2020. Sixty three-year old *Fagus sylvatica* trees  
498      were obtained from a local nursery in February 2020, transferred to 20 l plastic pots containing a 50/50  
499      sand/peat mixture, and kept outdoors under uniform conditions until the start of the experiment (15 June  
500      2020). Due to Covid19 restrictions, the experiment could not begin until June 15, but all trees were watered  
501      once a week to keep soil moisture constant. During the experiment (June 15 – December 1), all trees were  
502      kept outdoors and arranged in randomized blocks.

The experiment followed a 2 x 4 full-factorial design with two nutrient treatments (high versus low nitrogen, phosphorous, and potassium) and four irrigation treatments (High, Intermediate, Low, and No irrigation), resulting in a total of eight treatment combinations (Extended Data Fig. 10). The experimental and observational unit was a pot with a single individual. Each irrigation treatment consisted of 14 individuals of which eight individuals were exposed to high-nutrient and seven to low-nutrient conditions. In the *High Irrigation* treatment, plants were watered regularly (on average, every 3rd day); in the *Intermediate Irrigation* treatment, plants were watered every other time (i.e., every ~6 days); in the *Low Irrigation* treatment, plants were watered every fourth time (i.e., every ~12 days); in the *No Irrigation* treatment, plants were not watered and received only natural precipitation. On June 15 and August 12, the trees of the high-nutrient treatment were fertilized with 20 g organic NPK fertilizer (DCM ECO-XTRA 1), containing 8% nitrogen (1.6 g N), 5% phosphorous (1 g P<sub>2</sub>O<sub>5</sub>) and 6% potassium (1.2 g K<sub>2</sub>O). On July 15, all trees received 0.4 g micronutrients (DCM MICRO-MIX). For each irrigation treatment, soil moisture was measured weekly in 6 randomly chosen individuals. We observed strong differences in soil moisture among the irrigation treatments, with a median soil moisture between June and September of 22.1%, 11.4%, 7.6%. and 4.6% for the *High*, *Intermediate*, *Low*, and *No* irrigation treatments, respectively (Fig. S15a,b).

Leaf chlorophyll content measurements and autumn phenology scoring were done as in Experiment 1. Chlorophyll measurements were conducted at, on average, 2 wk intervals during summer and 1 wk intervals during October.

To test for differences in leaf senescence dates among treatments, we ran multivariate linear models including nutrient and irrigation treatment as categorical variables. We additionally included an interaction term between treatments to test if nutrient or irrigation effects depended on the other treatment but found no significant effect ( $P = 0.74$ ).

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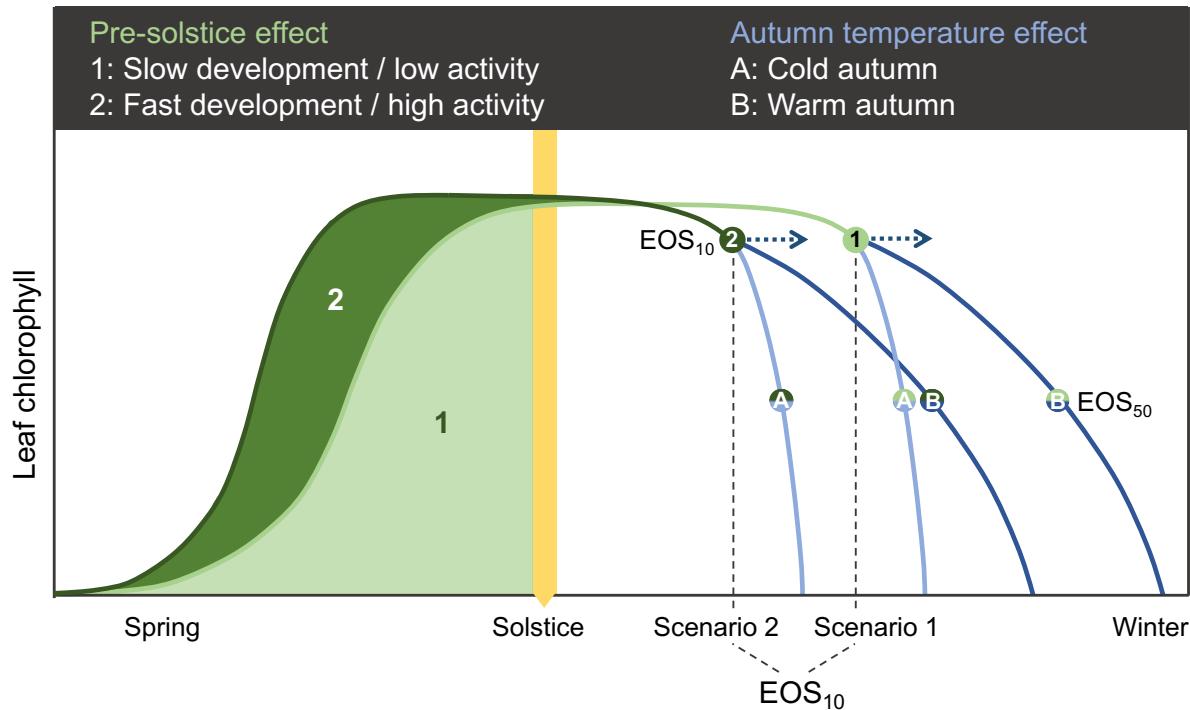
660 **Statement of authorship:** CMZ conceived and developed the study and wrote the first draft of the  
661 manuscript. LM contributed to the development of the study and the remote-sensing analysis. RB, DP and  
662 CMZ conducted the experiments. LMo contributed to the analysis. TWC, SSR, LM, YV, YHF and BDS  
663 contributed to the writing.

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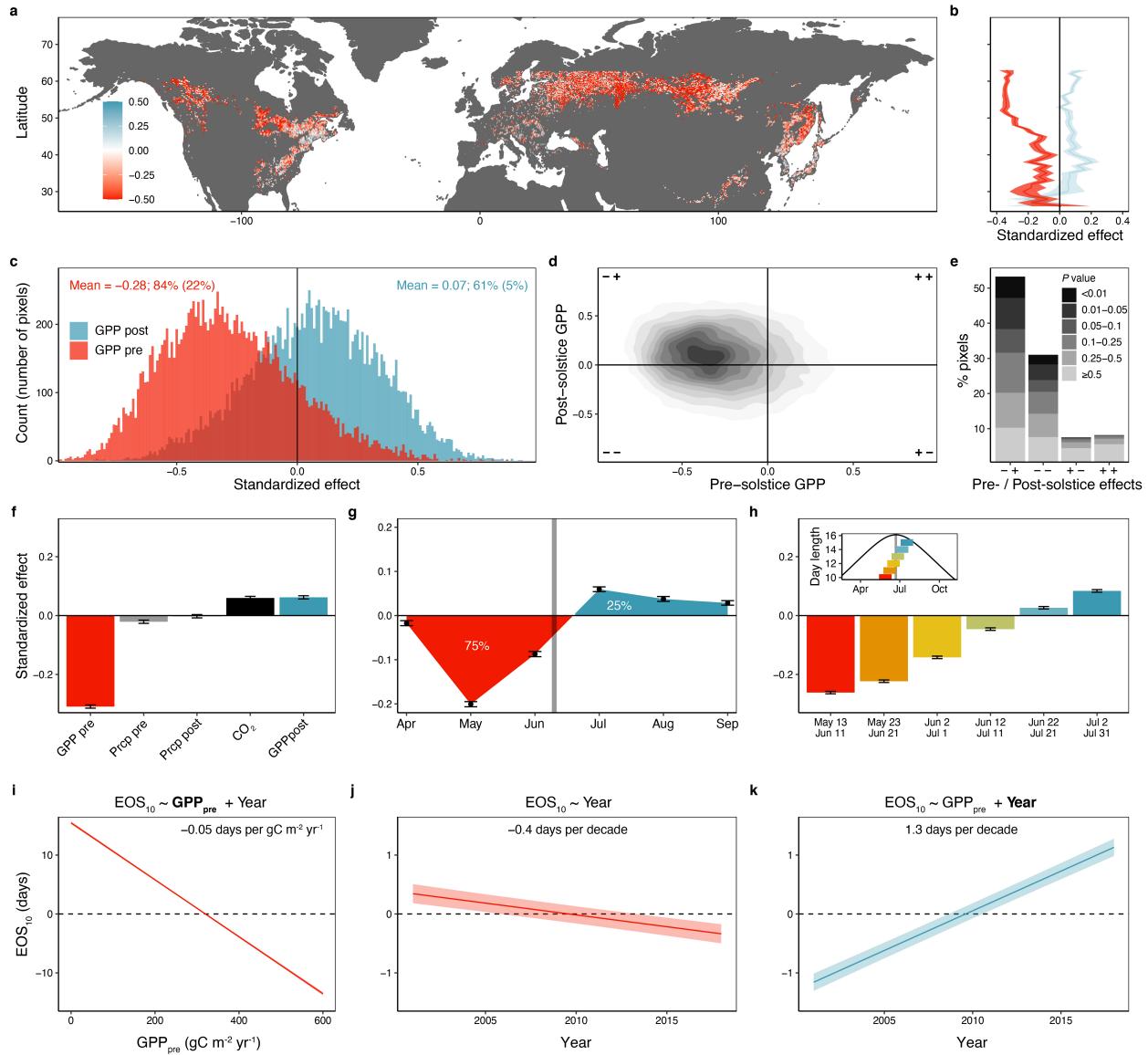
666   **Data and materials availability:** All source code and experimental data are available on github  
667   (<https://github.com/ConstantinZohner/AutumnPhenologySPS>). The PEP725 data used for this study are  
668   freely available at [www.PEP725.eu](http://www.PEP725.eu). The satellite-derived phenology observations are freely available at  
669   <https://doi.org/10.5067/MODIS/MCD12Q2.006>.

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671   **Competing interests:** The authors declare that there are no competing interests.  
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673 **Figures**  
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677  
678 **Fig. 1. Conceptual model of autumn phenological responses to pre-solstice and post-solstice**  
679 **growth and temperature (Solstice-as-Phenology-Switch [SPS] hypothesis).** The onset of autumnal  
680 senescence is estimated in this study as the date when the greenness index last dropped by >10% of the  
681 seasonal maximum (end-of-season, EOS<sub>10</sub>). In northern forests, stem growth and development rates and  
682 photosynthetic capacity are highest before the summer solstice and decline with shortening days<sup>25–27</sup>, the  
683 adaptive reason being the limited time remaining for tissue maturation and bud set before the first frost.  
684 According to the model, inter-annual variation in EOS<sub>10</sub> should be a function of pre-solstice growth due to  
685 developmental constraints on leaf longevity, with later EOS<sub>10</sub> in years with slow development / low activity  
686 before the solstice (scenario 1) and earlier EOS<sub>10</sub> in years with fast development / high activity (scenario 2).  
687 The progression of leaf senescence varies with autumn temperature, with faster chlorophyll breakdown in  
688 cold-autumn years (scenario A) than in warm-autumn years (scenario B), and the dates of 50% chlorophyll  
689 loss (EOS<sub>50</sub>) are therefore the combined result of pre- and post-solstice effects. An earlier start of  
690 senescence in high-activity years (scenario 2) also predicts that trees will become sensitive to autumn  
691 cooling earlier than in low-activity years (see blue arrows). Four fundamental predictions arise from this  
692 model that were tested in this study: 1) Enhanced pre-solstice vegetation activity should drive earlier EOS<sub>10</sub>  
693 (scenario 1 versus 2). 2) There should be a reversal of growth and temperature effects around the time of  
694 the summer solstice. 3) Autumn temperature should affect the speed of senescence and thus have a  
695 delaying effect on EOS<sub>50</sub> dates (scenario A versus B), but only little effect on EOS<sub>10</sub> dates. 4) The date when  
696 trees become sensitive to autumn temperature (blue arrows) should have advanced over recent decades  
697 because of an earlier onset of senescence (EOS<sub>10</sub>).



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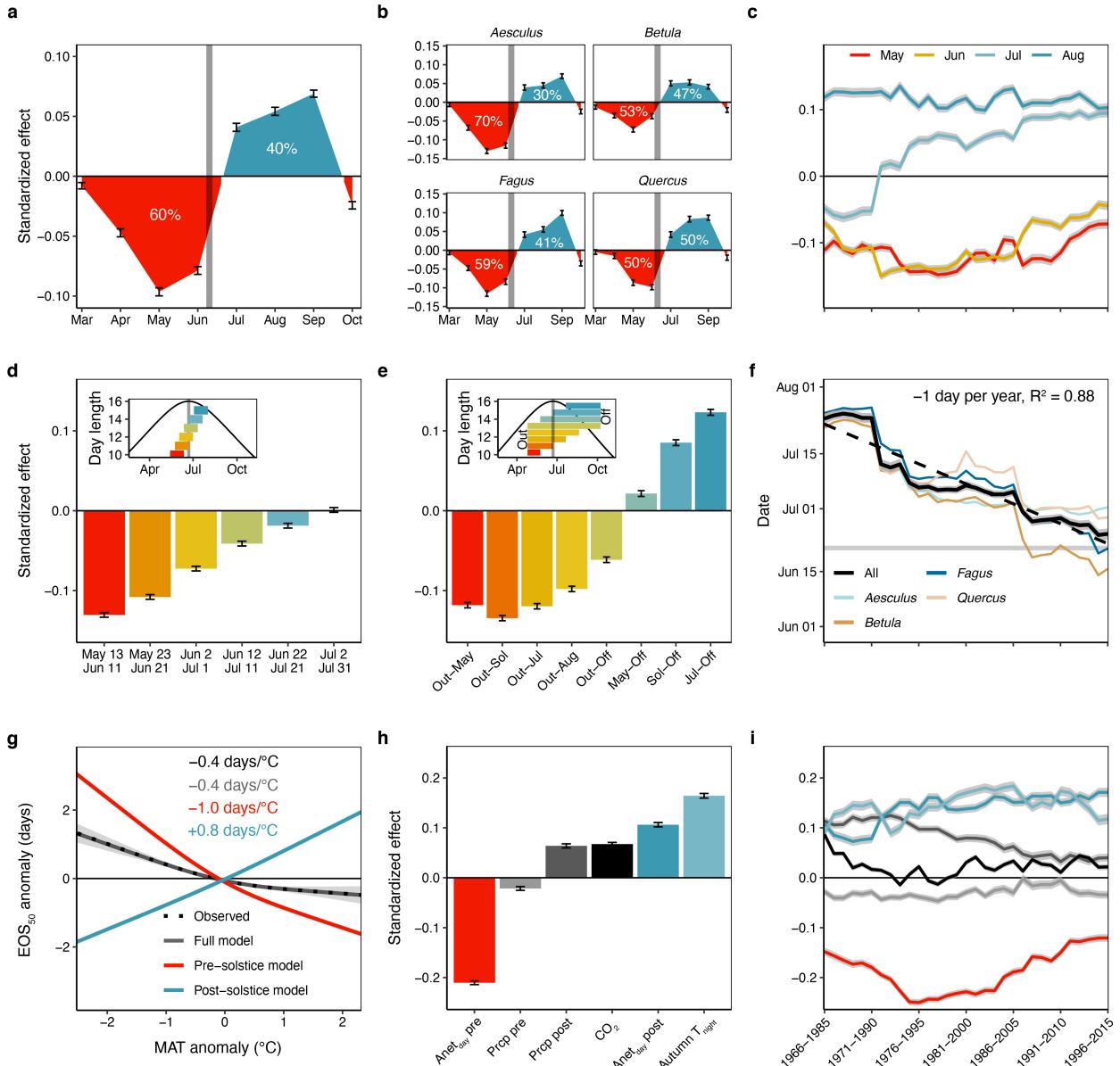
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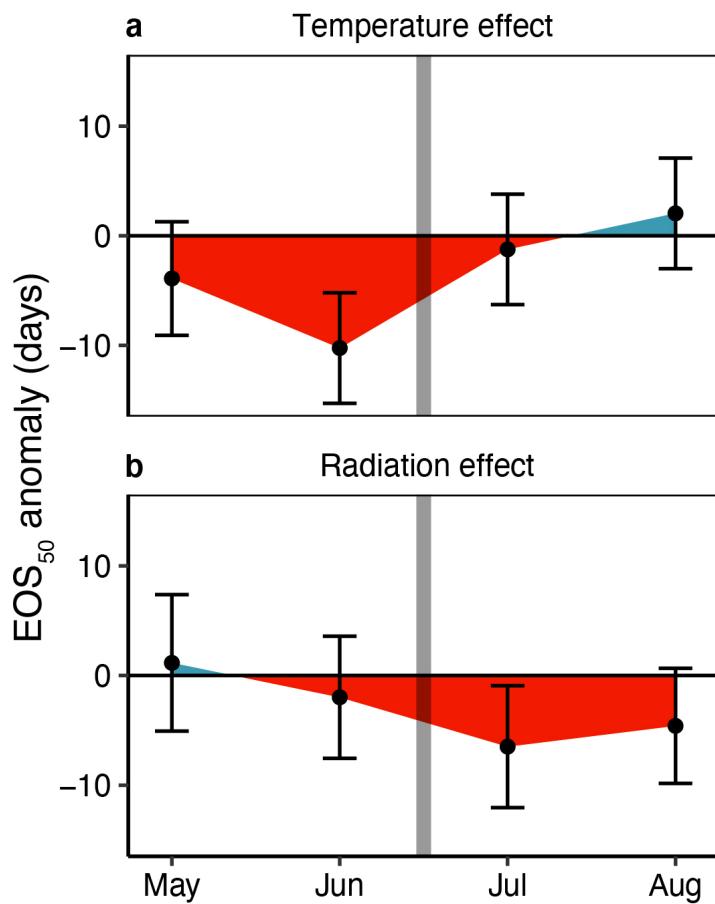
**Fig. 2. Satellite observations reveal consistent advances in the onset of senescence (EOS<sub>10</sub>) across northern forests in response to enhanced pre-solstice vegetation activity.** **a**, Map showing the standardized effects of pre-solstice (leaf-out to solstice) gross primary productivity (GPP) on EOS<sub>10</sub> timing at 0.25° resolution from linear models, including pre-solstice GPP and post-solstice (solstice to mean senescence) GPP as predictor variables. Red pixels indicate an earlier EOS<sub>10</sub> under enhanced pre-solstice GPP, blue pixels indicate a delayed EOS<sub>10</sub>. **b**, Effect size means and 95% confidence ranges summarized for each degree latitude (pre-solstice effects in red, post-solstice effects in blue). **c**, The distribution of the pre-solstice and post-solstice GPP effects across all pixels. Mean pre- and post-solstice GPP effect sizes and the percentage of pixels with an advancing pre-solstice GPP effect or delaying post-solstice GPP effect shown as red and blue text, respectively (percentage of significant pixels at  $P < 0.05$  in brackets). **d**, Two-dimensional density plot of pre- and post-solstice GPP effects. **e**, Barplot summarizing the effect direction across all analysed pixels. Grey scale indicates significance levels of pre-solstice GPP effects. **f**, The effects of pre-solstice and post-solstice GPP, pre-solstice (21 March to solstice) and post-solstice precipitation (prcp), and atmospheric CO<sub>2</sub>. **g**, Relationship between monthly GPP and EOS<sub>10</sub> dates. Percentages reflect the total positive and negative areas under the curve, i.e., the relative advancing versus delaying effects of day length. **h**, Day length vs month. **i**, **j**, **k**, Relationships between EOS<sub>10</sub> and GPP<sub>pre</sub> + Year.

714 seasonal GPP. **h**, The univariate effects of one-month-long GPP intervals around the summer solstice (May  
715 13 to June 11, May 23 to June 21, June 2 to July 1, June 12 to July 11, June 22 to July 21, and July 2 to  
716 July 31; see inset). Analyses in **f-h** show effect size means and 95% confidence ranges from pixel-level  
717 linear models with both predictor and dependent variables standardized. **i-j**, Mean effects ( $\pm 95\%$  confidence  
718 ranges) of pre-solstice GPP and year on  $EOS_{10}$  anomalies from mixed effects models where pixels are  
719 treated as grouping variables of random intercepts. **i**, Partial effect of pre-solstice GPP on  $EOS_{10}$  anomalies,  
720 including both pre-solstice GPP and year as fixed effects. **j**, Temporal trend in  $EOS_{10}$  anomalies with year  
721 as single fixed effect. **k**, Partial effect of year on  $EOS_{10}$  anomalies, where both pre-solstice GPP and year  
722 are treated as fixed effects.  
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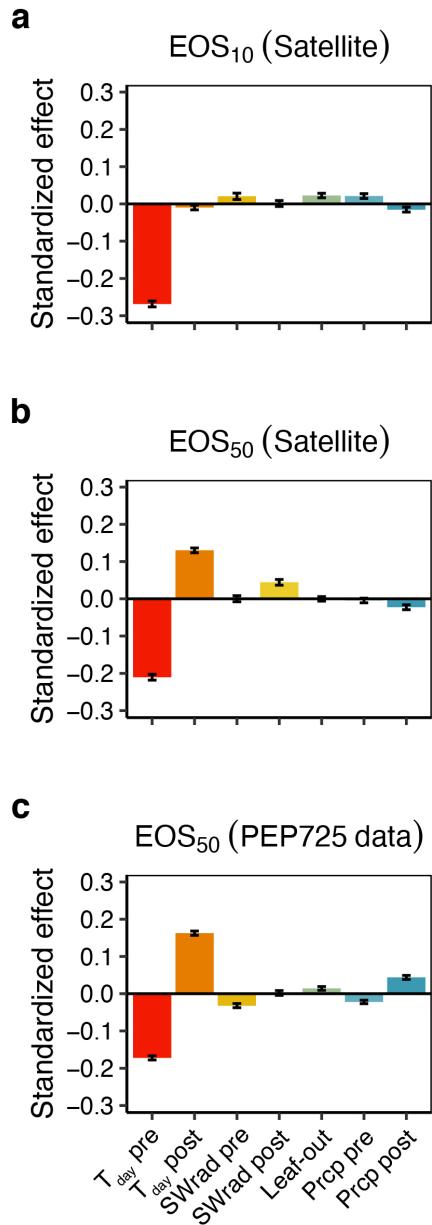


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 725 **Fig. 3. Relationships between seasonal photosynthesis and the timing of mid-senescence (EOS<sub>50</sub>)**  
 726 **from European long-term observations (PEP725 data).** **a,** Effects of monthly (March to October)  
 727 photosynthesis on EOS<sub>50</sub> dates. Percentages reflect the relative advancing versus delaying effects of  
 728 seasonal photosynthesis on EOS<sub>50</sub> dates. **b,** Species-level results with percentages as in panel a. **c,** Moving-  
 729 window analysis, showing the effects of May (leaf-out to 31 May), June, July, and August/September (1  
 730 August to 30 September) photosynthesis for each 20-year time period from 1966 to 2015. **d,** Effects of one-  
 731 month-long photosynthesis intervals around the summer solstice (May 13 to June 11, May 23 to June 21,  
 732 June 2 to July 1, June 12 to July 11, June 22 to July 21, and July 2 to July 31; see inset), including the  
 733 respective photosynthesis interval and autumn night-time temperature (Autumn T<sub>night</sub>) as fixed effects. **e,**  
 734 The effects of cumulative photosynthesis from leaf-out to May 22 (Out-May), leaf-out to solstice (Out-Sol),  
 735 leaf-out to July 21 (Out-Jul), leaf-out to August 20 (Out-Aug), leaf-out to mean EOS<sub>50</sub> (Out-Off), May 22 to  
 736 mean EOS<sub>50</sub> (May-Off), solstice to mean EOS<sub>50</sub> (Sol-Off), and July 21 to mean EOS<sub>50</sub> (Jul-Off), including  
 737 the respective photosynthesis interval as single fixed effect. **f,** Moving-window analysis, showing the  
 738 'reversal' dates when the photosynthesis effect switches from negative to positive for each 20-year time

739 period from 1966 to 2015 (based on monthly correlations, see panels **a–c**). On average, the reversal date  
740 advanced by 1 day per year. **g–i**, The effects of pre-solstice (leaf-out to solstice) and post-solstice (solstice  
741 to mean EOS<sub>50</sub>) photosynthesis, pre-solstice (21 March to solstice) and post-solstice precipitation,  
742 atmospheric CO<sub>2</sub>, and Autumn T<sub>night</sub>. **g**, Model predictions in response to mean annual temperature (MAT)  
743 anomalies (black dashed line: observed trend; black solid line: full model prediction including pre- and post-  
744 solstice effects; red line: model prediction including only pre-solstice photosynthesis and precipitation and  
745 CO<sub>2</sub> as predictors; blue line: model prediction including only post-solstice photosynthesis and precipitation,  
746 CO<sub>2</sub>, and Autumn T<sub>night</sub>). **h**, Standardised effects. **i**, 20-year moving-window analysis of the effects (colours  
747 as in panel **h**). Analyses show effect size means  $\pm$  2 s.e. from linear mixed models, including time series  
748 and species (**a,c–i**) or only time series (**b,f**) as random effects, with both predictor and dependent variables  
749 standardized.  
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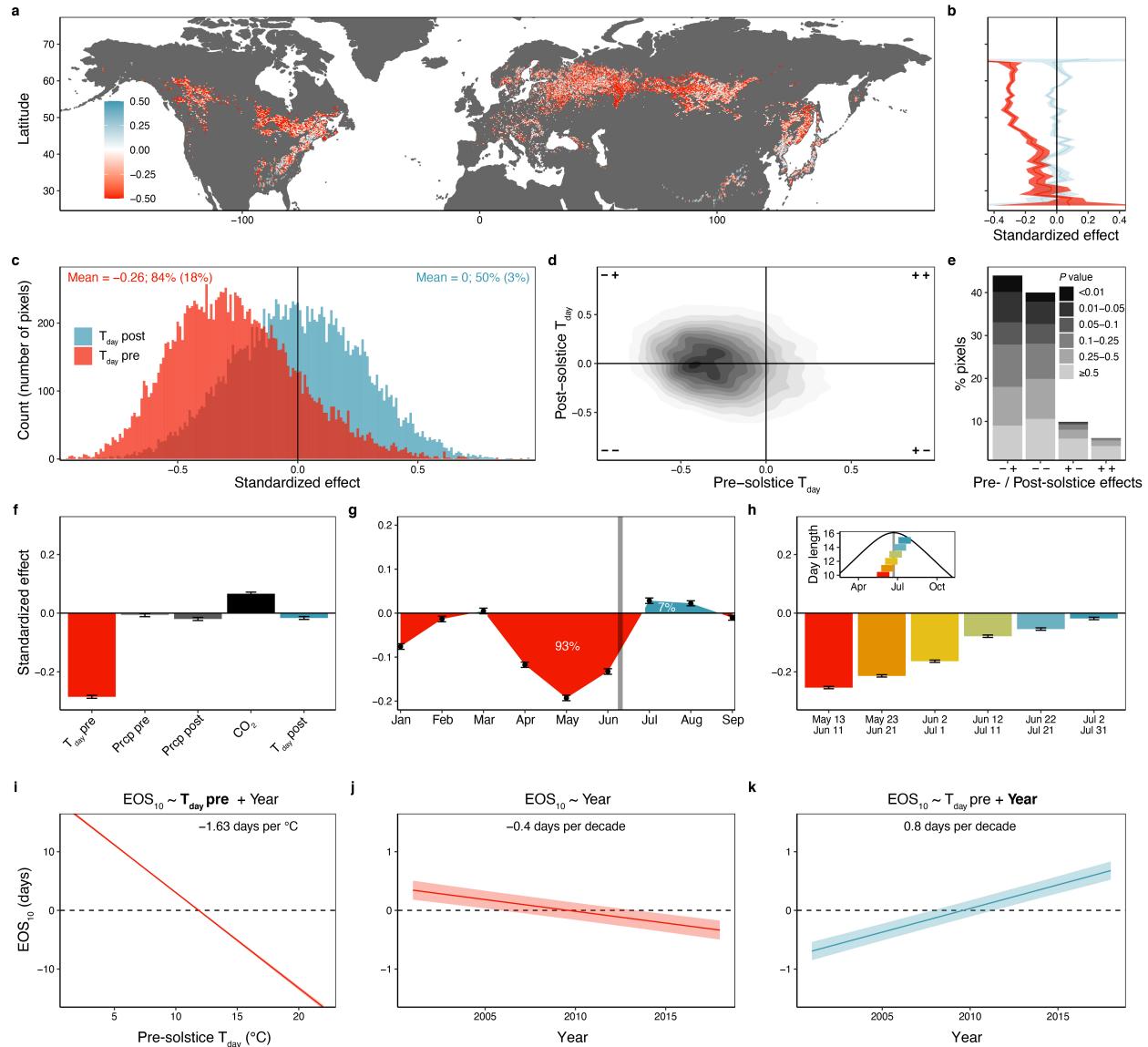
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 752 **Fig. 4. The seasonal effects of temperature (a) and shading (b) on autumn phenology in European**  
 753 **beech from experiment 1.** Effects of monthly (May to August) cooling (a) and shading (b) treatments on  
 754 EOS<sub>50</sub> dates. Analyses show effect size means  $\pm$  95% confidence intervals from linear models, including  
 755 treatment as fixed effect. Note that effect directions were reversed to facilitate comparison with Figs. 2 and  
 756 3, i.e., negative values indicate EOS<sub>50</sub> advances under warmer (a) or brighter (b) conditions. See methods  
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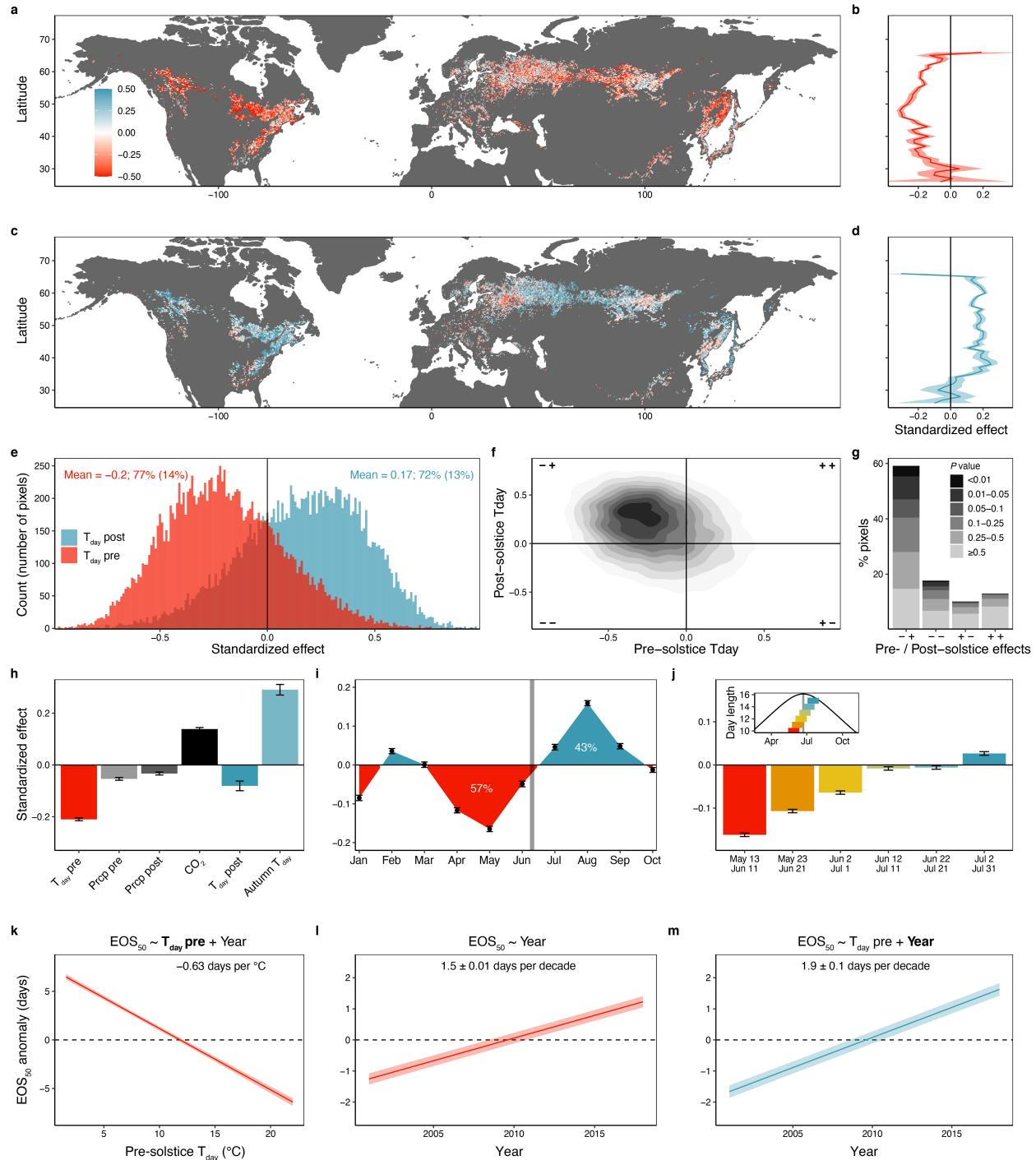
**Fig. 5. The effects of pre- and post-solstice temperature, radiation, water availability and spring leaf-out dates on inter-annual variation in the timing of EOS<sub>10</sub> (a) and EOS<sub>50</sub> (b, c).** We ran linear models including mean day-time temperature ( $T_{\text{day}}$ ) and short-wave radiation (SWrad) and the sums of precipitation (prcp) from March 20 to June 21 (pre-solstice) and from June 22 to the mean EOS date of each time series (post-solstice) as well as spring leaf-out dates as predictor variables. Models were run at the pixel-level (a, b) or individual-level (c) and the mean effects ( $\pm 95\%$  confidence intervals) are shown. All variables were standardized to allow for effect size comparison.

768 **Extended Data Figures**  
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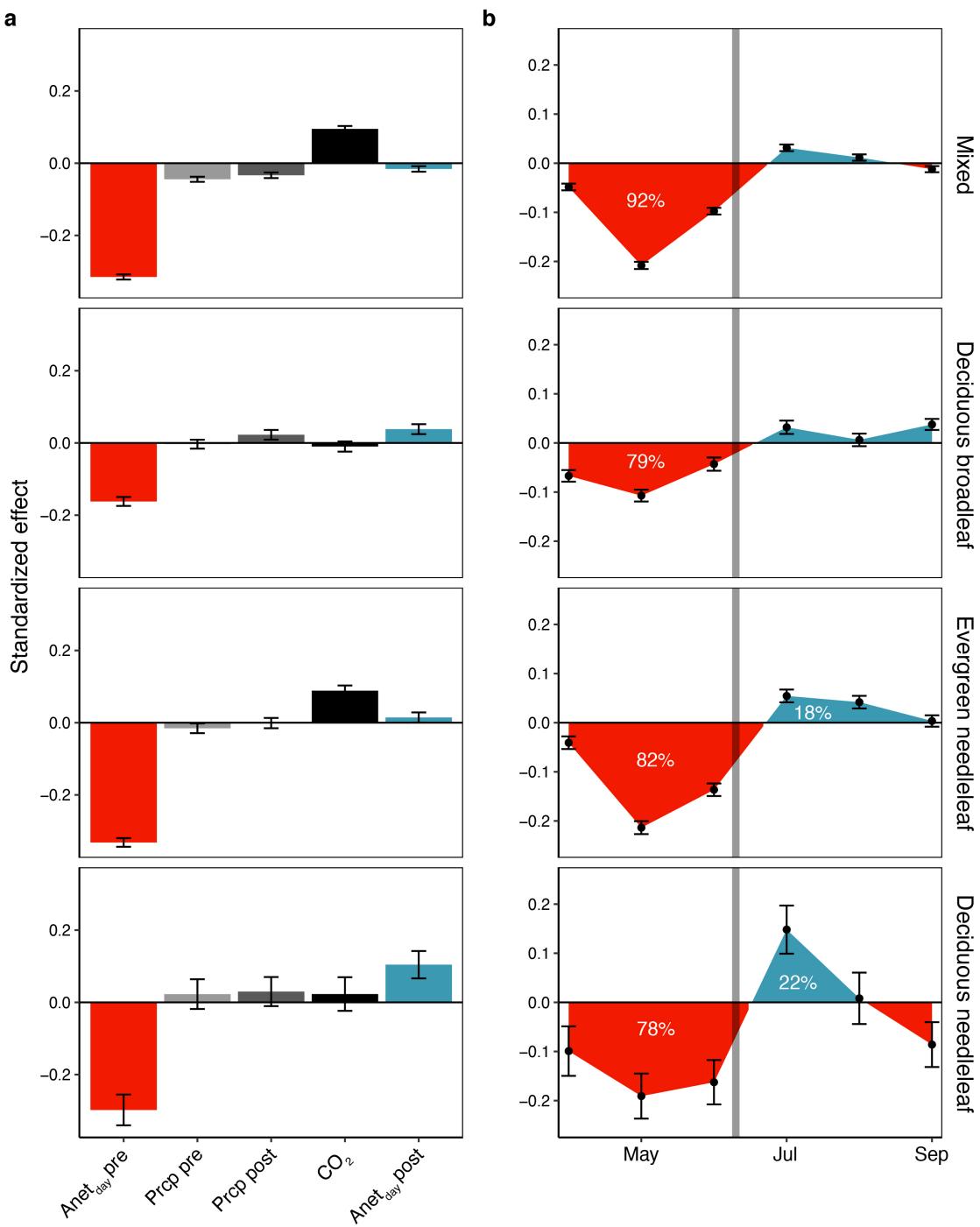
**Extended Data Fig. 1. The seasonal effects of day-time temperature ( $T_{\text{day}}$ ) on inter-annual variation in senescence onset (EOS<sub>10</sub> dates) [same as Fig. 2 but using  $T_{\text{day}}$  as predictor variable].** **a**, Map showing the standardized effects of pre-solstice (leaf-out to solstice)  $T_{\text{day}}$  on EOS<sub>10</sub> timing at 0.25° resolution from linear models, including pre-solstice  $T_{\text{day}}$  and post-solstice (solstice to mean senescence)  $T_{\text{day}}$  as predictor variables. Red pixels indicate an earlier EOS<sub>10</sub> under enhanced pre-solstice  $T_{\text{day}}$ , blue pixels indicate a delayed EOS<sub>10</sub>. **b**, Effect size means and 95% confidence ranges summarized for each degree latitude (pre-solstice effects in red, post-solstice effects in blue). **c**, The distribution of the pre-solstice and post-solstice  $T_{\text{day}}$  effects across all pixels. Mean pre- and post-solstice  $T_{\text{day}}$  effect sizes and the percentage of pixels with a negative pre-solstice  $T_{\text{day}}$  or positive post-solstice  $T_{\text{day}}$  effect (percentage of significant pixels at  $P < 0.05$  in brackets) shown as red and blue text, respectively. **d**, Two-dimensional density plot of pre- and post-solstice  $T_{\text{day}}$  effects. **e**, Barplot summarizing the effect direction across all analysed pixels. Grey scale indicates significance levels of pre-solstice  $T_{\text{day}}$  effects. **f**, The effects of pre-solstice and post-solstice  $T_{\text{day}}$ , pre-solstice (21 March to solstice) and post-solstice precipitation, and atmospheric CO<sub>2</sub>. **g**, Relationship between monthly  $T_{\text{day}}$  and EOS<sub>10</sub> dates. Percentages reflect the total positive and negative areas under the curve, i.e., the relative advancing versus delaying effects of seasonal  $T_{\text{day}}$ . **h**, The univariate effects of one-month-long  $T_{\text{day}}$  intervals around the summer solstice (May 13 to June 11, May 23 to June 21, June 2 to July 1, June 12 to July 11, June 22 to July 21, and July 2 to July 31; see inset). Analyses in **f-h** show effect size means and 95% confidence ranges from pixel-level linear models with both predictor and dependent variables standardized. **i-j**, Mean effects ( $\pm 95\%$  confidence ranges) of pre-solstice  $T_{\text{day}}$  and year on EOS<sub>10</sub> anomalies from mixed effects models where pixels are treated as grouping variables of random intercepts. **i**, Partial effect of pre-solstice  $T_{\text{day}}$ , including both pre-solstice  $T_{\text{day}}$  and year as fixed effects. **j**, Temporal trend in EOS<sub>10</sub> anomalies with year as single fixed effect. **k**, Partial effect of year, where both pre-solstice  $T_{\text{day}}$  and year are treated as fixed effects.

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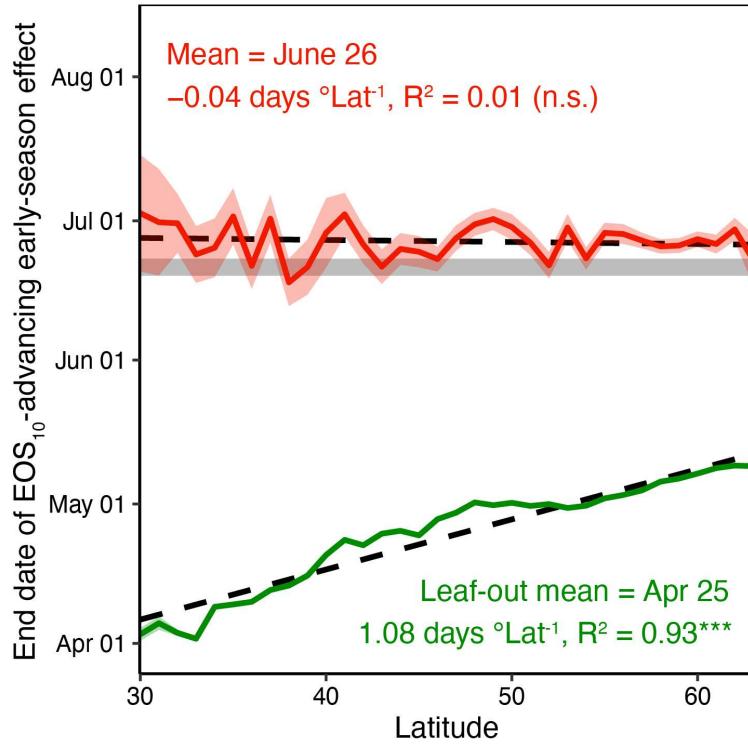


**Extended Data Fig. 2. The seasonal effects of  $T_{\text{day}}$  on inter-annual variation in mid-senescence ( $\text{EOS}_{50}$  dates). a, c, Maps showing the standardized effects of pre-solstice  $T_{\text{day}}$  (leaf-out to solstice; a) and post-solstice  $T_{\text{day}}$  (solstice to mean  $\text{EOS}_{50}$ , b) on  $\text{EOS}_{50}$  timing at  $0.25^{\circ}$  resolution from linear models, including pre-solstice  $T_{\text{day}}$  and post-solstice  $T_{\text{day}}$  as predictor variables. Red pixels indicate an earlier  $\text{EOS}_{50}$  under higher pre-solstice or post-solstice  $T_{\text{day}}$ , respectively, blue pixels indicate a delayed  $\text{EOS}_{50}$ . b, d, Effect size means and 95% confidence ranges summarized for each degree latitude (pre-solstice effects in red (b), post-solstice effects in blue (d)). e, The distribution of the pre-solstice and post-solstice  $T_{\text{day}}$  effects across all pixels. Mean pre- and post-solstice  $T_{\text{day}}$  effect sizes and the percentage of pixels with a negative pre-solstice  $T_{\text{day}}$  or positive post-solstice  $T_{\text{day}}$  effect (percentage of significant pixels at  $P < 0.05$  in brackets) shown as red and blue text, respectively. f, Two-dimensional density plot of pre- and post-solstice  $T_{\text{day}}$  effects. g, Barplot summarizing the effect direction across all analysed pixels. Grey scale indicates significance levels of pre-solstice  $T_{\text{day}}$  effects. h, The effects of pre-solstice and post-solstice  $T_{\text{day}}$ , pre-solstice (21 March to solstice) and post-solstice precipitation, atmospheric**

801 CO<sub>2</sub>, and autumn T<sub>day</sub>. **i**, Relationship between monthly T<sub>day</sub> and EOS<sub>50</sub> dates. Percentages reflect the total positive and negative areas  
802 under the curve, i.e., the relative advancing versus delaying effects of seasonal T<sub>day</sub>. **j**, The univariate effects of one-month-long T<sub>day</sub>  
803 intervals around the summer solstice (May 13 to June 11, May 23 to June 21, June 2 to July 1, June 12 to July 11, June 22 to July 21,  
804 and July 2 to July 31; see inset). Analyses in **h–j** show effect size means and 95% confidence ranges from pixel-level linear models  
805 with both predictor and dependent variables standardized. **k–m**, Mean effects ( $\pm 95\%$  confidence ranges) of pre-solstice T<sub>day</sub> and year  
806 on EOS<sub>50</sub> anomalies from mixed effects models where pixels are treated as grouping variables of random intercepts. **k**, Partial effect  
807 of pre-solstice T<sub>day</sub>, including both pre-solstice T<sub>day</sub> and year as fixed effects. **l**, Temporal trend in EOS<sub>50</sub> anomalies with year as single  
808 fixed effect. **m**, Partial effect of year, where both pre-solstice T<sub>day</sub> and year are treated as fixed effects.  
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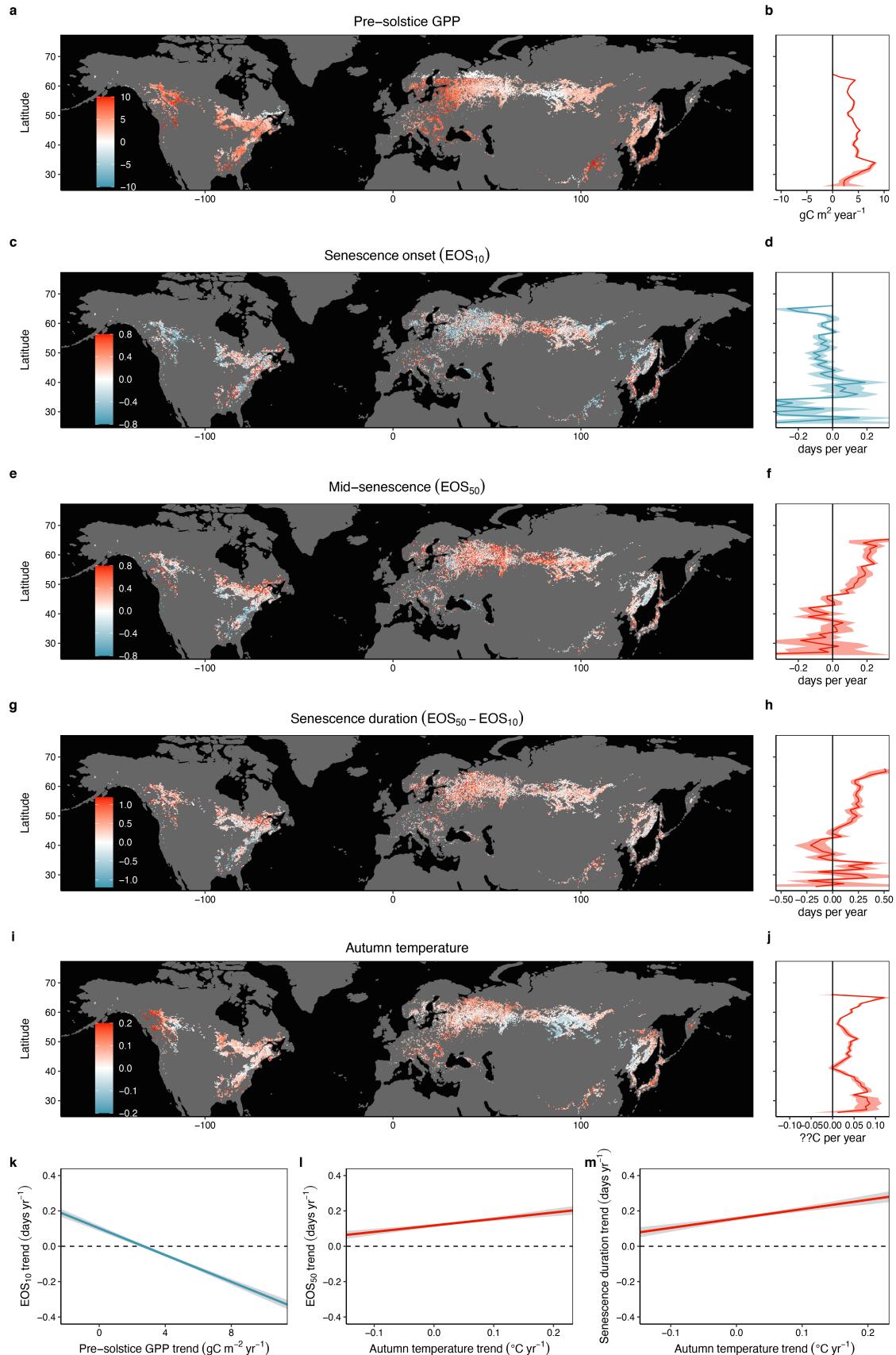


810  
 811 **Extended Data Fig. 3. Relationships between seasonal productivity (Anet<sub>day</sub>) and the timing of**  
 812 **senescence onset (EOS<sub>10</sub>) within mixed, deciduous broadleaf, deciduous needleleaf, and evergreen**  
 813 **needleleaf forests.** a, The effects of pre-solstice and post-solstice Anet<sub>day</sub>, pre-solstice (21 March to  
 814 the solstice) and post-solstice precipitation, and atmospheric CO<sub>2</sub> on EOS<sub>10</sub> dates. b, Relationship  
 815 between monthly Anet<sub>day</sub> and EOS<sub>10</sub> dates. Percentages reflect the total positive and negative areas under the curve,  
 816 i.e., the relative advancing versus delaying effects of seasonal Anet<sub>day</sub>.  
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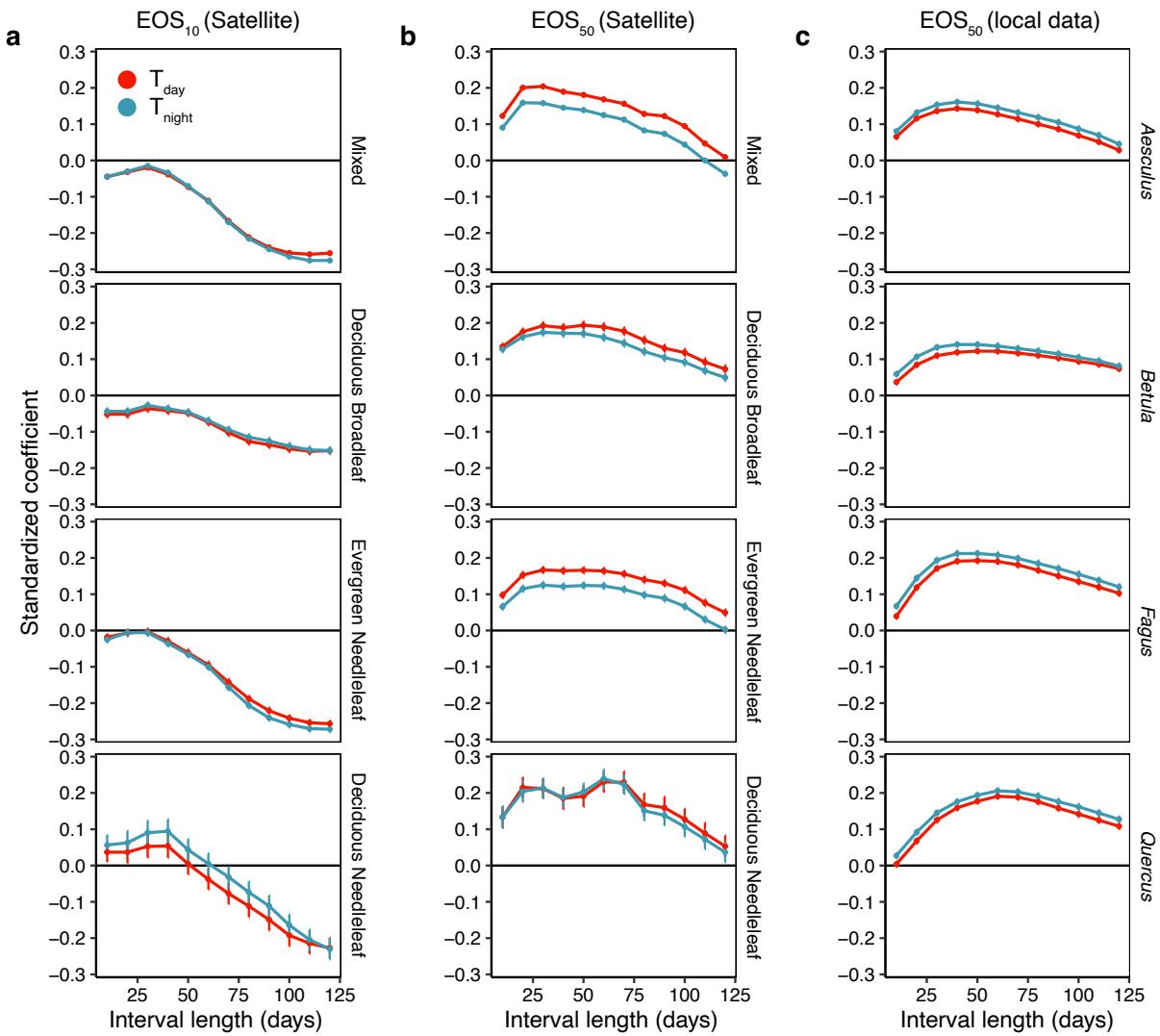


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**Extended Data Fig. 4. End date (red line) of the early-season growth period exhibiting an advancing effect on the onset of senescence ( $\text{EOS}_{10}$ ).** Pixel-level linear regression models were applied to test for the effect of gross primary productivity (GPP) on  $\text{EOS}_{10}$  dates. GPP summation always started at leaf-out and ended at different dates, using 30-day steps. For each pixel, we then obtained the period that showed the most negative effect on  $\text{EOS}_{10}$  dates. The red line shows the end date of this period along latitude, whereby pixel-level estimates were averaged for each degree latitude. Across the entire latitudinal range, the end date of the early-season effect consistently occurred right after the summer solstice at June ~26. Red text shows the mean date as well as the slope and  $R^2$  for the correlation between latitude and the end date of the early-season effect ( $R^2 = 0.01$ ). The green line represents the average spring leaf-out dates for each degree latitude, showing an average delay in leaf-out of 1.08 days per each degree increase in northern latitude ( $R^2 = 0.93$ ). Grey line represents the summer solstice (21 June). Non-significant (n.s.):  $P > 0.05$ ; \*\*\*  $P < 0.001$ .

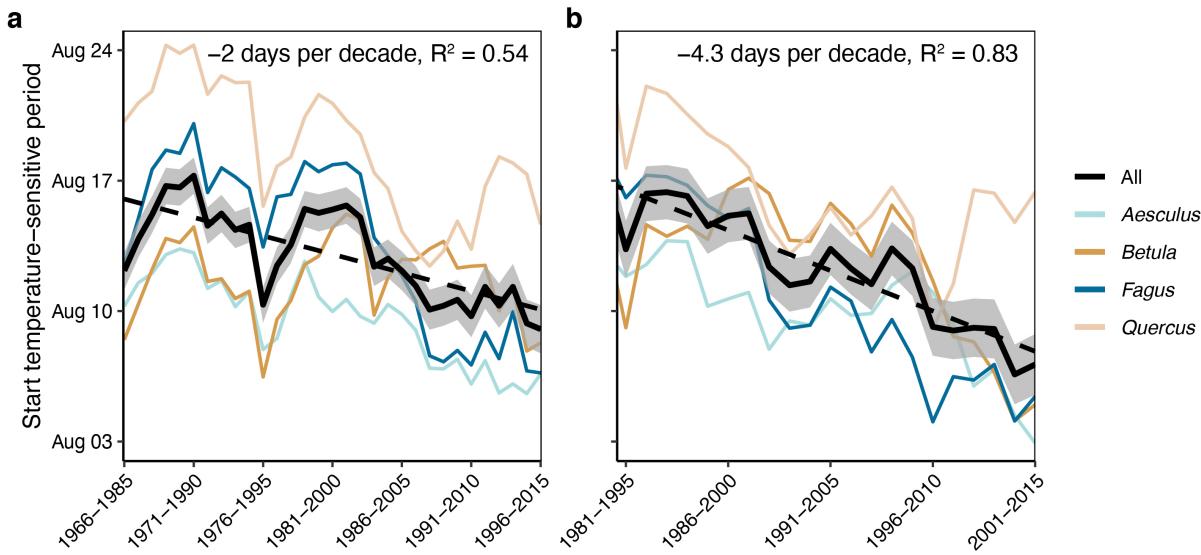


834 **Extended Data Fig. 5. Temporal trends in (a) pre-solstice gross primary productivity [GPP], (c)**  
835 **senescence onset ( $\text{EOS}_{10}$ ) dates, (e) mid-senescence ( $\text{EOS}_{50}$ ) dates, (g) senescence duration ( $\text{EOS}_{10}$ -**  
836 **to- $\text{EOS}_{50}$ ) and (i) autumn temperature at  $0.25^\circ$  resolution for the 2001–2018 period.** Red pixels indicate  
837 delays in  $\text{EOS}_{10/50}$  dates (c, e), a longer duration of the senescence period (g), or increases in pre-solstice  
838 GPP (a) or autumn temperature (i); blue pixels indicate advances in  $\text{EOS}_{10/50}$ , a shorter duration of the  
839 senescence period, or decreases in pre-solstice GPP and autumn temperature. b, d, f, h, j, Trend means  
840 and 95% confidence ranges summarized for each degree latitude. All trends were inferred from linear,  
841 univariate models. k-m, Linear regression ( $\pm 95\%$  confidence interval) between pixel-level temporal trends  
842 in k) pre-solstice GPP and  $\text{EOS}_{10}$  dates, l) autumn temperature and  $\text{EOS}_{50}$  dates, and m) autumn  
843 temperature and senescence duration. Areas with large increases in pre-solstice GPP also show larger  
844 advances in  $\text{EOS}_{10}$  dates, whereas areas in which GPP has been declining tend to show delays in  $\text{EOS}_{10}$   
845 (k). Areas with large increases in autumn temperature show larger delays in  $\text{EOS}_{50}$  dates (l) and,  
846 accordingly, a prolongation of senescence duration (m). Autumn temperature represents the mean day-time  
847 autumn temperature for the autumn period that was most highly correlated with  $\text{EOS}_{50}$  dates (Autumn  $T_{\text{day}}$ ;  
848 see *Autumn temperature intervals* in methods section).  
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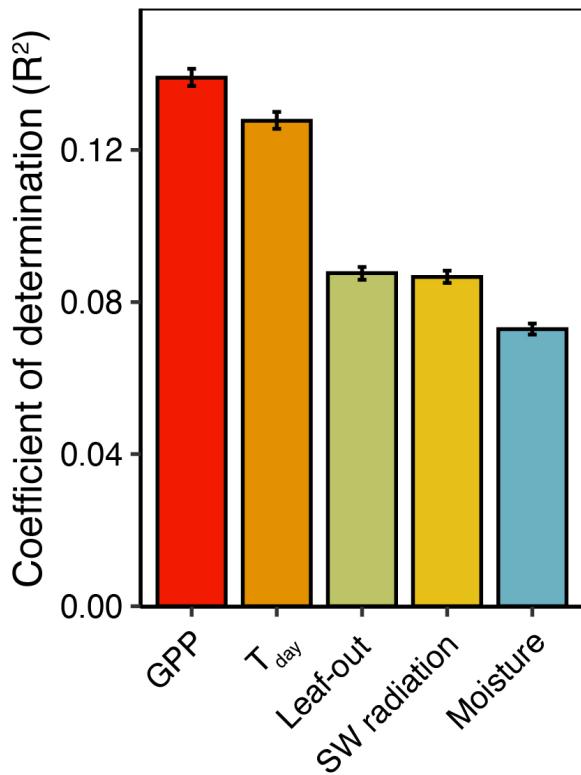
**Extended Data Fig. 6. The effect of autumn temperature on  $\text{EOS}_{10}$  (a) and  $\text{EOS}_{50}$  dates (b,c).**  
 Standardized regression coefficients for the univariate correlations between autumn temperature intervals and EOS dates. Temperature intervals refer to the mean night-time ( $T_{\text{night}}$ ) or day-time ( $T_{\text{day}}$ ) temperatures for the periods 10 to 120 days before the mean  $\text{EOS}_{10}$  or  $\text{EOS}_{50}$  date at each time series. Models were run at the pixel-level (a, b) or individual-level (c) and the mean time series-level effects ( $\pm 95\%$  confidence intervals) are shown separately for mixed, deciduous broadleaf, evergreen needleleaf, and deciduous needleleaf forests for the satellite-based analyses and for the four European species included in the PEP725 dataset.

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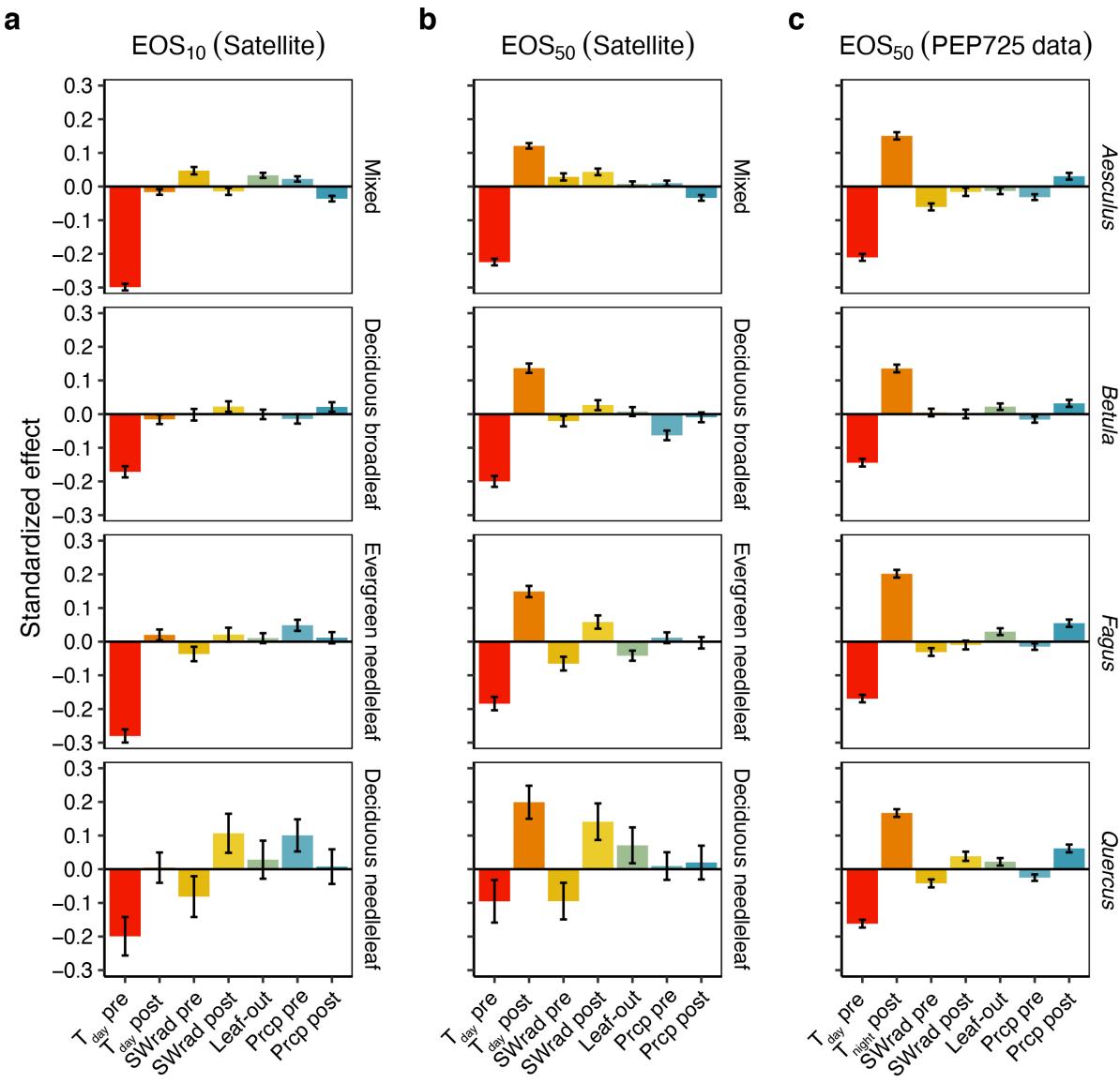
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**Extended Data Fig. 7. Moving-window analysis based on European long-term observations (PEP725 data), showing the average dates when trees became sensitive to autumn temperatures for each 20-year time period from 1966 to 2015 (a) and for each 15-year time period from 1981 to 2015 (b).** Coloured lines indicate species-specific results, the black line represents the mean ( $\pm 95\%$  confidence interval) across all species, the black dashed line indicates the trend from a linear model. This trend line shows that the start date of the temperature-sensitive autumn period advanced by  $2.0 \pm 0.7$  days (mean  $\pm 95\%$  confidence interval) per decade (a) or by  $4.3 \pm 0.9$  days per decade for the 1981–2015 period (b).



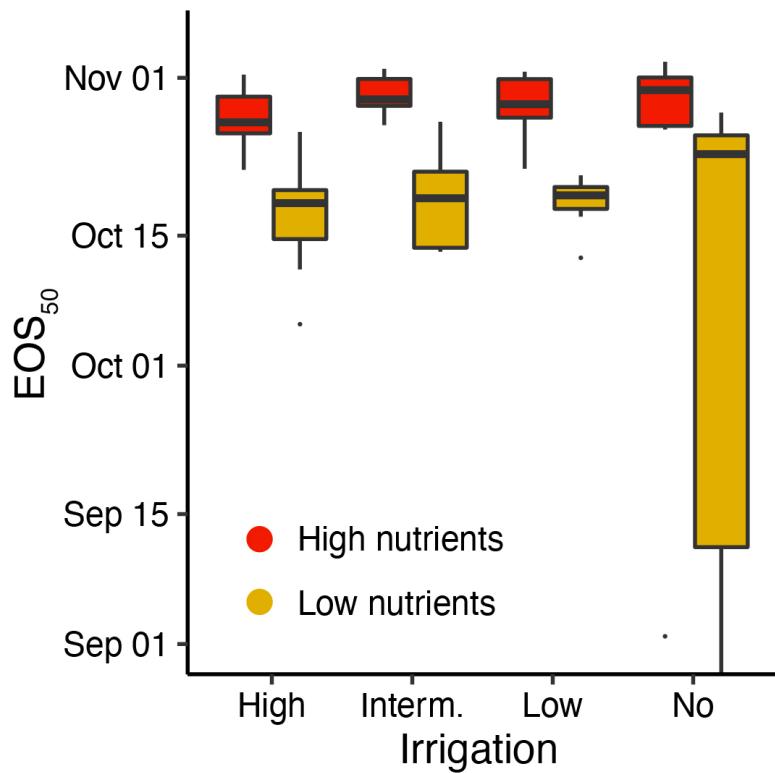
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**Extended Data Fig. 8. Coefficients of determination for the univariate effects of pre-solstice productivity (GPP), pre-solstice temperature, spring leaf-out dates, pre-solstice short-wave radiation, and pre-solstice soil moisture on the timing of senescence onset ( $\text{EOS}_{10}$ ).** For each variable, we ran univariate linear models, with GPP representing the cumulative productivity from leaf-out to June 21 (summer solstice),  $T_{\text{day}}$ , SW radiation, and moisture representing the average day-time temperature, short-wave radiation, or soil moisture from March 20 to June 21, and leaf-out representing the spring leaf-out date in the respective year. Models were run at the pixel-level and the mean coefficients of determination ( $\pm 95\%$  confidence intervals) are shown.



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**Extended Data Fig. 9. The effects of pre- and post-solstice temperature, radiation, precipitation and spring leaf-out dates on inter-annual variation in the timing of EOS<sub>10</sub> (a) and EOS<sub>50</sub> (b, c) for each forest type (a,b) and tree species (c). We ran linear models including mean day-time temperature ( $T_{\text{day}}$ ) and short-wave radiation (SWrad) and the sums of precipitation (prcp) from March 20 to June 21 (pre-solstice) and from June 22 to the mean EOS date of each time series (post-solstice) as well as spring leaf-out dates as predictor variables. Models were run at the pixel-level (a, b) or individual-level (c) and the mean effects ( $\pm 95\%$  confidence intervals) are shown separately for mixed, deciduous broadleaf, evergreen needleleaf, and deciduous needleleaf forests for the satellite-based analyses and for the European species included in the PEP725 dataset. All variables were standardized to allow for effect size comparison.**



**Extended Data Fig. 10. Results of the nutrient and drought experiment.** EOS<sub>50</sub> dates (day of 50% chlorophyll loss) for the eight treatment combinations, i.e., low and high soil nutrient status and no, low, intermediate and high irrigation.  $P < 0.01$  for the nutrient treatment and  $P = 0.17$  for the irrigation treatment.

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## Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- [ZohneretalSPSSupplement.pdf](#)