

1 *Article*

2 **Leaf senescence exhibits stronger climatic responses during warm than during**
3 **cold autumns**

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20 **A warmer world could extend growing seasons for plants. Changes in spring**
21 **phenology have been studied, yet autumn phenology remains poorly understood.**
22 **Using >500,000 phenological records of four temperate tree species between 1951 and 2013**
23 **in Europe, we show that leaf senescence in warm autumns exhibits significantly**
24 **stronger climate responses, with a higher phenological plasticity, than in cold autumns,**
25 **indicating a nonlinear response to climate. The onset of leaf senescence in warm autumns was**
26 **delayed due to the stronger climate response, primarily caused by nighttime warming.**
27 **However, daytime warming, especially during warm autumns, imposes a drought stress**
28 **which advances leaf senescence. This may counteract the extension of growing season under**
29 **global warming. These findings provide guidance for more reliable predictions of plant**
30 **phenology and biosphere-atmosphere feedbacks in the context of global warming.**

31 Plant phenology, the timing of periodic developmental events, influences carbon, water, nutrient
32 cycling, fitness and distribution of tree species, trophic interactions, and community structures¹⁻³.
33 Under global warming, advanced spring phenology has been widely reported in recent decades^{1,4}.
34 Contrary to spring phenology, autumn phenology responses to climate warming are inconsistent,
35 with advanced and delayed trends as well as no response having been reported⁵; the mechanisms
36 of the complex climatic responses of autumn phenology remain poorly understood^{1,6}. Consequently,
37 current tree phenology models often fail to simulate and predict autumn phenological changes^{7,8}.
38 This leaves the ability of the models to forecast responses of growing season length and biosphere–
39 atmosphere feedbacks under future climatic scenarios in doubt⁹.

40 In addition to temperature, autumn phenology has been found to be influenced by other
41 environmental cues, i.e., photoperiod, precipitation, and solar radiation^{5,10,11}. In particular,
42 photoperiod provides a more consistent and reliable signal of seasonality than the other climatic

43 factors. Accordingly, when trees rely on photoperiodic cues to signal the arrival of autumn, leaf
44 senescence would be expected to show no or limited climatic responses¹². For example, plants in
45 cold regions with frequent frosts track photoperiod to determine the growth cessation in autumn¹²
46 in order to reduce the risk of frost damage¹³. However, whether photoperiodic sensitivity and
47 climatic responses of plant phenology are consistent under different autumn conditions remains
48 unclear. Using >500,000 records of leaf senescence timing of four temperate tree species monitored
49 *in situ* between 46 °N and 55 °N during 1951-2013 in Europe (Supplementary Fig. 1), we
50 investigated and compared the effects of climatic factors on the onset of leaf senescence in years
51 with warm and cold autumn seasons.

52 **Climatic response in cold and warm autumns**

53 The concept of climatic sensitivity has been widely used to quantify and predict the climatic
54 responses of plant phenology under global warming¹⁴. To investigate the difference in the climatic
55 responses of leaf senescence under cold and warm conditions, we calculated the climatic
56 sensitivities of leaf senescence in cold and warm autumns at cold and warm sites (G1-G4). The
57 classification of the cold and warm sites was based on their latitudes and elevations (see Methods),
58 representing a temperature gradient from the coldest (G1) to the warmest (G4) sites
59 (Supplementary Table 1). The cold and warm autumns were identified by comparing whether mean
60 daily maximum temperature (T_{\max} , °C) during the period 1st August – 31st October of each year
61 and site group was below or above its long-term average for 1951-2013, respectively.

62 In order to calculate the climatic sensitivities, we first used partial correlation analysis to
63 calculate the optimal pre-season length for each combination of climatic factor, species, and site
64 group. The optimal pre-season was defined as the period before the onset of leaf senescence with
65 the highest absolute partial correlation coefficient^{14,15} between leaf senescence dates and the

66 particular climatic factor for the period of 1951-2013. The length of the optimal preseason ranged
67 from 8 to 120 days across different species, consistent with earlier results of both spring and autumn
68 phenology^{4,14,24}(Supplementary Fig. 2). Ridge regression reduces the variance of regression
69 coefficients and improves the estimations when multicollinearity occurs^{16,17}, as was the case in
70 this work. We first calculated the average of each climatic factor during the optimal preseason and
71 those of leaf senescence dates at each site group for each species. Then, ridge regression models
72 were applied to calculate the climatic sensitivities of leaf senescence for daily maximum
73 temperature (T_{\max} , °C), daily minimum temperature (T_{\min} , °C), daily sunshine duration (hour), and
74 daily precipitation (mm) in cold and warm autumns. In all models, normalized anomalies of
75 response and predictor variables were used to calculate the climatic sensitivities, which were then
76 used in the comparisons of the effects of different climatic factors on leaf senescence in cold and
77 warm autumn seasons¹⁸. Positive and negative sensitivities indicate delayed and advanced
78 senescence, respectively.

79 We found that average climatic sensitivities of leaf senescence to T_{\min} , sunshine duration
80 and precipitation during 1951-2013 were significantly higher in warm than in cold autumns across
81 the four studied species ($P<0.001$, Fig. 1a). Furthermore, the climatic sensitivities of leaf
82 senescence to T_{\max} were significantly more negative in warm than in cold autumns ($P<0.001$, Fig.
83 1a and Supplementary Fig. 3a), i.e., leaf senescence advanced more in warm than in cold autumns
84 with the increase in T_{\max} . In order to assess the extent to which the climatic factors influence the
85 onset of leaf senescence in cold and warm autumns, without considering the direction of the effect
86 (delay or advance), the concept of climatic signal, defined as the absolute value of climatic
87 sensitivity, was introduced. We found that climatic signals were significantly stronger in warm
88 than in cold autumns ($P<0.001$, Fig. 1b and Supplementary Fig. 3b). To further test the generality

89 of this finding, we collected records of five additional species and examined their climatic
90 responses of leaf senescence in cold and warm autumns. As with the four initial species, the average
91 climatic signals of all of the five additional species were significantly higher in warm than in cold
92 autumns ($P < 0.01$, Supplementary Fig. 4). These results suggest that leaf senescence exhibited
93 significantly stronger climatic response in warm than in cold autumns.

94 To test the robustness of our results, we calculated the climatic sensitivity for each climatic
95 factor based on a fixed preseason in autumn (1st August to 31st October). Consistent with the result
96 based on the optimal preseason, we observed significantly stronger climatic responses of autumn
97 leaf senescence in warm than in cold autumns also when using the fixed preseason ($P < 0.001$,
98 Supplementary Fig. 5). Because previous studies reported autumn phenology is influenced by
99 spring phenology^{19,20}, we further accounted for the effects of spring leaf unfolding using a joint
100 modelling approach, where both spring leaf unfolding dates and climatic factors were incorporated
101 into the ridge regression models. In all species, leaf unfolding dates had positive effects on leaf
102 senescence dates (Supplementary Fig. 6a), indicating delayed leaf senescence with delayed leaf
103 unfolding, and vice-versa. This is consistent with previous findings^{19,20}. After accounting for the
104 effects of spring phenology, leaf senescence of all species still showed significantly stronger
105 climatic responses in warm than in cold autumns ($P < 0.01$, Supplementary Fig. 6b).

106 **Phenological plasticity in cold and warm autumns**

107 We compared the plasticity of autumn leaf senescence in each species at each site group between
108 cold and warm autumn seasons based on the coefficient of variation (CV) of leaf senescence. In
109 accordance with the stronger climatic responses found in warm than in cold autumns, a
110 significantly higher phenological plasticity, as indicated by a higher CV, was observed in warm

111 than in cold autumn seasons ($P < 0.001$, Fig. 2). In addition, the onset of leaf senescence occurred
112 later in warm than in cold autumns (Fig. 3 and Supplementary Fig. 7).

113 Limited climatic responses, with a lower plasticity of phenological events, is expected when
114 trees are under a strong photoperiodic control¹². We found such conservative climatic responses
115 and reduced plasticity of leaf senescence in cold, but not in warm, autumn seasons (Figs. 1 and 2).
116 On one hand, before leaf senescence, trees need to assimilate sufficient carbohydrate and nutrients
117 for overwintering and budburst during the following spring¹⁰. The accumulated GDD was
118 significantly higher in warm than in cold autumns across all of the site groups ($P < 0.001$, Fig. 4).
119 Under the favorable conditions, trees may therefore prefer to delay leaf senescence and increase
120 carbon uptake in warm autumns¹⁰, especially in warmer sites. This is supported by the observed
121 later onset of leaf senescence in warm autumns (Fig. 3 and Supplementary Fig. 7). On the other
122 hand, trees also need to harden sufficiently early to avoid frost damage²¹. As a compensating factor,
123 photoperiod may act as a safety mechanism for trees to avoid too late leaf senescence to reduce the
124 risk of frost in cold autumns. This may explain why, compared to warm autumns, the onset of leaf
125 senescence showed a lower phenological plasticity (Fig. 2) and occurred earlier (Fig. 3 and
126 Supplementary Fig. 7) in cold autumns.

127 **Effects of daytime and night-time warming**

128 Among all of the climatic factors analyzed, the mean climatic signal was highest for T_{\max} , and
129 second highest for T_{\min} ($P < 0.05$, Fig. 5a). This is in accordance with the earlier findings of stronger
130 influence of daytime than nighttime temperature on spring phenology²². However, it is noteworthy
131 that here climatic sensitivities of T_{\max} and T_{\min} were negative and positive, respectively (Fig. 5b).
132 This indicates that the onset of leaf senescence was advanced by daytime warming, but it was
133 delayed by nighttime warming. Wu et al.¹⁵ recently observed advanced leaf senescence caused by

134 daytime warming in regions with continental climates. A possible explanation for the observed
135 advanced leaf senescence by daytime warming is drought stress^{15,23}. To test this hypothesis, we
136 calculated the Standardized Precipitation-Evapotranspiration Index (SPEI), which considers effects
137 of both precipitation and potential evapotranspiration on drought severity²⁴, and examined the
138 effect of drought stress on the onset of leaf senescence. The averaged SPEI was positive in cold
139 autumn seasons, but negative in warm autumn seasons (Supplementary Fig. 8). This indicated drier
140 environmental conditions in warm autumn seasons. We further observed a significant effect of
141 drought stress on the onset of leaf senescence, with a stronger effect in warm autumns ($P < 0.001$,
142 Supplementary Table 2). This suggests that a higher daytime temperature may increase evaporative
143 demand and impose a drought stress on tree growth, especially in warm autumns, and eventually
144 advance autumn leaf senescence^{10,15}.

145 Among the four studied species, leaf senescence advanced by daytime warming was greater
146 in *Fagus sylvatica* L. and *Quercus robur* L. than in *Aesculus hippocastanum* L. and *Betula pendula*
147 Roth (Fig. 1a). This is possibly due to a difference in the drought tolerance among species^{25,26}.
148 Accordingly, under drought stress, onset of leaf senescence is less likely to advance in a species
149 with a high drought tolerance than in a species with a low drought tolerance. However, the
150 physiological mechanisms behind the species-specific climatic response of leaf senescence remain
151 to be tested experimentally. Using the simulated climate data by Community Earth System Model
152 (CESM) Large Ensemble (CESM-LENS) ([http://www.cesm.ucar.edu/projects/community-
153 projects/LENS/](http://www.cesm.ucar.edu/projects/community-projects/LENS/))²⁷, we investigated the trends in the T_{\max} and T_{\min} in the autumn season (1st August-
154 31st October) during 2021-2050 in Europe. We found both average T_{\max} and T_{\min} showed
155 significant increases through the years of 2021-2050 ($P < 0.001$, Supplementary Fig. 9). Therefore,
156 drought-induced advance of leaf senescence might continue in the future decades. This may

157 counteract the delayed leaf senescence and offset the extension of growing season duration in
158 Europe.

159 **Conclusion**

160 Using a long-term and large-scale dataset of field observations in Europe, we demonstrated that:
161 (1) climatic response of leaf senescence was significantly stronger in warm than in cold autumns,
162 and (2) the onset of leaf senescence was delayed by nighttime warming, but was advanced by
163 daytime warming. These findings provide important guidance for the understanding of complicated
164 climatic responses of plants' autumn phenology in the context of global climate change. Our results
165 can be used to facilitate more reliable predictions of the timing of autumn phenological events, and,
166 as a result, biosphere-atmosphere feedbacks under future climatic scenarios. However, further
167 studies should experimentally investigate the physiological mechanisms behind the species-
168 specific climatic responses in controlled environments and examine whether the observed
169 nonlinear climatic response of autumn phenology also exists in other parts of Northern Hemisphere,
170 including Asia and North America.

171 172 **References**

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236 **Methods**

237 **Leaf phenology and climate data**

238 The leaf senescence dataset was obtained from the Pan European Phenology (PEP) network
239 (www.pep725.eu), which provides an open access to *in situ* phenology records across central
240 Europe²⁸. The leaf senescence dates, expressed as the day of year (DOY), were defined according
241 to the BBCH (Biologische Bundesanstalt, Bundessortenamt und CHEmische Industrie) code. Most
242 of the records used in the study are from between the 46th and 55th parallels (Supplementary Fig.
243 1). Because records of PEP725 network may include erroneous data points, median absolute
244 deviation (MAD) method (Leys et al., 2013) was used to identify and exclude outliers^{14,29,30}. MAD
245 is a robust alternative to the standard deviation measure of the central tendency in a dataset. For a
246 dataset with values of X_1, X_2, \dots, X_i , the MAD is defined as follows:

$$247 \quad \text{MAD} = \text{median} (|X_i - \text{median}(X)|).$$

248 Using a conservative criterion, any data point deviating more than 2.5 times MAD was considered
249 as an outlier and removed from the dataset before the analyses³¹. In this way, we selected 547,000
250 records of leaf senescence during 1951-2013 from approximately 10,000 sites between 46°N and
251 55°N across all nine temperate tree species examined. The primary analysis focused on four species:
252 *Betula pubescens* Ehrh. (Downy birch), *Fagus sylvatica* L. (European beech), *Quercus robur* L.
253 (European oak), *Aesculus hippocastanum* L. (Horse chestnut). An additional five species were
254 examined in supplementary analysis: *Sorbus aucuparia* L. (Mountain ash), *Acer platanoides* L.
255 (Norway maple), *Betula pendula* Roth (Silver birch), *Tilia cordata* Mill. (Small-leaved lime), early
256 cultivar of *Prunus avium* (L.) L. (Wild cherry (early)), and late cultivar of *Prunus avium* (L.) L.
257 (Wild cherry (late)). Note that the two cultivars of *Prunus avium* (L.) L. were examined separately.

258 Gridded daily maximum temperature (T_{\max} , °C), minimum temperature (T_{\min} , °C) and
259 precipitation (mm) data between 1951 and 2013 with a spatial resolution of 0.25° were downloaded
260 from the database E-OBS (<http://ensembles-eu.metoffice.com>). Because gridded solar radiation
261 dataset with 0.25° spatial resolution was only available since 1980, the daily measured sunshine
262 duration (hours) dataset between 1951 and 2013 obtained from E-OBS database was used to
263 account for the effect of solar radiation on leaf senescence. In addition, daily measured temperature
264 and precipitation datasets between 1951 and 2013 were downloaded from E-OBS database. In the
265 E-OBS climate database, the quality of the observations is classified into valid, suspect, or missing.
266 We used only the values classified as valid in the data analysis.

267 To investigate differences in the climate-phenology relationship in cold and warm regions,
268 we divided the phenological observation sites into four groups based on their latitudes and
269 elevations: elevation > 300 m a.s.l. and latitude > 51 °N (G1), elevation > 300 m a.s.l. and latitude
270 < 51 °N (G2), elevation < 300 m a.s.l. and latitude > 51 °N (G3), and elevation < 300 m a.s.l. and
271 latitude < 51 °N (G4). The four groups represent a temperature gradient from the coldest (G1) to
272 the warmest (G4) sites (Supplementary Table 1). We also tried other grouping criteria (e.g.,
273 elevation <100 or 200 m) and obtained similar results.

274 Among the nine selected species, there were approximately 517, 000 records for *Aesculus*
275 *hippocastanum* L., *Betula pendula* Roth, *Fagus sylvatica* L., and *Quercus robur* L. These records
276 accounted for 95% of all of the records and were also well-distributed across the four site groups.
277 In contrast, the records of other five species were more limited and only distributed across one or
278 two site groups. We therefore mainly present results based on the four widely distributed species
279 with massive records in this study. The results of the additional other five species were used to test
280 the generality of the results found from the more representative abovementioned four species.

281 **Climatic sensitivity and climatic signal**

282 In order to calculate climatic sensitivities of each species to each climatic factor, we first used
283 partial correlation analysis to calculate the optimal length of pre-season of each climatic factor for
284 each species at each site group. For each climatic factor, the optimal pre-season was defined as the
285 period before the onset of leaf senescence with the highest absolute partial correlation coefficient
286 ^{14,15} between leaf senescence dates and corresponding climatic factors during 1951-2013 (with 8-d
287 steps). Using the period corresponding to the optimal length of pre-season, we then calculated the
288 climatic sensitivity as the slope of a ridge regression^{16,17} between the onset of leaf senescence
289 (DOY) and the averaged climatic factor during the pre-season period for each species at a site group.
290 The climatic sensitivity was calculated in this way for the daily maximum temperature (T_{\max} , °C),
291 daily minimum temperature (T_{\min} , °C), daily sunshine duration (hour), and daily precipitation (mm).
292 Positive and negative sensitivities indicate delayed and advanced senescence, respectively.
293 Climatic signal was defined as the absolute value of climatic sensitivity. It indicates the extent to
294 which the climatic factor influences the onset of leaf senescence, without considering the direction
295 of the effect (delay, advance).

296 In addition to the full data set used, the results of climatic sensitivities are reported
297 separately for species and for site groups, and for years with cold and warm autumn seasons. The
298 seasons were classified into cold and warm ones based on whether mean daily T_{\max} during the
299 autumn season (1st August – 31st October) of the particular year at the particular site was below
300 or above its long-term average for 1951 – 2013, respectively.

301 Multicollinearity is a problem when two or more predictors in multiple regression models
302 are highly correlated¹⁶. The estimated regression coefficients based on ordinary least square
303 regression can be unreliable when multicollinearity occurs¹⁶. By adding a penalty parameter in the

304 model, ridge regression reduces the variance of regression coefficient and produces more reliable
305 estimates¹⁷. In order to take into account the potential multicollinearity between climatic factors,
306 ridge regressions were therefore used in the calculations of climatic sensitivity^{16,17}. The spatial
307 resolution of sunshine duration dataset was too coarse to obtain the sunshine duration hours for
308 each site. To address this, we averaged climatic data, including T_{\max} , T_{\min} , precipitation and
309 sunshine duration, and leaf senescence dates for each site group (G1-G4), and analyzed the effect
310 of the averaged climatic factors on autumn leaf senescence. A total of 128 models were applied to
311 calculate the climatic sensitivities, one for each combination of site group, species, and season type
312 (4 climate factors \times 4 climate groups \times 4 species \times 2 season types). The response variable was the
313 mean leaf senescence date, the predictors were the averaged climatic factors during the optimal
314 pre-season of each species at each site group. Normalized anomalies of climatic factors and leaf
315 senescence dates were used in all of the models when calculating the climatic sensitivities, which
316 were then used for comparing the effects of different climatic factors on the onset of leaf senescence
317 in cold and warm autumns in different species and different site groups¹⁸. To test the robustness of
318 our results, we calculated the climatic sensitivity also based on a fixed pre-season in autumn (1st
319 August to 31st October) for each climatic variable. We also addressed the effects of spring
320 phenology on autumn leaf senescence in cold and warm autumns via a joint modelling approach where
321 both spring leaf unfolding dates and climatic factors were incorporated into the ridge regression
322 models. Both the response variables and the predictors were normalized also in these models.

323 Due to the coarse spatial resolution of sunshine duration dataset, we could not analyze
324 the effects of all of the four climatic factors on leaf senescence at the site level. To address this, we
325 performed an additional analysis using the climatic data that could be obtained for each site (see
326 Supplementary Fig. 10). Specifically, we first excluded the outliers deviating more than 2.5 times

327 MAD and selected sites with at least 40 years records of leaf senescence between 1951 and 2013.
328 Second, we used the bilinear interpolation method to extract the daily T_{\max} , daily T_{\min} , and daily
329 precipitation between 1951 and 2013 for each site using the “raster” package³² in R version 3.6.1³³.
330 After determining the optimal preseason length of climatic factors, we calculated the mean
331 temperature and precipitation during the optimal preseason for each year at each site. Finally, we
332 obtained year-to-year normalized anomalies (relative to average year) of both climatic variables
333 and leaf senescence dates, and calculated climatic signals in cold and warm autumns for each
334 species at each site using ridge regressions.

335 Linear mixed models are widely used to analyze hierarchical data, because they allow
336 inclusion of both fixed and random effects³⁴. By pooling all of the species at different site groups,
337 a linear mixed model was used to examine the difference in climatic sensitivity or climatic signal
338 between cold and warm autumn seasons. In the linear mixed model, the response variable was
339 climatic sensitivity or signal, the fixed effect was autumn season type (a categorical variable with
340 two levels: cold and warm autumn), with random intercepts among species. Tukey's HSD
341 (Honestly Significant Difference) test is a common post-hoc test used to compare the means
342 between groups based on the studentized range distribution³⁵. Here Tukey's HSD test followed by
343 linear mixed model was used to examine the differences in climatic signals among the climatic
344 factors addressed.

345 **Growing degree days**

346 Based on the following equation, we calculated the growing degree days (GDD) to assess the
347 climatic forcing in cold and warm autumns at different site groups:

$$348 \quad GDD = \left[\frac{(T_{\max} + T_{\min})}{2} \right] - T_{base} \quad \text{Eq. (1),}$$

349 where $GDD = 0$ when $(T_{max}+T_{min})/2 < T_{base}$. Based on Eq. (1), we calculated the accumulated
350 GDD5 ($T_{base} = 5\text{ }^{\circ}\text{C}$) and GDD10 ($T_{base} = 10\text{ }^{\circ}\text{C}$) during the optimal preseason³⁶ of leaf senescence.
351 These calculations were carried out separately for years with cold and warm autumns. Linear mixed
352 models were used to examine the difference in the accumulated GDD5 and GDD10 between years
353 with cold and warm autumns. The response variable was GDD5 or GDD10, the fixed effect was
354 autumn season type (a categorical variable with two levels: warm and cold) with random intercepts
355 among species.

356 **Phenological plasticity**

357 We calculated the coefficient of variation (CV) of leaf senescence dates to indicate the plasticity
358 of autumn leaf senescence for each species at each site group during years with cold and warm
359 autumn seasons. A total of 32 CV values were obtained to quantify the autumn phenological
360 plasticity, one for each of the combinations of 4 site groups \times 4 species \times 2 season types. A linear
361 mixed model was used to test the mean difference of the CV between the years with warm and cold
362 autumn seasons. The response variable was the CV of leaf senescence dates, the fixed effect was
363 autumn season type (a categorical variable with two levels: warm and cold) with random intercepts
364 among species.

365 **Effects of drought on leaf senescence**

366 The Standardized Precipitation-Evapotranspiration Index (SPEI), which considers effects of both
367 precipitation and potential evapotranspiration on drought severity²⁴, was calculated to examine the
368 effects of drought stress on the onset of leaf senescence. The mean SPEI during the autumn season
369 (1st August – 31st October) across different site groups was selected to examine the effects of
370 drought on leaf senescence. A linear mixed model was used to test the effects of drought on the

371 timing of leaf senescence during years with cold and warm autumn seasons. The response variable
372 was the leaf senescence DOY, the predictor variables were the SPEI and the type of the season (a
373 categorical variable with two levels: warm and cold autumn season), with random intercepts among
374 site groups. Both response variable and predictors were normalized in the models.

375 Using the simulated climate data by Community Earth System Model (CESM) Large
376 Ensemble (CESM-LENS) (<http://www.cesm.ucar.edu/projects/community-projects/LENS/>)²⁷, we
377 investigated the trends in the averaged T_{\max} and T_{\min} in autumn (1 August-31 October) under
378 RCP8.5 scenario³⁷ during 2021-2050 in Europe to project the effect of drought on the onset of leaf
379 senescence under future climate scenarios.

380 **Data availability**

381 Phenology data are available from the Pan European Phenology (PEP) network (www.pep725.eu).
382 Climate data can be downloaded from E-OBS site: <http://ensembles-eu.metoffice.com>.

383 **Code availability**

384 The codes used for data processing and analysis in this study are available on Figshare:
385 <https://doi.org/10.6084/m9.figshare.12291245.v6>.

386 **Methods references**

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416 **Author contributions**

417 L.C., J.L. and Z.L. designed this research. L.C. and Z.L. performed the data analysis. L.C. drafted
418 the paper with the inputs of H.H., S. R., N.G.S., Z.L., S.P., G.F., J.G. and J.L. All authors
419 contributed to the interpretation of the results and approved the final manuscript.

420 **Competing interests**

421 The authors declare no competing interests.

422 **Figure legends**

423 **Fig. 1** Climatic responses of leaf senescence of four temperate tree species in Europe during 1951-
424 2013. (a) Climatic sensitivity, (b) climatic signal, with the results given separately for warm (red)
425 and cold (blue) autumn seasons, based on whether mean T_{\max} during the autumn season from 1st
426 August to 31st October of the particular year was above or below its long-term average for 1951 –
427 2013, respectively. Climatic sensitivities were calculated for daily maximum temperature (T_{\max} ,
428 °C), daily minimum temperature (T_{\min} , °C), daily sunshine duration (Sun, hours), and daily
429 precipitation (Prec, mm) during the optimal pre-season (see Methods for details). Climatic signal,
430 the absolute value of climatic sensitivity, indicates the extent to which climatic factors influence
431 leaf senescence without considering the direction of the effect (delay, advance). The averaged
432 climatic signal represents the mean of the four climatic factors. The climatic sensitivities and
433 signals reported were calculated using normalized response and predictor variables. Length of each
434 box indicates the interquartile range, the horizontal line inside each box the median, and the bottom
435 and top of the box the first and third quartiles, respectively. The black points outside the boxes
436 represent outliers. The four temperate tree species addressed are *Aesculus hippocastanum* L.,

437 *Betula pendula* Roth, *Fagus sylvatica* L. and *Quercus robur* L. The asterisks in (b) indicate
438 significant differences between cold and warm autumns ($P<0.05$).

439
440 **Fig. 2** Coefficient of variation (CV) of the leaf senescence onset day of four temperate tree species
441 in Europe during 1951 – 2013. (a) Averaged over the four species and all observation sites and (b)
442 separately for each species at different phenological observation site groups. The site groups
443 represent a climatic gradient from cold (G1) to warm (G4) observation sites (see Supplementary
444 Table 1). The results are presented separately for cold (blue) and warm (red) autumn seasons (1st
445 August – 31st October), based on whether mean daily T_{\max} during the autumn season of the
446 particular year was below or above its long-term average for 1951 – 2013, respectively. Total
447 number of CV values is equal to 32 (4 species \times 4 site groups \times 2 season types). In (a), the length
448 of each box indicates the interquartile range, the horizontal line inside each box the median, and
449 the bottom and top of the box the first and third quartiles, respectively. The black points outside
450 the boxes represent outliers. The four temperate tree species addressed are *Aesculus hippocastanum*
451 L., *Betula pendula* Roth, *Fagus sylvatica* L., and *Quercus robur* L. The asterisks in (a) indicate
452 significant differences between cold and warm autumns ($P<0.05$).

453
454 **Fig. 3** Average leaf senescence dates of four temperate tree species at different phenological
455 observation site groups in Europe during 1951 – 2013. The site groups represent a climatic gradient
456 from cold (G1) to warm (G4) observation sites (see Table S1). The results are presented separately
457 for cold (blue) and warm (red) autumn seasons (1 August – 31 October), based on whether mean
458 daily T_{\max} during the autumn season of the particular year was below or above its long-term average
459 for 1951-2013, respectively. Error bars indicate standard error of the mean. The four temperate tree

460 species addressed are *Aesculus hippocastanum* L., *Betula pendula* Roth, *Fagus sylvatica* L., and
461 *Quercus robur* L.

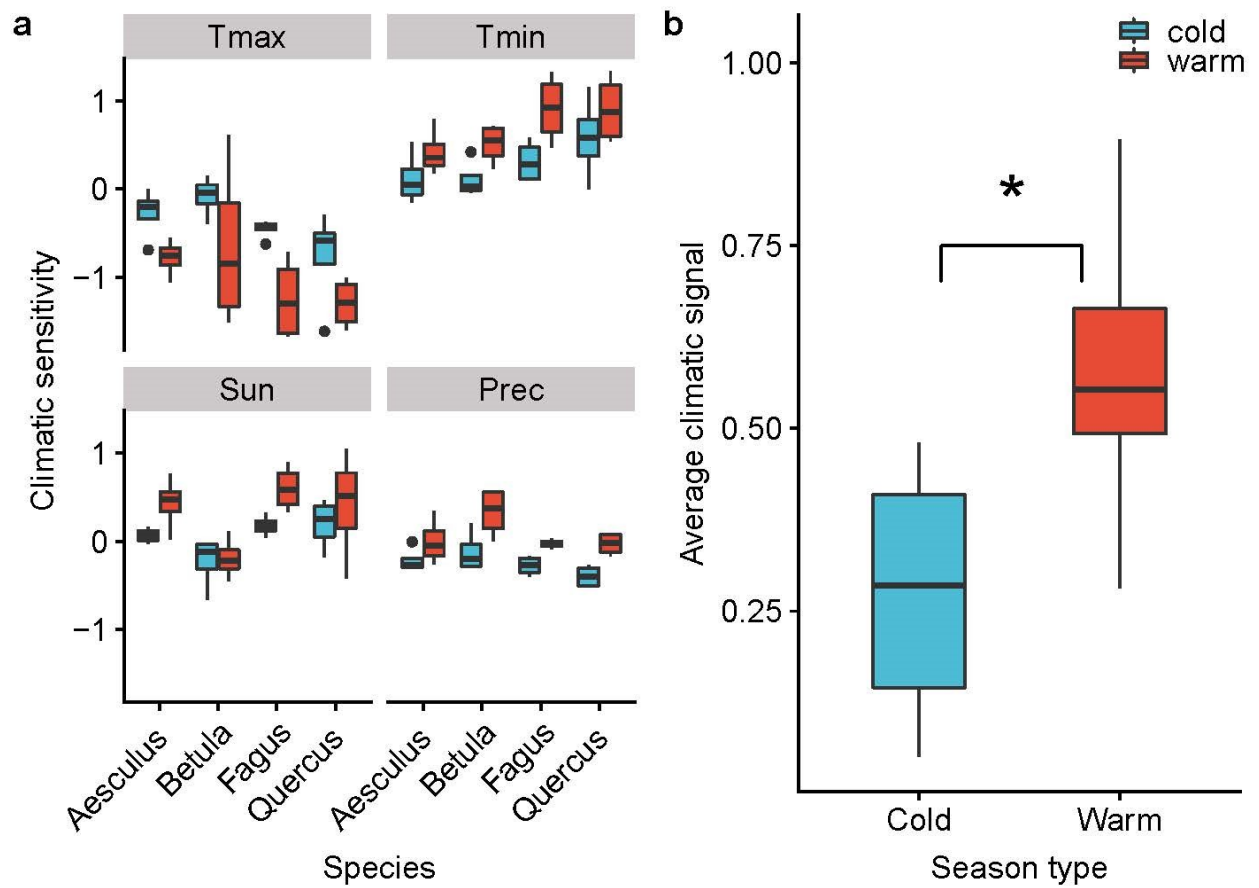
462
463 **Fig. 4** Growing degree days (GDD) at different site groups in Europe during 1951 – 2013. The site
464 groups represent a climatic gradient from cold (G1) to warm (G4) observation sites (see Table S1).
465 The results are presented separately for cold (blue) and warm (red) autumn seasons (1st August –
466 31st October), based on whether mean daily T_{\max} during the autumn season of the particular year
467 was below or above its long-term average for 1951 – 2013, respectively. The growing degree days
468 were calculated based on the optimized pre-season of leaf senescence. (a) GDD5 and (b) GDD10
469 represent accumulated GDDs calculated with base temperatures $T_{\text{base}} = +5$ °C and $T_{\text{base}} = +10$ °C,
470 respectively. Different letters indicate significant differences between site groups based on Tukey's
471 honest significant difference (HSD) test ($P < 0.05$).

472
473 **Fig. 5** Climatic responses of leaf senescence of four temperate tree species in Europe during 1951-
474 2013. (a) Climatic sensitivity and (b) climatic signal. Climatic signal is defined as the absolute value
475 of climatic sensitivity. Unlike climatic sensitivity, climatic signal does not address direction of the
476 effect of climatic factor on leaf senescence. The values of both indicators are calculated for daily
477 maximum temperature, T_{\max} (days per °C), daily minimum temperature, T_{\min} (days per °C), daily
478 sunshine duration, Sun (days per h), and daily precipitation, Prec (days per mm) during the optimal
479 pre-season (see Methods for details). The climatic sensitivities reported were calculated using
480 normalized response and predictor variables. Length of each box indicates the interquartile range,
481 the horizontal line inside each box the median, and the bottom and top of the box the first and third
482 quartiles, respectively. The black points outside the boxes represent outliers. The four temperate

483 tree species addressed are *Aesculus hippocastanum* L., *Betula pendula* Roth, *Fagus sylvatica* L.,
484 and *Quercus robur* L. Different letters indicate significant differences among the climatic factors
485 based on Tukey's honest significant difference (HSD) test ($P < 0.05$).

486

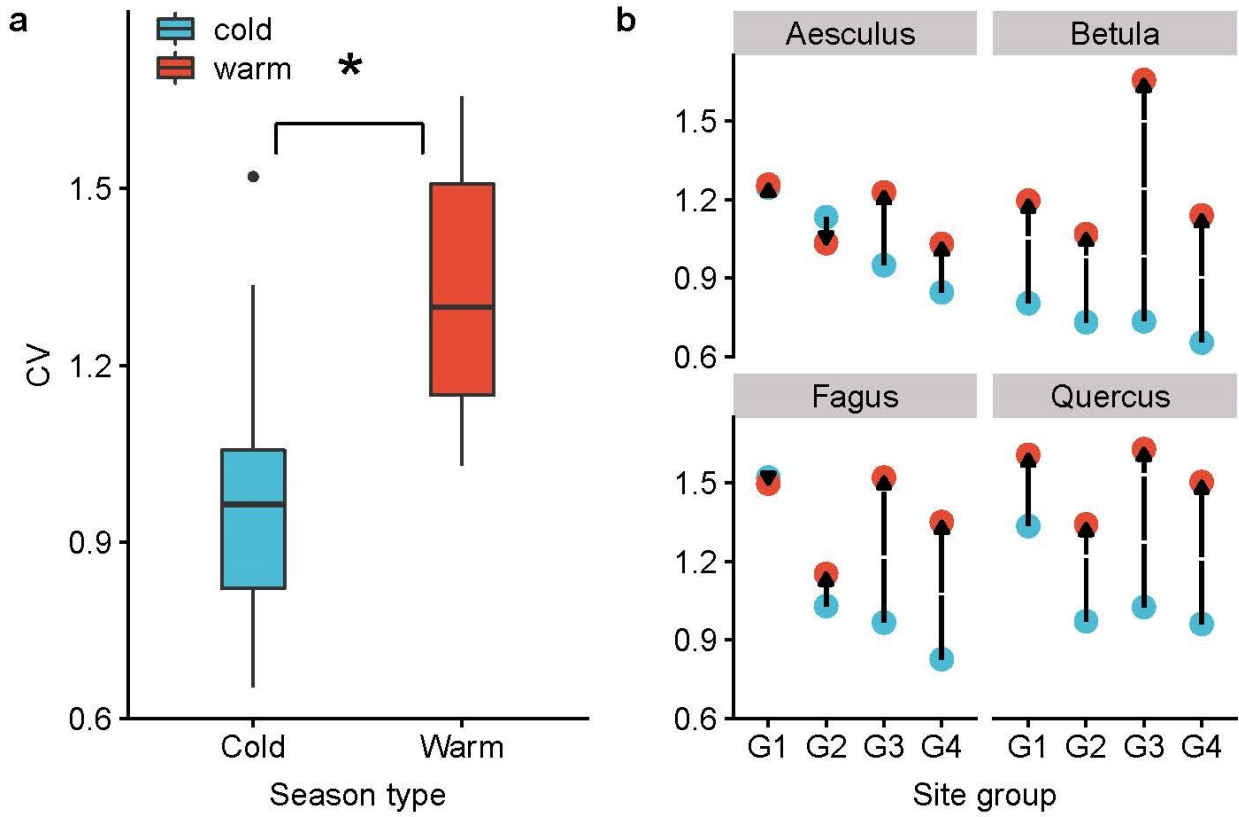
487 Figure 1



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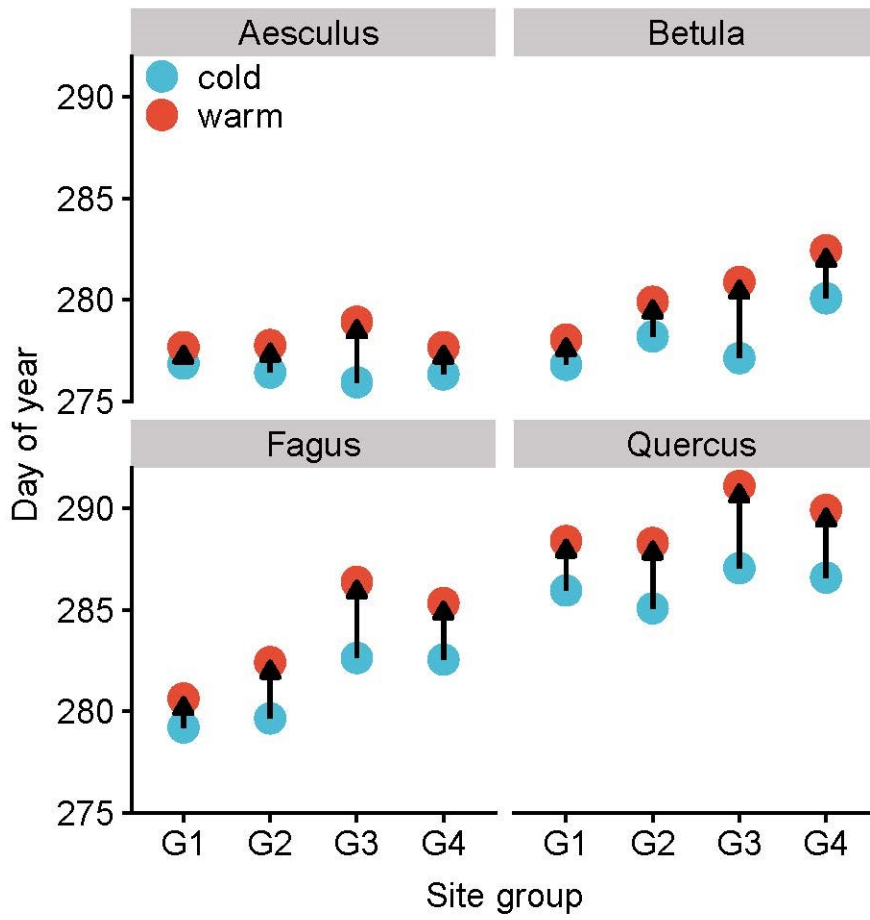
490 Figure 2



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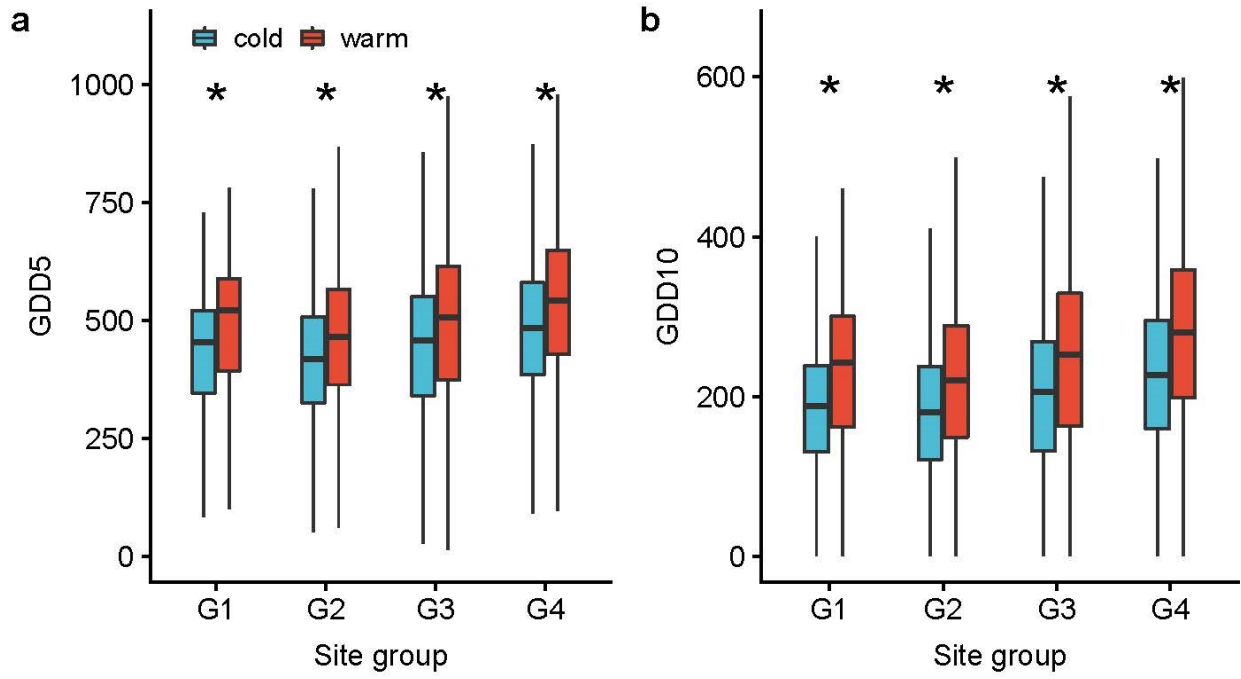
493 Figure 3



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495

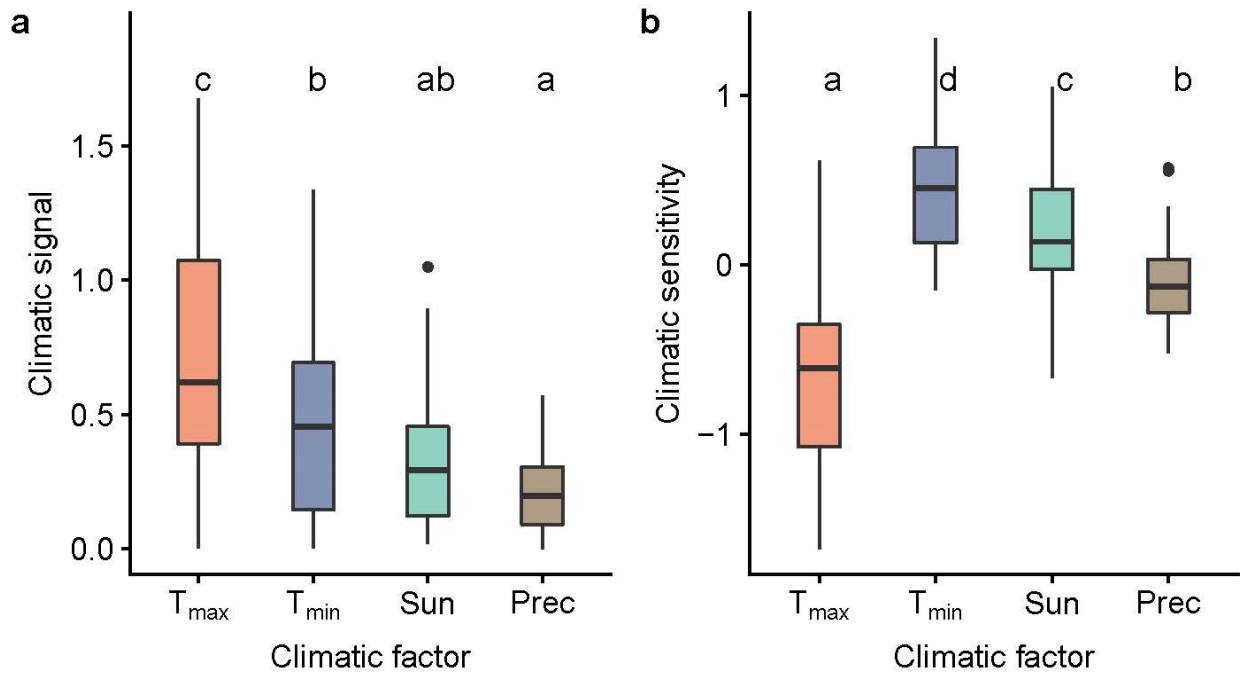
496 Figure 4



497

498

499 Figure 5



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