

# Declining global warming effects on the phenology of spring leaf unfolding

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Earlier spring leaf unfolding is a frequently observed response of plants to climate warming<sup>1–4</sup>. Many deciduous tree species require chilling for dormancy release, and warming-related reductions in chilling may counteract the advance of leaf unfolding in response to warming<sup>5,6</sup>. Empirical evidence for this, however, is limited to saplings or twigs in climate-controlled chambers<sup>7,8</sup>. Using long-term *in situ* observations of leaf unfolding for seven dominant European tree species at 1,245 sites, here we show that the apparent response of leaf unfolding to climate warming ( $S_T$ , expressed in days advance of leaf unfolding per °C warming) has significantly decreased from 1980 to 2013 in all monitored tree species. Averaged across all species and sites,  $S_T$  decreased by 40% from  $4.0 \pm 1.8$  days °C<sup>-1</sup> during 1980–1994 to  $2.3 \pm 1.6$  days °C<sup>-1</sup> during 1999–2013. The declining  $S_T$  was also simulated by chilling-based phenology models, albeit with a weaker decline (24–30%) than observed *in situ*. The reduction in  $S_T$  is likely to be partly attributable to reduced chilling. Nonetheless, other mechanisms may also have a role, such as ‘photo-period limitation’ mechanisms that may become ultimately limiting when leaf unfolding dates occur too early in the season. Our results provide empirical evidence for a declining  $S_T$ , but also suggest that the predicted strong winter warming in the future may further reduce  $S_T$  and therefore result in a slowdown in the advance of tree spring phenology.

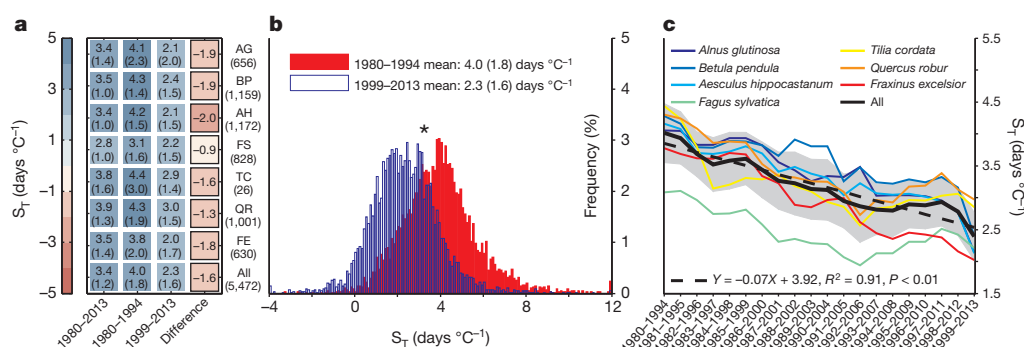
The phenology of spring leaf unfolding influences regional and hemispheric-scale carbon balances<sup>2</sup>, the long-term distribution of tree species<sup>9</sup>, and plant–animal interactions<sup>10</sup>. Changes in the phenology of spring leaf unfolding can also exert biophysical feedbacks on climate by modifying the surface albedo and energy budget<sup>11,12</sup>. Recent studies have reported substantial advances in spring phenology as a result of warming in most Northern Hemisphere regions<sup>1,3,4</sup>. Climate warming is projected to further increase<sup>13</sup>, but the future evolution of the phenology of spring leaf unfolding remains uncertain—in view of the imperfect understanding of how the underlying mechanisms respond to environmental stimuli<sup>12,14</sup>. In addition, the relative contributions of each environmental stimulus, which together define the apparent temperature sensitivity of the phenology of spring leaf unfolding ( $S_T$ ), may also change over time<sup>6,8,15</sup>. An improved characterization of the variation in phenological responses to spring temperature is thus valuable, provided that it addresses temporal and spatial scales relevant for regional projections.

Many studies have reported advanced spring leaf unfolding which matches warming trends over recent decades<sup>1,3,4</sup>. However, there is still debate regarding the linearity of the leaf unfolding response to climate warming<sup>6,7</sup>. Recent experimental studies of warming using saplings have shown that  $S_T$  weakens as warming increases<sup>7</sup>. Experimental

manipulation of temperature for saplings or twigs, however, might elicit phenological responses that do not accurately reflect the response of mature trees<sup>16,17</sup>. We therefore investigated the temporal changes in  $S_T$  in adult trees monitored *in situ* and exposed to real-world changes in temperature and other climate variables. These long-term data series were obtained across Central Europe from the Pan European Phenology Project (<http://www.pep725.eu/>). Data were collected from 1,245 sites for seven dominant tree species (see Methods and the distribution of the sites in Extended Data Fig. 1). The aims of our analysis are to determine the temporal changes in  $S_T$  at the species level during 1980–2013, a period during which Europe has substantially warmed<sup>13</sup>, and to relate these changes in  $S_T$  to differences in other physiological and environmental factors.

For each species at each observation site, we first determined the pre-season length as the period before leaf unfolding for which the partial correlation coefficient between leaf unfolding and air temperature was highest (see Methods). We used a gridded climate data set, including daily maximum and minimum air temperature, precipitation and absorbed downward solar radiation, with a spatial resolution of 0.25° (approximately 25 km)<sup>18</sup>. The optimal length of the pre-season ranged between 15 days and 4 months across the seven species (Extended Data Fig. 2), in agreement with earlier results<sup>11,14</sup>. We then calculated the average temperature during the pre-season for each year at each site and calculated  $S_T$  using ordinary least squares linear regression for the entire period and for two 15-year periods, 1980–1994 and 1999–2013, that had a slight difference in pre-season lengths (Extended Data Fig. 3a). The leaf unfolding dates were negatively correlated with the pre-season temperature, with a mean linear correlation coefficient of  $-0.61 \pm 0.16$ , determined using the pre-season defined from the time period 1980–2013. Almost all individual tree-level correlations were negative (99.7%) and the vast majority of these correlations was statistically significant at  $P < 0.05$  (93.4%) (Extended Data Fig. 4). Consistent with previous studies<sup>1,4</sup>, the timing of leaf unfolding substantially advanced in all species for 1980–2013, with an average advancing rate of  $3.4 \pm 1.2$  days °C<sup>-1</sup> across all species sites (hereafter, a positive value indicates advancement) (Fig. 1a). But the surprising result is that  $S_T$  significantly decreased by 40.0% from  $4.0 \pm 1.8$  days °C<sup>-1</sup> during 1980–1994 to  $2.3 \pm 1.6$  days °C<sup>-1</sup> during 1999–2013 ( $t = -37.3$ ,  $df = 5,473$ ,  $P < 0.001$ ) (Fig. 1b). All species show similar significant decreases in  $S_T$  (Fig. 1a), although the extent of reduction was species-specific. For example, *Aesculus hippocastanum* (see caption to Fig. 1 for English common names) had the largest decrease in  $S_T$  ( $-2.0$  days °C<sup>-1</sup>), whereas  $S_T$  decreased only slightly (but still significantly) in *Fagus sylvatica* ( $-0.9$  days °C<sup>-1</sup>) (Fig. 1a). Similar results were also obtained using a fixed pre-season length deter-

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**Figure 1 | Changes of apparent temperature sensitivity of leaf unfolding ( $S_T$ ) over time.** **a**, Species-specific  $S_T$  and s.d. (in brackets) across all sites in three periods and its difference between 1999–2013 and 1980–1994. The  $S_T$  was determined using the pre-season fixed at the time period 1980–2013 and using ordinary least squares linear regression. The colour scale indicates the magnitude of  $S_T$ . AG, alder (*Alnus glutinosa*); BP, silver birch (*Betula pendula*); AH, horse chestnut (*Aesculus hippocastanum*); FS, beech (*Fagus sylvatica*); TC, lime (*Tilia cordata*); QR, oak (*Quercus robur*); FE, ash (*Fraxinus excelsior*).

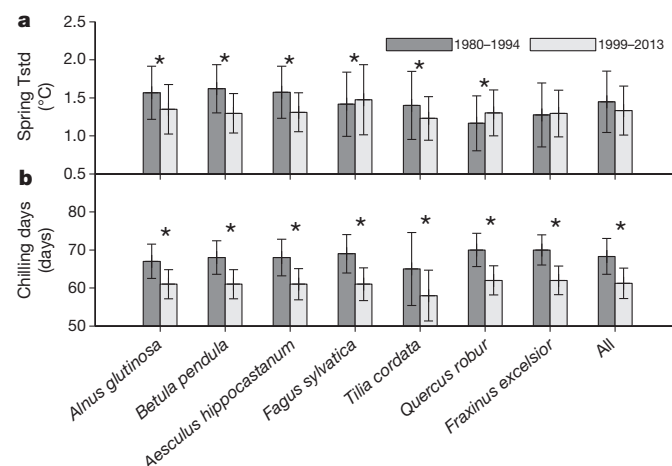
mined either in the time period 1980–1994 or in 1999–2013 (Extended Data Fig. 3b, c). The declining  $S_T$  could, however, also have been an artefact resulting from the ‘encroachment’ of leaf unfolding dates into the pre-season period that was used to calculate the temperature sensitivity. We therefore calculated the number of ‘encroachment days’ and found it is very small compared to the pre-season length even in the warmest period (Extended Data Fig. 3d, e). Because the timescale of the analysis could affect the estimates of  $S_T$ <sup>19</sup>, we also calculated  $S_T$  using 10-year intervals (instead of 15-year intervals) and found consistent results,  $S_T$  significantly decreased between the 1980s and the last decade for all species except *Tilia cordata* (Extended Data Fig. 5a). We further calculated  $S_T$  with a 15-year moving window from 1980 to 2013 and found a significant decrease ( $P < 0.01$ ) for each of the seven species (Fig. 1c).  $S_T$  decreased by an average of 0.7 days °C<sup>-1</sup> per decade across all species. Similar results were also reached when a 10-year interval was used (Extended Data Fig. 6). These results suggest a remarkable reduction in the response of leaf unfolding to the ongoing climate warming in all studied tree species in Central Europe.

As there is no single accepted theory to account for the decreased  $S_T$  over the period 1980–2013, we propose three mutually non-exclusive hypotheses: (1) adaptation to increased variance in spring temperature, (2) photoperiodic limitations (due to earlier leaf unfolding) overriding temperature controls, or (3) reduced duration and/or sum of cold temperatures during dormancy, a ‘lost chilling’ mechanism.

The first hypothesis relates to possible effects of an increased variance in temperature. A recent study reported substantial spatial differences in  $S_T$ , with smaller absolute values at sites with a higher variance of local spring temperature<sup>20</sup>. Trees may indeed develop conservative strategies (or higher phenological plasticity) of spring leaf unfolding in places where temperature fluctuates more, for example, in order to avoid spring frost damage<sup>21</sup>. The observed declining  $S_T$  could therefore partly result from an increase in the variance in spring temperature. However, the variance in spring temperature only significantly increased at sites of two species and decreased for all the other species except *Fraxinus excelsior* (Fig. 2a). This suggests that increased variance in spring temperature cannot account for the decreased  $S_T$ . We further studied the fluctuations in daily mean temperature and diurnal temperature amplitude ( $T_{\max} - T_{\min}$ ) over the pre-season for the two periods 1980–1994 and 1999–2013, and for three groups of sites with comparable mean annual temperature (MAT). The fluctuations in daily temperature and diurnal temperature amplitude during the pre-season were similar during the two time periods between which  $S_T$  declined (Extended Data Fig. 7), suggesting that altered temperature variability is not an obvious cause for the declining apparent temperature sensitivity of leaf unfolding.

The number of sites for each species are in brackets below the species name. **b**, The distribution of  $S_T$  across all species and sites in two different periods and the mean  $S_T$  and s.d. (in brackets). The asterisk indicates a significant difference of  $S_T$  between the two periods at  $P < 0.05$ . **c**, Temporal change of  $S_T$  for individual species and for combined totals for all species across all sites with a 15-year moving window from 1980 to 2013. The black line indicates the average across all species, and the grey area indicates one s.d. either side of the mean. The dotted line indicates the linear regression.

Precocious leaf unfolding in warm springs may increase the risk of late frost events for trees<sup>21</sup>. To overcome this risk during warm springs, many species have evolved a protective mechanism related to photoperiod<sup>22</sup>, which hinders the warming response when days are still short and the risk for subsequent frost events is thus high. Our second, alternative, hypothesis to account for the observed decrease in  $S_T$  in recent decades is therefore a change in the relationship between chilling accumulation and heat requirement, due to the shortening days as warming advances leaf unfolding. However, we did not observe changes in  $S_T$  with latitude, neither across all species, nor for individual species (Extended Data Fig. 8), as one may expect if photoperiod was a strong co-limitation of leaf unfolding. Nonetheless, we have no evidence to exclude photoperiod as a controlling mechanism for the decline of  $S_T$  as different populations may have different genetic adaptations to photoperiod<sup>23</sup>. In addition, the lack of relation between



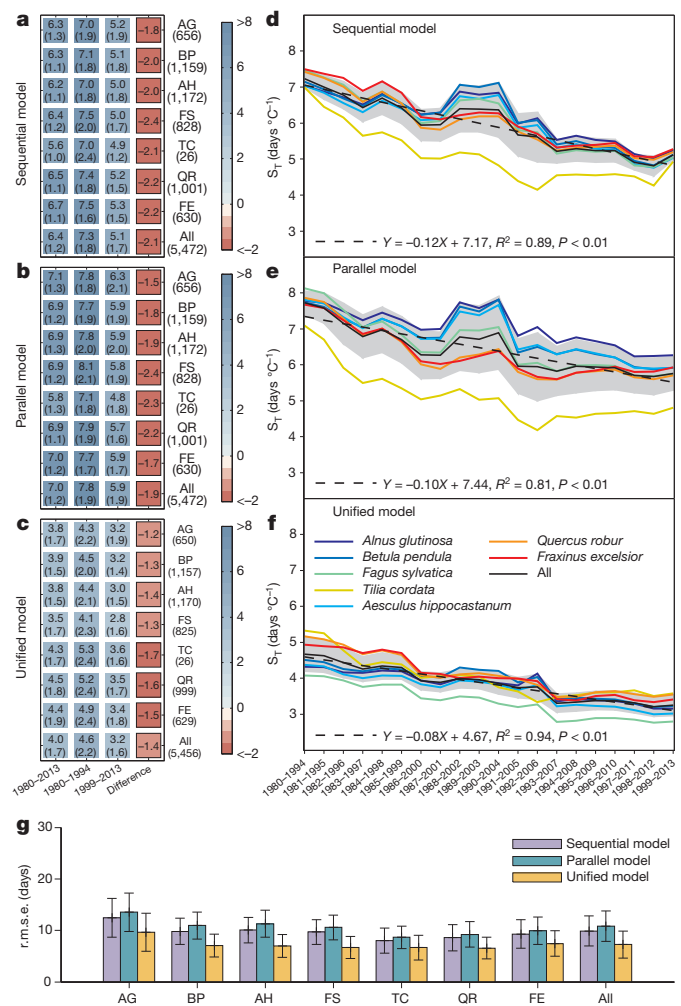
**Figure 2 | Changes of chilling and spring temperature variation between 1980–1994 and 1999–2013.** **a**, **b**, Species-specific Tstd (the standard deviation of mean spring temperature) (**a**) and chilling accumulation (**b**) across all sites over two periods, 1980–1994 and 1999–2013. The Tstd was calculated as the s.d. of mean spring temperature during the pre-season over these two periods. The pre-season was defined as the period before leaf unfolding for which the correlation coefficient between leaf unfolding and temperature was highest. The chilling accumulation was calculated as chilling days when daily temperature was between 0 °C and 5 °C from 1 November to the average date of leaf unfolding. The asterisks indicate significant differences at  $P < 0.05$ .

$S_T$  and latitude may have been because the response of spring phenology to photoperiod can be associated with many confounding factors, such as tree age<sup>17</sup>, successional niche<sup>23</sup> (although there is some contradictory evidence<sup>8</sup>), xylem anatomy<sup>24</sup> or chilling conditions<sup>8</sup>. We can therefore not conclude that photoperiod did not influence  $S_T$ , but how it might directly or indirectly affect spring phenology still remains unclear and is currently under debate<sup>6,15,22</sup>.

The third hypothesis to explain the decreased  $S_T$  is based on the control of spring phenology by cold temperatures during the dormancy period. In general, temperate and boreal trees require a certain amount of heat (heat requirement) after they come out of the rest period to initiate leaf unfolding in spring<sup>25</sup>. This heat requirement is met sooner during warmer springs, which explains the advance of leaf unfolding in response to global warming. The heat requirement, however, is negatively correlated with chilling<sup>7,8,25</sup>, that is, the accumulation of cold temperatures during the dormancy period. As the dormancy period warmed during the study period, the accumulated chilling is progressively reduced, thereby increasing the heat requirement and slowing down the advance of leaf unfolding. The net effect of lost chilling can thus be a reduced  $S_T$ . This effect may be further exacerbated by the nonlinearity of the negative correlation between the heat requirement and the accumulation of chilling<sup>7,25</sup>.

To test this hypothesis, we calculated the accumulation of chilling that was defined as the sum of days when daily air temperature was within the range between 0 °C and 5 °C from 1 November in the year before leaf unfolding (see Methods), and found a significant decrease ( $P < 0.001$ ) in chilling accumulation for all species (Fig. 2b). Chilling accumulation was 10% lower for 1999–2013 than for 1980–1994. Chilling accumulation was also significantly decreased with a 15-year moving window (Extended Data Fig. 9a) and when defined by different temperature thresholds (Extended Data Fig. 9b). To further test the importance of the ‘lost chilling’ hypothesis, we applied three chilling-based phenology models to the data (see Supplementary Information). All three models captured the declining  $S_T$  after their calibration at each site and their integration with observed climate forcing, irrespective of species (Fig. 3). The modelled relative reductions in  $S_T$  between the two periods 1980–1994 and 1999–2013 were, however, smaller than the observed decline, that is, simulated  $S_T$  was reduced by 28.8%, 24.4% and 30.4% for the sequential, parallel and unified chilling-based models, respectively, whereas the observed  $S_T$  was reduced by 40.0%. This may suggest that either other protective or adaptive mechanisms, such as photoperiod or adaptation mechanisms, are affecting the decline in  $S_T$  or that the three models do not completely accurately represent all chilling mechanisms. There are also uncertainties related to the 0.25° gridded climate product that may not represent local air temperature at each site (snow effects, shading, slope, elevation). Furthermore, using the unified model, we applied idealized step-wise increases of winter temperature over the period 1980–2013 by +1 °C to +5 °C, and consistently obtained a decrease in  $S_T$  induced by the loss of chilling in these idealized tests (Extended Data Fig. 9c). However, we did not find marked differences in  $S_T$  between years with more chilling days and years with less chilling days (Extended Data Fig. 10a–c), which can probably be explained by the different climate conditions between years with more and less chilling days. For example, the relatively high spring radiation sum in years with less chilling days might buffer the effects of less chilling days (Extended Data Fig. 10d), and eventually result in a similar  $S_T$ , but this remains a matter of speculation. Clearly, further studies are needed to support these inferences and their role in the control over phenology. Overall, these results support the third hypothesis that the decline in chilling accumulation is, at least partly, driving the decline in  $S_T$ , although the possible constraint of photoperiod/radiation could not be excluded.

Changes in spring phenology associated with climate warming have direct effects on regional and global carbon cycling<sup>12</sup>. Studies have reported that an extension of the growing season can increase the



**Figure 3 | Changes of modelled apparent temperature sensitivity of leaf unfolding.** a–c, As in Fig. 1a, the panels show the modelled species-specific  $S_T$ , including the s.d. (in brackets), across all sites during three periods and its difference between 1999–2013 and 1980–1994 for the sequential model (a), parallel model (b) and unified model (c). d–f, As in Fig. 1c, the panels show the modelled temporal change of  $S_T$  for individual species and for combined totals for all species across all sites with a 15-year moving window from 1980 to 2013 for the sequential model (d), parallel model (e) and unified model (f). g, The model performance. The  $S_T$  was determined using the pre-season fixed at the time period 1980–2013 and using ordinary least squares linear regression. The colour scale indicates the magnitude of  $S_T$ . r.m.s.e., root mean square error; AG, alder (*Alnus glutinosa*); BP, silver birch (*Betula pendula*); AH, horse chestnut (*Aesculus hippocastanum*); FS, beech (*Fagus sylvatica*); TC, lime (*Tilia cordata*); QR, oak (*Quercus robur*); FE, ash (*Fraxinus excelsior*). The number of sites for each species are in brackets under the species name.

photosynthetic production of forests by 0.5–1% per day<sup>26–28</sup>. We found that the apparent sensitivity of spring phenology to warming for seven temperate tree species in Central Europe has declined significantly as winter and spring temperatures increased over the past three decades. These findings indicate that the early spring phenologically driven increases in carbon uptake may slow down for temperate forests under future conditions of climate warming. On the other hand, the declining apparent temperature sensitivity of spring phenology may be beneficial for the trees. Extreme climatic events have dramatically increased in recent decades, especially warm winters and springs<sup>29</sup>, and the decreased apparent temperature sensitivity would thus reduce the risk of late spring frost damage by avoiding premature leaf unfolding.



**Online Content** Methods, along with any additional Extended Data display items and Source Data, are available in the online version of the paper; references unique to these sections appear only in the online paper.

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**Supplementary Information** is available in the online version of the paper.

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**Author Contributions** Y.H.F. and H.Z. contributed equally to this work. S.Pi., Y.H.F. and I.A.J. designed the research; H.Z., Y.H.F., M.P., S.Pe. and G.Z. performed the analysis; Y.H.F., S.Pi. and I.A.J. drafted the paper; and Y.H.F., S.Pi., I.A.J., H.Z., M.P., S.Pe., G.Z., P.C., M.H., A.M., J.P., Y.S., Y.V. and Z.Z. contributed to the interpretation of the results and to the writing of the paper.

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## METHODS

**Data sets.** *In situ* phenological observations were obtained from the Pan European Phenology network (<http://www.pep725.eu/>), which provides an open European phenological database comprising multiple plant phenological records. We selected the records of leaf unfolding dates for seven tree species at 1,245 sites for 1980–2013 from sites in an area stretching from north Germany to the Adriatic Sea (see Extended Data Fig. 1). The leaf unfolding dates were defined according to the BBCH code (Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie). Dates were excluded from the analysis when the trees flushed later than the end of June. The daily mean air temperature of each site was derived from a gridded climate data set of daily maximum and minimum temperature at 0.25° spatial resolution (approximately 25 km)<sup>18</sup>. We also applied another climate forcing data set (CRU-NCEP v5, with spatial resolution of 0.5° and temporal resolution of 6 h, (<http://dods.extra.cea.fr/data/p529viov/cruncep/>)), and returned very similar results (Extended Data Fig. 5c).

**Data reporting.** No statistical methods were used to predetermine sample size.

**Analysis.** The relevant period for leaf unfolding is several months before the phenological event<sup>1</sup>, and periods differ among species and locations. To remove covariate effects of precipitation and radiation on leaf unfolding, we applied a partial correlation analysis to determine the optimal length of the pre-season for each species at each site<sup>30</sup>. The optimal pre-season for each species at each station was defined as the period (with 15-day steps) before the mean leaf unfolding date for which the partial correlation coefficient between leaf unfolding and air temperature was highest during 1980–2013. Using a similar method, we also defined pre-season for two 15-year periods (for example, 1980–1994, 1999–2013) to further assess the robustness of the inferred decline of apparent temperature sensitivity of leaf unfolding over the last three decades (Extended Data Fig. 3a–c).

Linear regression analyses (using both ordinary least squares and reduced major axis regressions) of the dates of leaf unfolding against mean air temperature over the pre-season were performed for each species at each site during the three study periods: 1980–2013 (minimum 15-year records required per site), 1980–1994, and 1999–2013 (minimum 7-year records required per site, satisfied simultaneously for the two latter study periods). Similar results, that is, significant decreases in  $S_T$ , were observed using reduced major axis regression method (Extended Data Fig. 5b), we therefore only present the results using ordinary least squares method. The regression coefficient was defined as the apparent temperature sensitivity of leaf unfolding ( $S_T$ ) that reflects the change in leaf unfolding date per unit increase in mean temperature during the pre-season. This is not the ‘actual’ physiological sensitivity to temperature, given that other climate-related variables, such as

chilling, photoperiod, solar radiation and precipitation, also co-determine the leaf unfolding process and determine the emerging  $S_T$  value diagnosed from the pre-season temperature<sup>8,12,22</sup>. The mean  $S_T$  across all sites was calculated for individual species and for combined totals for all species for these three periods. The frequency distributions of  $S_T$  across all species and sites for 1980–1994 and 1999–2013 were determined. The differences in mean  $S_T$  during 1999–2013 and 1980–1994 were tested using independent *t*-tests for each and across species.

To investigate the effect of the chilling requirement and variance in spring temperature on  $S_T$ , we calculated species-specific variances in spring temperature and chilling requirements at each site. The spring temperature variance was calculated as the s.d. of mean temperature during the pre-season. The chilling requirement is normally defined as the length of the period (days or hours) during which temperature remains within a specific range. Most previous studies have reported that temperatures slightly above freezing are most effective in satisfying the chilling requirement<sup>31</sup> and have suggested that the temperature range between 0 °C and 5 °C is the most effective across species. To calculate the chilling requirement, we therefore summed the days when daily temperature was within this range:

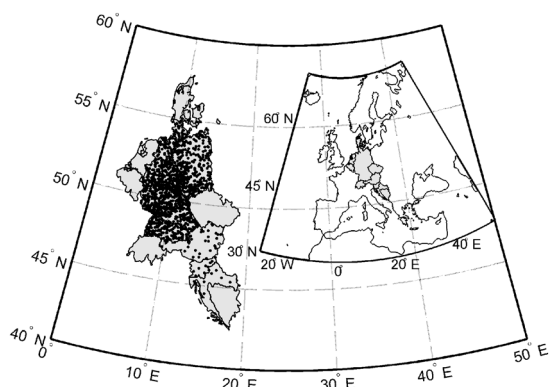
$$CD_{req}(t) = \sum_{t_0}^{t_{LF}} 1 \quad \text{if } 0 \leq T_t \leq 5$$

where  $CD_{req}$  is the chilling requirement,  $t_{LF}$  is the day of leaf unfolding,  $T_t$  is the daily mean temperature on day  $t$ , and  $t_0$  is the start date for chilling accumulation.  $t_0$  was fixed at 1 November in the year before leaf unfolding. We also tested another commonly used temperature threshold, 5 °C<sup>24</sup>, and included all temperatures below this threshold.

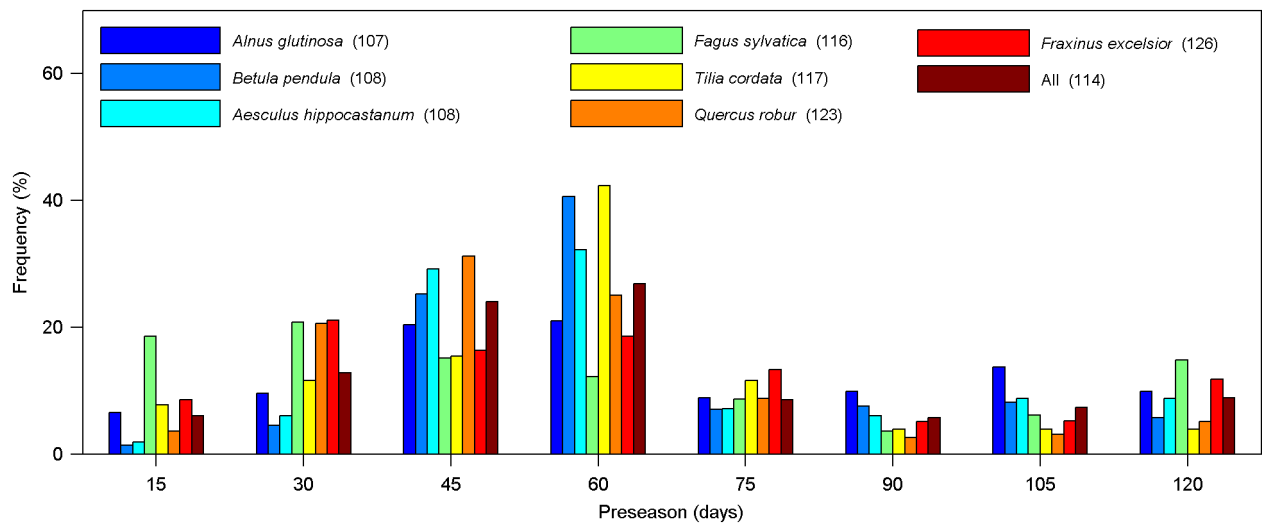
$$CD_{req}(t) = \sum_{t_0}^{t_{LF}} 1 \quad \text{if } T_t \leq 5$$

The differences in mean during 1999–2013 and 1980–1994 were tested using independent *t*-tests for each and across species. Ordinary least squares linear regression was applied to determine the temporal change in the chilling requirement for 1980–2013 and to determine the correlation between chilling accumulation and  $S_T$ .

30. Fu, Y. S. H. *et al.* Variation in leaf flushing date influences autumnal senescence and next year's flushing date in two temperate tree species. *Proc. Natl Acad. Sci. USA* **111**, 7355–7360 (2014).
31. Coville, F. V. The influence of cold in stimulating the growth of plants. *Proc. Natl Acad. Sci. USA* **6**, 434–435 (1920).

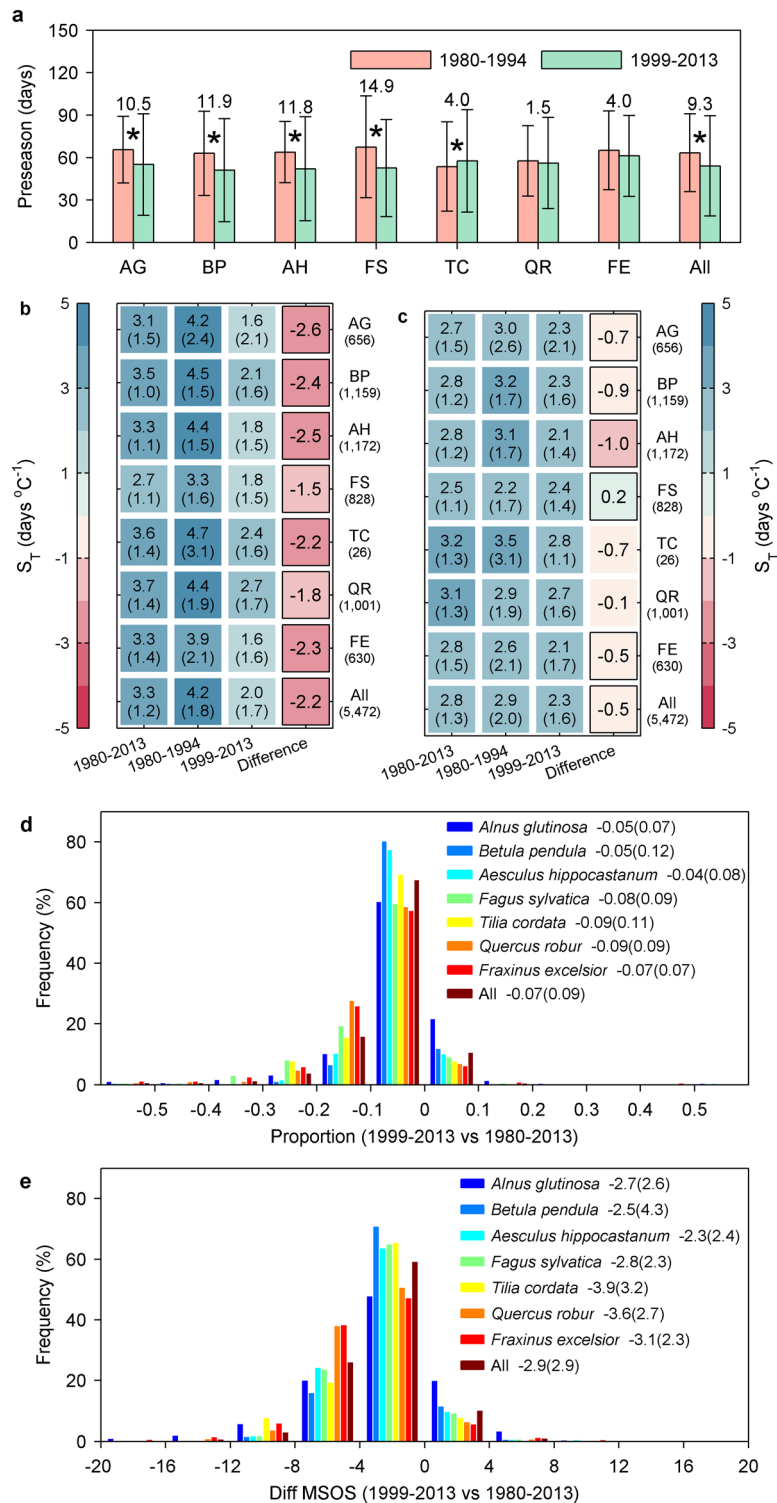


**Extended Data Figure 1 | The distribution of the sites.** The data were obtained from the Pan European Phenology network (<http://www.pep725.eu/>).



**Extended Data Figure 2 | The distribution of preseason length for individual species and for combined totals for all species.** The optimal preseason was defined as the period before leaf unfolding for which the

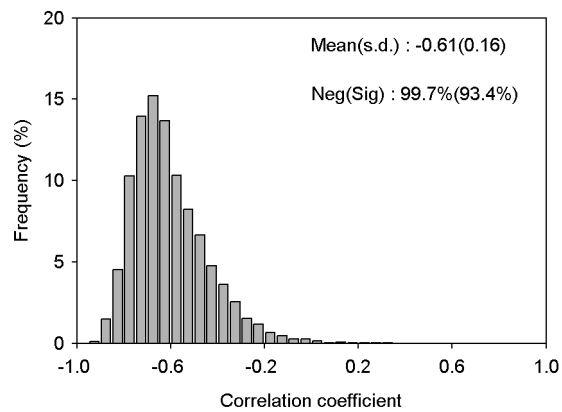
correlation coefficient between leaf unfolding and temperature was highest. The numbers in the brackets are the mean dates of leaf unfolding across all sites.



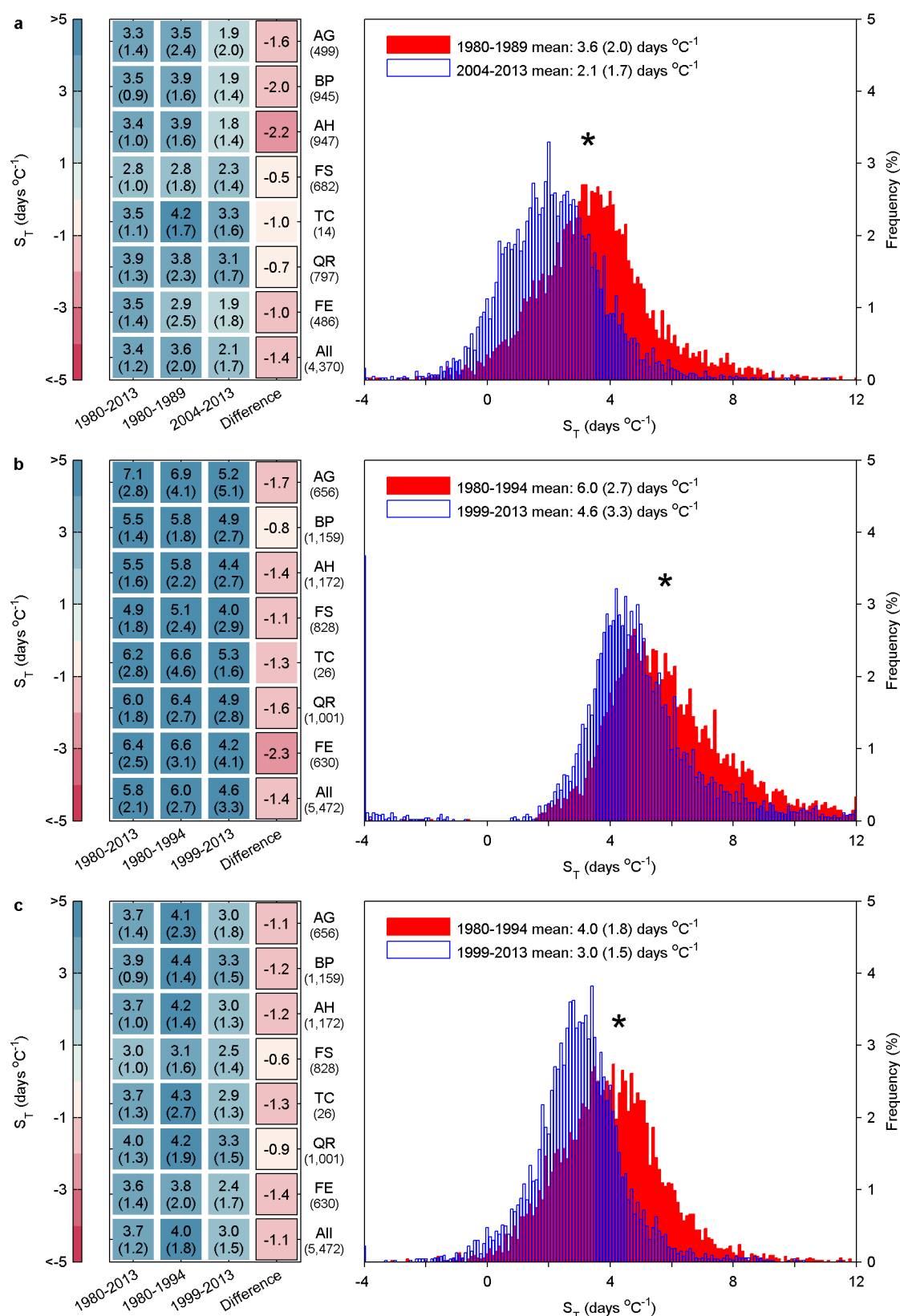
**Extended Data Figure 3 | Changes of apparent temperature sensitivity of leaf unfolding between 1980–1994 and 1999–2013.** **a–c,** Same as Fig. 1, but the  $S_T$  was calculated based on the preseason that was determined either in the time period 1980–1994 (**b**) or in 1999–2013 (**c**). The differences in preseason lengths are provided for individual species and for combined totals for all species (**a**), and the figures above bars are the mean absolute preseason difference between two periods. For **b** and **c**, species-specific  $S_T$  and its s.d. (in brackets) across all sites in three periods and its difference between 1999–2013 and 1980–1994. The colour scale indicates the magnitude of  $S_T$ .

The number of sites for each species are in brackets under the species name. **d, e,** The distribution of the proportion and corresponding days (**e**) of the encroachment of phenology dates into the preseason temperature that the preseason was determined on the period 1980–2013. The proportion was defined as the difference of the mean leaf unfolding dates (diff MSOS) between the period 1999–2013 and 1980–2013 (which is the end date of the preseason temperature that was used to calculate the  $S_T$ ) divided by the preseason length in days. The mean values and s.d. (in brackets) are provided for individual species and for combined totals for all species.



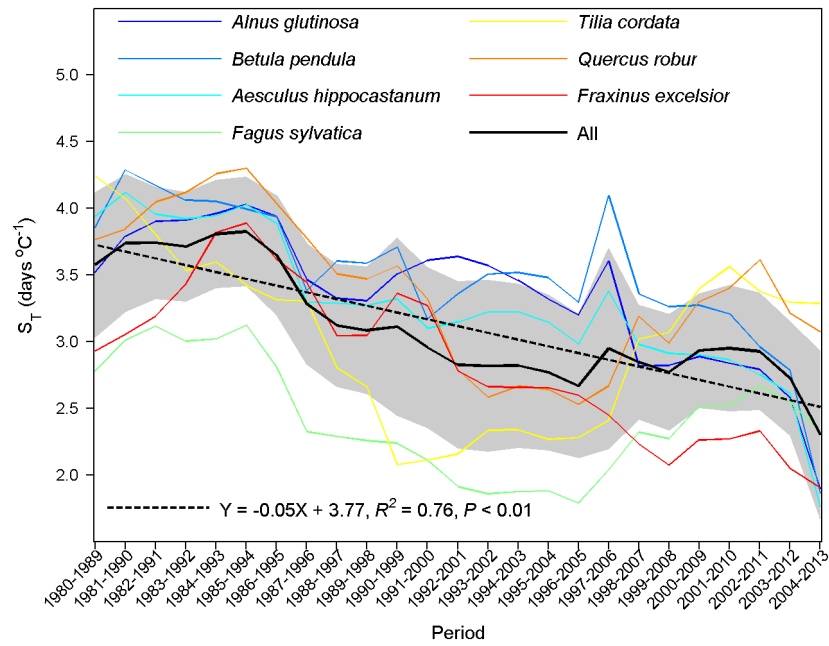


**Extended Data Figure 4 | The distribution of partial correlation coefficients between preseason temperature and leaf unfolding dates over the time period 1980–2013.** The mean (and s.d.) of the correlation coefficients across all species and sites are provided. The percentages of negative correlations and statistically significant negative correlations (Neg(Sig)) are also provided.



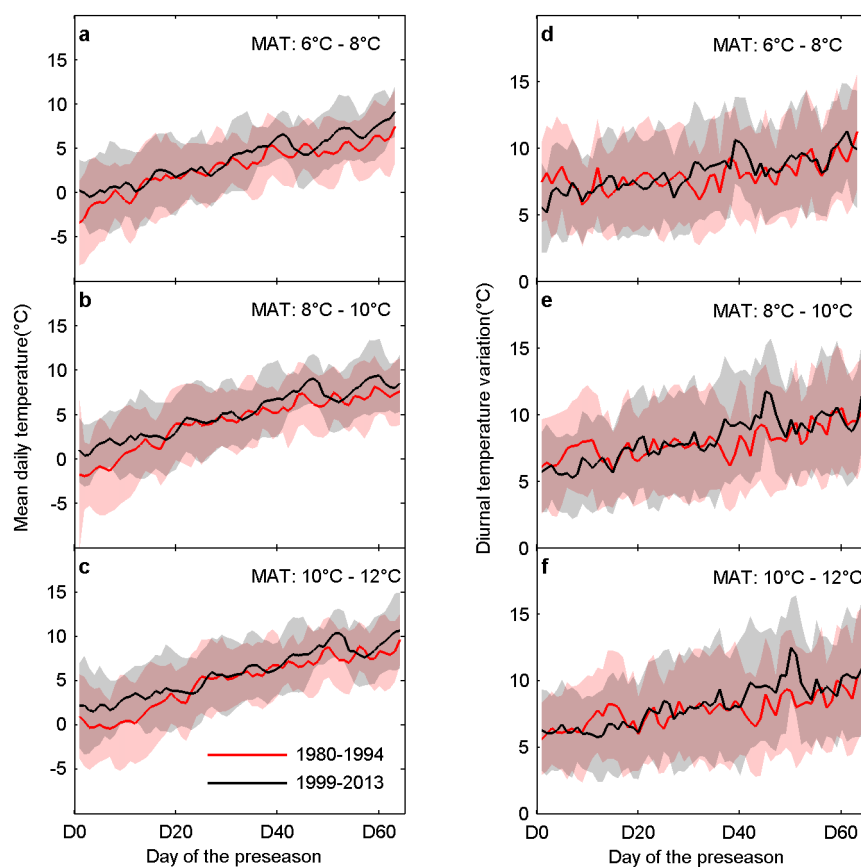
**Extended Data Figure 5 | Changes of apparent temperature sensitivity of leaf unfolding determined by different methods.** a–c, The  $S_T$  were analysed in two 10-year periods (a), were calculated using the reduced major axis (RMA) regression (b), or were calculated based on another climate forcing data set (CRU-NCEP v5, c). Species-specific  $S_T$  and s.d. (in brackets) across all sites in three periods and the difference between the two study periods are provided.

The colour scale indicates the magnitude of  $S_T$ . The number under the species name is the number of sites. The histograms show the distribution of  $S_T$  across all species and sites in two different periods and the mean  $S_T$  and s.d. (in brackets). The asterisk indicates a significant difference of  $S_T$  between the two periods at  $P < 0.05$ .



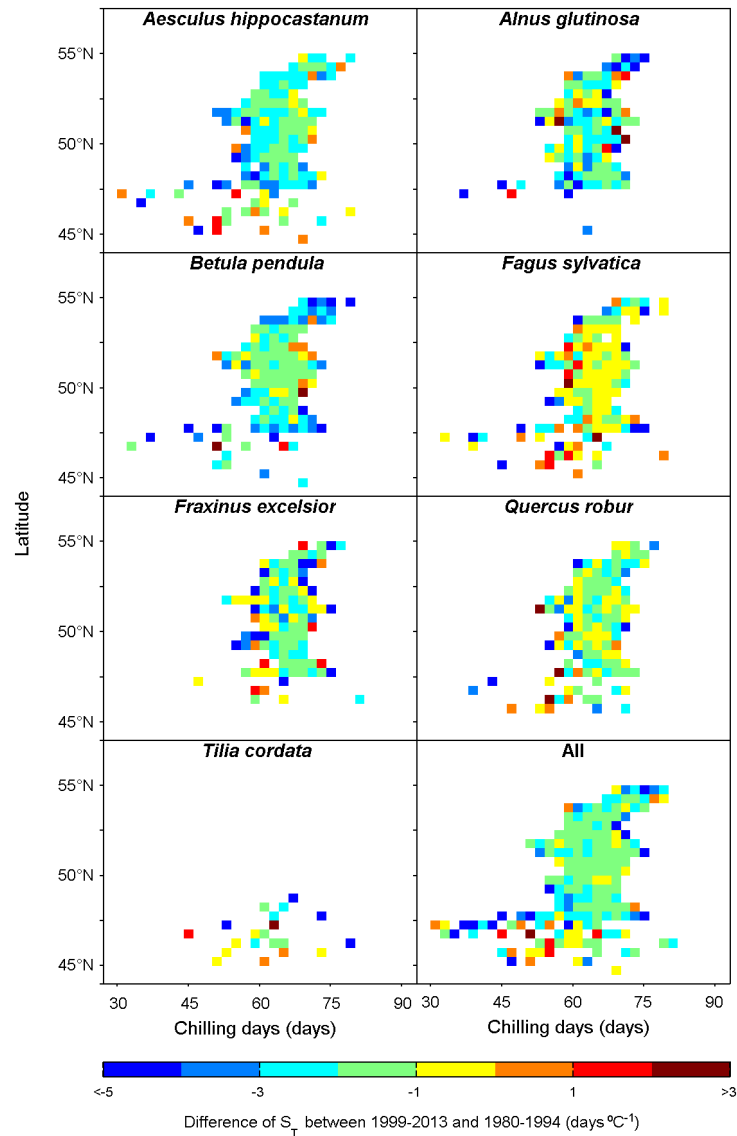
**Extended Data Figure 6 | Changes of apparent temperature sensitivity of leaf unfolding over time.** Same as Fig. 1c, but temporal change of  $S_T$  with 10-year moving windows from 1980 to 2013. The  $S_T$  was calculated using

simple linear regression. The black line indicates the average across all species, and the grey area indicates one s.d. either side of the mean. The dotted line indicates the linear regression.



**Extended Data Figure 7 | The differences in climatology over the preseason.** The fluctuations in mean daily temperature (left) and diurnal variation temperature ( $T_{\max} - T_{\min}$ , right) over the preseason across all sites during the

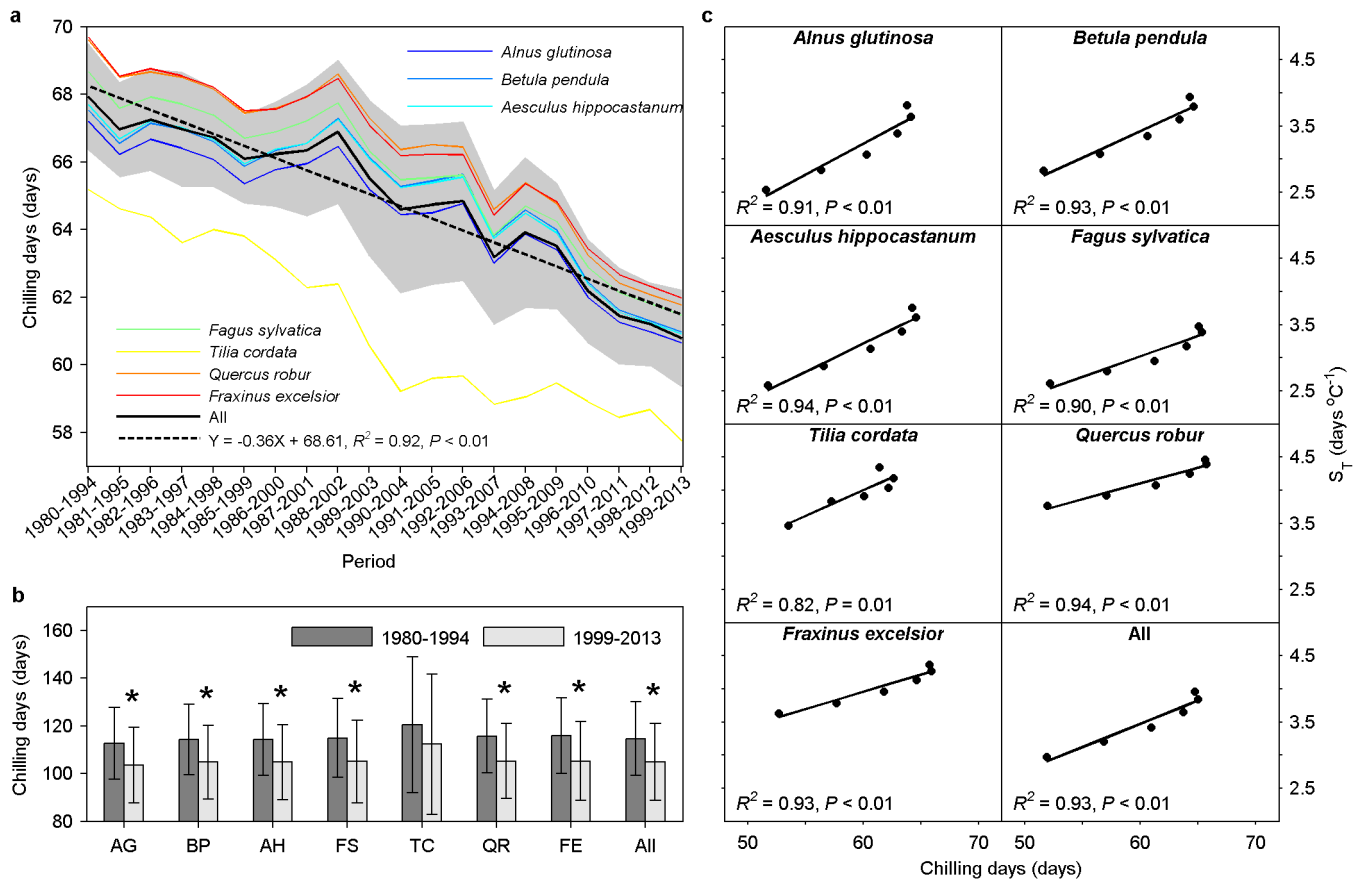
time period 1980–1994 and 1999–2013 in three MAT groups, that is, (top panels) 6–8 °C, (middle panels) 8–10 °C and (bottom panels) 10–12 °C. The preseason was determined over the period 1980–2013.



**Extended Data Figure 8 | Spatial difference in apparent temperature sensitivity of leaf unfolding reduction.** The difference of  $S_T$  for each species and across all species studied between two time periods, 1999–2014 and

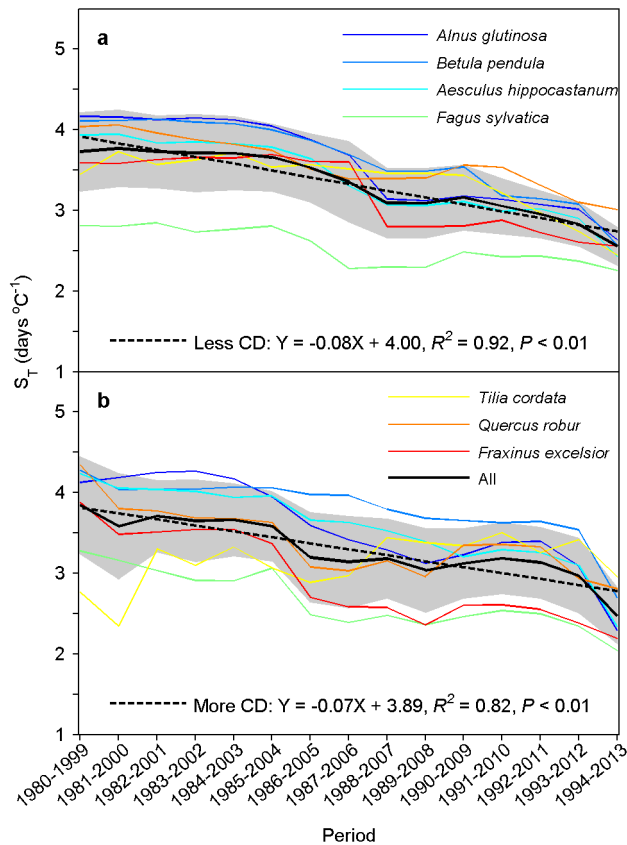
1980–1994, at different latitudes (bin: 0.5 °) and chilling conditions (bin: two chilling days). The colour scales indicate the differences of  $S_T$  between the two periods.



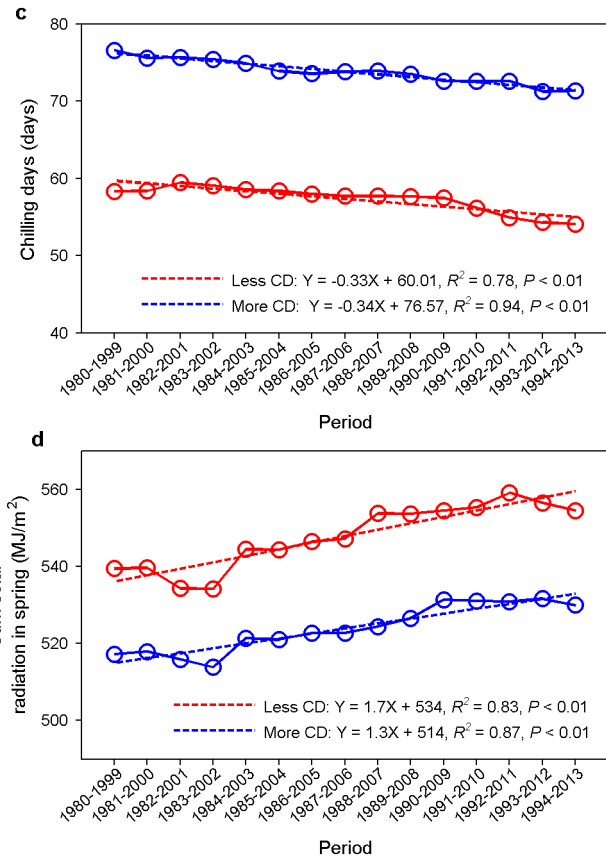


**Extended Data Figure 9 | Changes in chilling accumulation and modelled correlation between chilling and apparent temperature sensitivity of leaf unfolding.** **a**, Chilling accumulation for individual species and for combined totals for all species with 15-year moving windows from 1980 to 2013. The chilling accumulation was calculated as chilling days when daily temperature was between 0 °C and 5 °C from 1 November to the average date of leaf unfolding. The black line indicates the average across all species, and the grey area indicates one s.d. either side of the mean. The dotted line indicates the linear regression. **b**, Same as Fig. 2b, but chilling accumulation was calculated as

chilling days when daily temperature was below 5 °C from 1 November to the average date of leaf unfolding. The asterisks indicate significant differences at  $P < 0.05$ . **c**, The modelled (unified model)  $S_T$  under different artificial winter warming conditions. The temperature in winter, defined as the period from the 1 November to 31 January, was warmed by +1 °C to +5 °C over the period 1980–2013. The points with most chilling days indicate the real winter temperatures, and each of the other points indicate one winter warming treatment. The lines indicate simple linear regressions.



**Extended Data Figure 10 | Changes in apparent temperature sensitivity of leaf unfolding between years with more or less chilling.** **a**, **b**,  $S_T$  for years with less chilling (**a**) and more chilling (**b**) with a 20-year moving window for 1980–2013. For each 20-year series, we divided the 20 years into two groups based on the mean chilling accumulation (chilling was accumulated when daily temperature within the temperature range between 0 °C and 5 °C from 1 November to the day of leaf unfolding). The 10 years with chilling higher than the overall mean were defined as more chilling, and the other 10 years were



defined as less chilling. The black lines indicate the average across all species, and the grey area indicates one s.d. either side of the mean. The dotted lines are the linear regressions. **c**, Chilling accumulation for years with less chilling (red line) and more chilling (blue line) with a 20-year moving window for 1980–2013. **d**, The mean radiation sum over the pre-season for years with less chilling (red line) and more chilling (blue line) with a 20-year moving window for 1980–2013. The pre-season was determined over the period 1980–2013.