

Declining global warming effects on the phenology of spring leaf unfolding

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1 **Earlier spring leaf unfolding is a frequently observed response of northern trees to climate**
2 **warming^{1,2,3,4}. Many deciduous tree species require chilling for dormancy release, and**
3 **warming-related reductions in chilling may counteract the advance of leaf unfolding in**
4 **response to warming^{5,6}. Empirical evidence for this, however, is limited to saplings or twigs**
5 **in climate-controlled chambers^{7,8}. Using long-term *in situ* observations of leaf unfolding for**
6 **seven dominant European tree species at 1,245 sites, we show here that the apparent**
7 **response of leaf unfolding to climate warming (S_T , expressed in days advance per °C) has**
8 **significantly decreased from 1980 to 2013 in all monitored tree species. Averaged across all**
9 **species and sites, S_T decreased by 40% from 4.0 ± 1.8 days °C⁻¹ during 1980-1994 to $2.3 \pm$**
10 **1.6 days °C⁻¹ during 1999-2013. The declining S_T was also simulated by chilling-based**
11 **phenology models, albeit with a weaker decline (24%-30%) than observed *in situ*. The**
12 **reduction in S_T is likely to be partly attributable to reduced chilling. Nonetheless, other**
13 **mechanisms may also play a role, such as ‘photoperiod limitation’ mechanisms that may**
14 **become ultimately limiting when leaf unfolding dates occur too early in the season. Our**
15 **results provide empirical evidence for a declining S_T , but also suggest that the predicted**
16 **strong winter warming in the future may further reduce S_T and therefore result in a**
17 **slowdown in the advance of tree spring phenology.**

18

19 The phenology of spring leaf unfolding influences regional and hemispheric-scale carbon
20 balances², the long-term distribution of tree species⁹, and plant-animal interactions¹⁰. Changes in
21 the phenology of spring leaf unfolding can also exert biophysical feedbacks on climate by
22 modifying the surface albedo and energy budget^{11,12}. Recent studies have reported significant
23 advances in spring phenology as a result of warming in most northern hemisphere regions^{1,3,4}.
24 Climate warming is projected to further increase¹³, but the future evolution of the phenology of
25 spring leaf unfolding remains uncertain — in view of the imperfect understanding of how the
26 underlying mechanisms respond to environmental stimuli^{12,14}. In addition, the relative
27 contributions of each environmental stimulus, which together define the apparent temperature
28 sensitivity of the phenology of spring leaf unfolding (advances in days per degree Celsius
29 warming, S_T), may also change over time^{6,8,15}. An improved characterization of the variation in

1 phenological responses to spring temperature is thus valuable, provided that it addresses temporal
2 and spatial scales relevant for regional projections.

3 Numerous studies have reported advanced spring leaf unfolding which matches warming trends
4 over recent decades^{1,3,4}. However, there is still debate regarding the linearity of leaf unfolding
5 response to the climate warming^{6,7}. Recent experimental studies of warming using saplings have
6 shown that S_T weakens as warming increases⁷. Experimental manipulation of temperature for
7 saplings or twigs, however, might elicit phenological responses that do not accurately reflect the
8 response of mature trees^{16,17}. We therefore investigated the temporal changes in S_T in adult trees
9 monitored *in situ* and exposed to real-world changes in temperature and other climate variables.
10 These long-term data series were obtained across Central Europe from the Pan European
11 Phenology Project (<http://www.pep725.eu/>). Data were collected from 1,245 sites for seven
12 dominant tree species (see methods and the distribution of the sites in Extended Data Fig. 1). The
13 aims of our analysis are to determine the temporal changes in S_T at the species level during 1980-
14 2013, a period during which Europe has substantially warmed¹³, and to relate these changes in S_T
15 to differences in other physiological and environmental factors.

16

17 For each species at each observation site, we first determined the preseason length as the period
18 before leaf unfolding for which the partial correlation coefficient between leaf unfolding and air
19 temperature was highest (see methods). We used a gridded climate dataset, including daily
20 maximum and minimum air temperature, precipitation and absorbed downward solar radiation,
21 with a spatial resolution of 0.25° (approximately 25 km)¹⁸. The optimal length of the preseason
22 ranged between 15 days and four months across the seven species (Extended Data Fig. 2), in
23 agreement with earlier results^{1,14}. We then calculated the average temperature during the
24 preseason for each year at each site and calculated S_T using ordinary least squares linear
25 regression for the entire period and for two 15-year periods, namely 1980-1994 and 1999-2013,
26 that had slight difference in preseason lengths (Extended Data Fig. 3a). The leaf unfolding dates
27 were negatively correlated with the preseason temperature, with a mean linear correlation
28 coefficient of -0.61 ± 0.16 , determined using the preseason defined from the time period 1980-
29 2013. Almost all individual tree-level correlations were negative (99.7%) and the vast majority of
30 these correlations was statistically significant at $P < 0.05$ (93.4%) (Extended Data Fig. 4). In line

1 with previous studies^{1,4}, the timing of leaf unfolding substantially advanced in all species for
2 1980-2013, with an average advancing rate of 3.4 ± 1.2 days $^{\circ}\text{C}^{-1}$ across all species-sites
3 (hereafter, a positive value indicates advancement) (Fig. 1a). But the surprising result is that S_T
4 significantly decreased by 40.0% from 4.0 ± 1.8 days $^{\circ}\text{C}^{-1}$ during 1980-1994 to 2.3 ± 1.6 days $^{\circ}\text{C}^{-1}$
5 during 1999-2013 ($t=-37.3$, $df=5473$, $P<0.001$) (Fig. 1b). All species show similar significant
6 decreases in S_T (Fig. 1a), although the extent of reduction was species-specific. For example,
7 *Aesculus hippocastanum* (see caption to Fig. 1 for English common names) had the largest
8 decrease in S_T (-2.0 days $^{\circ}\text{C}^{-1}$), while S_T decreased only slightly (but still significantly) in *Fagus*
9 *sylvatica* (-0.9 days $^{\circ}\text{C}^{-1}$) (Fig. 1a). Similar results were also obtained using a fixed preseason
10 length determined either in the time period 1980-1994 or in 1999-2013 (Extended Data Fig. 3b
11 and 3c). The declining S_T could, however, also have been an artifact resulting from the
12 ‘encroachment’ of leaf unfolding dates into the preseason period that was used to calculate the
13 temperature sensitivity. We therefore calculated the number of ‘encroachment days’ and found it
14 is very small compared to the pre-season length even in the warmest period (Extended Data Fig.
15 3d and 3e). Because the time scale of the analysis could affect the estimates of S_T ¹⁹, we also
16 calculated S_T using 10-year intervals (instead of 15 years) and found consistent results, i.e., S_T
17 significantly decreased between the 1980s and the last decade for all species except *Tilia cordata*
18 (Extended Data Fig. 5a). We further calculated S_T with a 15-year moving window from 1980 to
19 2013 and found a significant decrease ($P<0.01$) for each of the seven species (Fig. 1c). S_T
20 decreased by an average of 0.7 days $^{\circ}\text{C}^{-1}$ per decade across all species. Similar results were also
21 reached when a 10-year interval was used (Extended Data Fig. 6). These results suggest a
22 significant change in the response of leaf unfolding to the ongoing climate warming in all studied
23 tree species in Central Europe.

24
25 Since there is no single accepted theory to account for the decreased S_T over the period 1980-
26 2013, we propose three mutually non-exclusive hypotheses: (1) adaptation to increased variance
27 in spring temperature, (2) photoperiodic limitations (due to earlier leaf unfolding) overriding
28 temperature controls, and (3) reduced duration and/or sum of cold temperatures during dormancy,
29 a ‘lost chilling’ mechanism.

30

1 The first hypothesis relates to possible effects of an increased variance in temperature. A recent
2 study reported substantial spatial differences in S_T , with smaller absolute values at sites with a
3 higher variance of local spring temperature²⁰. Trees may indeed develop conservative strategies
4 (or higher phenological plasticity) of spring leaf unfolding in places where temperature fluctuates
5 more, in order for instance to avoid spring frost damage²¹. The observed declining S_T could
6 therefore partly result from an increase in the variance in spring temperature. However, the
7 variance in spring temperature only significantly increased at sites of two species and decreased
8 for all the other species except *Fraxinus excelsior* (Fig. 2a). This suggests that increased variance
9 in spring temperature cannot account for the decreased S_T . We further studied the fluctuations in
10 daily mean temperature and diurnal temperature amplitude ($T_{\max} - T_{\min}$) over the preseason for
11 the two periods 1980-1994 and 1999-2013, and for three groups of sites with comparable mean
12 annual temperature (MAT). The fluctuations in daily temperature and diurnal temperature
13 amplitude during the preseason were similar during the two time periods between which S_T
14 declined (Extended Data Fig. 7), suggesting that altered temperature variability is not an obvious
15 cause for the declining apparent temperature sensitivity of leaf unfolding.

16

17 Precocious leaf unfolding in warm springs may increase the risk of late frost events for trees²¹. To
18 overcome this risk during warm springs, many species have evolved a protective mechanism
19 related to photoperiod²², which hinders the warming response when days are still short and the
20 risk for subsequent frost events is thus high. Our second, alternative, hypothesis to account for
21 the observed decrease in S_T in recent decades is therefore a change in the relationship between
22 chilling accumulation and heat requirement, due to the shortening days as warming advances leaf
23 unfolding. However, we did not observe changes in S_T with latitude, neither across all species,
24 nor for individual species (Extended Data Fig. 8), as one may expect if photoperiod was a strong
25 co-limitation of leaf unfolding. Nonetheless, we have no evidence to exclude photoperiod as a
26 controlling mechanism for the decline of S_T since different populations may have different
27 genetic adaptations to photoperiod²³. In addition, the lack of relation between S_T and latitude may
28 have been because the response of spring phenology to photoperiod can be associated with many
29 confounding factors, such as tree age¹⁷, successional niche²³ (although there is some
30 contradictory evidence⁸), xylem anatomy²⁴, or chilling conditions⁸. We can therefore not

1 conclude that photoperiod did not influence S_T , but how it might directly or indirectly affect
2 spring phenology still remains unclear and is currently under debate^{6,15,22}.

3

4 The third hypothesis to explain for the decreased S_T is based on the control of spring phenology
5 by cold temperatures during the dormancy period. In general, temperate and boreal trees require a
6 certain amount of heat (heat requirement) after they come out of the rest period to initiate leaf
7 unfolding in spring²⁵. Logically, this heat requirement is met sooner during warmer springs,
8 which explains the advance of leaf unfolding in response to global warming. The heat
9 requirement, however, is negatively correlated with chilling^{7,8,25}, i.e. the accumulation of cold
10 temperatures during the dormancy period. Since the dormancy period warmed during the study
11 period, the accumulated chilling is progressively reduced, thereby increasing heat requirement
12 and slowing down the advance of leaf unfolding. The net effect of lost chilling can thus be a
13 reduced S_T . This effect may be further exacerbated by the non-linearity of the negative
14 correlation between the heat requirement and the chilling accumulation^{7,25}.

15

16 To test this hypothesis, we calculated the accumulated chilling that was defined as the sum of
17 days when daily air temperature was within the range between 0 and 5 °C from 1st November in
18 the year prior to leaf unfolding (see methods), and found a significant decrease ($P<0.001$) in
19 chilling accumulation for all species (Fig. 2b). Chilling accumulation was 10% lower for 1999-
20 2013 than for 1980-1994. Chilling accumulation was also significantly decreased with a 15-year
21 moving window (Extended Data Fig. 9a) and when defined by different temperature thresholds
22 (Extended Data Fig. 9b). To further test the importance of the ‘lost chilling’ hypothesis, we
23 applied three chilling-based phenology models to the data (See Supplementary information). All
24 three models captured the declining S_T after their calibration at each site and their integration
25 with observed climate forcing, irrespective of species (Fig. 3). The modelled relative reductions
26 in S_T between the two periods 1980-1994 and 1999-2013 were, however, smaller than the
27 observed decline, i.e. simulated S_T was reduced by 28.8 %, 24.4% and 30.4% for the Sequential,
28 Parallel and Unified chilling-based models, respectively, whereas the observed S_T was reduced
29 by 40.0%. This may suggest that either other protective or adaptive mechanisms, such as
30 photoperiod or adaptation mechanisms, are affecting the decline in S_T , or that the three models do

1 not completely accurately represent all chilling mechanisms. There are also uncertainties related
2 to the 0.25° gridded climate product that may not represent local air temperature at each site
3 (snow effects, shading, slope, elevation). Furthermore, using the Unified model, we applied
4 idealized stepwise increases of winter temperature over the period 1980-2013 by +1°C to +5°C,
5 and consistently obtained a decrease in S_T induced by the loss of chilling in these idealized tests
6 (Extended Data Fig. 9c). However, we did not find marked differences in S_T between years with
7 more chilling days and years with less chilling days (Extended Data Fig. 10a-c), which can
8 probably be explained by the different climate conditions between years with more and less
9 chilling days. For example, the relatively high spring radiation sum in years with less chilling
10 days might buffer the effects of less chilling days (Extended Data Fig. 10d), and eventually
11 resulted in a similar S_T , but this remains speculation. Clearly, further studies are needed to
12 support these inferences and their role in the control over phenology. Overall, these results
13 support the third hypothesis that the decline in chilling accumulation is, at least partly, driving the
14 decline in S_T , although the possible constraint of photoperiod/radiation could not be excluded.

15
16 Changes in spring phenology associated with climate warming have direct impacts on regional
17 and global carbon cycling¹². Studies have reported that an extension of the growing season can
18 increase the photosynthetic production of forests by 0.5-1% per day^{26,27,28}. We found that the
19 apparent sensitivity of spring phenology to warming for seven temperate tree species in Central
20 Europe has declined significantly as winter and spring temperatures increased over the past three
21 decades. These findings indicate that the early spring phenologically-driven increases in carbon
22 uptake may slow down for temperate forests under future conditions of climate warming. On the
23 other hand, the declining apparent temperature sensitivity of spring phenology may be beneficial
24 for the trees. Extreme climatic events have dramatically increased in recent decades, especially
25 warm winters and springs²⁹, and the decreased apparent temperature sensitivity would thus
26 reduce the risk of late spring frost damage by avoiding premature leaf unfolding.

27

28 **Methods**

29 **Data sets.** *In situ* phenological observations were obtained from the Pan European Phenology
30 network (<http://www.pep725.eu/>), which provides an open European phenological database

1 comprising multiple plant phenological records. We selected the records of leaf unfolding dates
2 for seven tree species at 1,245 sites for 1980-2013 from sites in an area stretching from north
3 Germany to the Adriatic Sea (see Extended Data Fig. 1). The leaf unfolding dates were defined
4 according to the BBCH code (Biologische Bundesanstalt, Bundessortenamt und Chemische
5 Industrie). Dates were excluded from the analysis when the trees flushed later than the end of
6 June. The daily mean air temperature of each site was derived from a gridded climate data set of
7 daily maximum and minimum temperature at 0.25° spatial resolution (approximately 25 km)¹⁸.
8 We also applied another climate forcing dataset (CRU-NCEP v5, with spatial resolution of 0.5°
9 and temporal resolution of 6h, <http://dods.extra.cea.fr/data/p529viov/cruncpe/>), and returned very
10 similar results (Extended Data Fig. 5c).

11

12 **Analysis.** The relevant period for leaf unfolding is several months prior to the phenological
13 event¹, and periods differ among species and locations. To remove covariate effects of
14 precipitation and radiation on leaf unfolding, we applied a partial correlation analysis to
15 determine the optimal length of the preseason for each species at each site³⁰. The optimal
16 preseason for each species at each station was defined as the period (with 15-day steps) before
17 the mean leaf unfolding date for which the partial correlation coefficient between leaf unfolding
18 and air temperature was highest during 1980-2013. Using a similar method, we also defined
19 preseason for two 15-year periods (e.g., 1980-1994, 1999-2013) to further assess the robustness
20 of the inferred decline of apparent temperature sensitivity of leaf unfolding over the last three
21 decades (Extended Data Fig. 3a-c).

22

23 Linear regression analyses (using both ordinary least squares and reduced major axis regressions)
24 of the dates of leaf unfolding against mean air temperature over the preseason were performed for
25 each species at each site during the three study periods: 1980-2013 (minimum 15-year records
26 required per site), 1980-1994, and 1999-2013 (minimum 7-year records required per site,
27 satisfied simultaneously for the two latter study periods). Similar results, i.e. significant decreases
28 in S_T , were observed using reduced major axis regression method (Extended Data Fig. 5b), we
29 therefore only present the results using ordinary least squares method. The regression coefficient
30 was defined as the apparent temperature sensitivity of leaf unfolding (S_T) that reflects the change

1 in leaf unfolding date per unit increase in mean temperature during the preseason. This is not the
2 ‘actual’ physiological sensitivity to temperature, given that other climate-related variables, such
3 as chilling, photoperiod, solar radiation and precipitation, also co-determine the leaf unfolding
4 process and determine the emerging S_T value diagnosed from the preseason temperature^{8,12,22}.
5 The mean S_T across all sites was calculated for each and all species for these three periods. The
6 frequency distributions of S_T across all species and sites for 1980-1994 and 1999-2013 were
7 determined. The differences in mean S_T during 1999-2013 and 1980-1994 were tested using
8 independent *t*-tests for each and across species.

9
10 To investigate the effect of the chilling requirement and variance in spring temperature on S_T , we
11 calculated species-specific variances in spring temperature and chilling requirements at each site.
12 The spring temperature variance was calculated as the standard deviation of mean temperature
13 during the preseason. The chilling requirement is normally defined as the length of the period
14 (days or hours) during which temperature remains within a specific range. Most previous studies
15 have reported that temperatures slightly above freezing are most effective in satisfying the
16 chilling requirement³¹ and have suggested that the temperature range between 0 and 5 °C is the
17 most effective across species. To calculate the chilling requirement, we therefore summed the
18 days when daily temperature was within this range:

$$19 CD_{req}(t) = \sum_{t_0}^{t_{LF}} 1 \quad if \quad 0 \leq T_t \leq 5$$

20 where CD_{req} is the chilling requirement, t_{LF} is the day of leaf unfolding, T_t is the daily mean
21 temperature on day t , and t_0 is the start date for chilling accumulation. t_0 was fixed at 1 November
22 in the year prior to leaf unfolding. We also tested another commonly used temperature threshold,
23 5°C²⁴, and included all temperatures below this threshold.

$$24 CD_{req}(t) = \sum_{t_0}^{t_{LF}} 1 \quad if \quad T_t \leq 5$$

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

1

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16

17 **Supplementary Information** is linked to the online version of the paper at
18 www.nature.com/nature.

19

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3

4 **Author contributions**

5 S.L.P., Y.H.F. and I.A.J. designed the research; H.F.Z., Y.H.F., M. P., S.S.P. and G.Y.Z
6 performed the analysis; Y.H.F., S.L.P. and I.A.J. drafted the paper; and all authors contributed to
7 the interpretation of the results and to the text.

8 **Author Information**

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10 have no competing financial interests. Correspondence and requests for materials should be
11 addressed to S.L.P. (slpiao@pku.edu.cn).

12

13 **Figure Legends**

14 **Figure 1. Changes of apparent temperature sensitivity of leaf unfolding (S_T , advances in
15 days per degree Celsius warming) over time.** (a) Species-specific S_T and its standard deviation
16 (in brackets) across all sites in three periods and its difference between 1999-2013 and 1980-
17 1994. The S_T was determined using the preseason fixed at the time period 1980-2013 and using
18 ordinary least squares linear regression. The colour scale indicates magnitude of S_T . AG, alder
19 (*Alnus glutinosa*); BP, silver birch (*Betula pendula*); AH, horse chestnut (*Aesculus
20 hippocastanum*); FS, beech (*Fagus sylvatica*); TC, lime (*Tilia cordata*); QR, oak (*Quercus
21 robur*); FE, ash (*Fraxinus excelsior*). The number of sites for each species are in brackets under
22 the species name. (b) The distribution of S_T across all species and sites in two different periods
23 and the mean S_T and standard deviations (in brackets). The asterisk indicates a significant
24 difference of S_T between the two periods at $P<0.05$. (c) Temporal change of S_T for each and all
25 species across all sites with a 15-year moving window from 1980 to 2013. The black line
26 indicates the average across all species, and the grey area indicates one standard deviation either
27 side of the mean. The dotted line indicates the linear regression.

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

10
11 **Figure 3. Changes of modeled apparent temperature sensitivity of leaf unfolding (S_T ,**
12 **advances in days per degree Celsius warming).** As in Fig. 1a, panels a-c show the modelled
13 species-specific S_T , including the standard deviations (in brackets), across all sites during three
14 periods and its difference between 1999-2013 and 1980-1994. (a) Sequential model, (b) Parallel
15 model and (c) Unified model. As in Fig. 1c, panels d-f show the modelled temporal change of S_T
16 for each and all species across all sites with a 15-year moving window from 1980 to 2013. (d)
17 Sequential model, (e) Parallel model and (f) Unified model. The model performance is provided
18 in (g). The S_T was determined using the preseason fixed at the time period 1980-2013 and using
19 ordinary least squares linear regression. The colour scale indicates magnitude of S_T . RMSE, root
20 mean square error; AG, alder (*Alnus glutinosa*); BP, silver birch (*Betula pendula*); AH, horse
21 chestnut (*Aesculus hippocastanum*); FS, beech (*Fagus sylvatica*); TC, lime (*Tilia cordata*); QR,
22 oak (*Quercus robur*); FE, ash (*Fraxinus excelsior*). The number of sites for each species are in
23 brackets under the species name.

24
25 **Extended Data Figure Legends:**
26 **Extended Data Figure 1. The distribution of the sites.** The data were obtained from the Pan
27 European Phenology network (<http://www.pep725.eu/>).

1 **Extended Data Figure 2. The distribution of preseason length for each and all species.** The
2 optimal preseason was defined as the period before leaf unfolding for which the correlation
3 coefficient between leaf unfolding and temperature was highest. The numbers in the brackets are
4 the mean dates of leaf unfolding across all sites.

5 **Extended Data Figure 3. Changes of apparent temperature sensitivity of leaf unfolding (S_T ,
6 **advances in days per degree Celsius warming) between 1980-1994 and 1999-2013.** Same as
7 Fig. 1, but the S_T was calculated based on the preseason that was determined either in the time
8 period 1980-1994 (b) or in 1999-2013 (c). The differences in preseason lengths are provided for
9 each and all species (a), and the figures above bars are the mean absolute preseason difference
10 between two periods. For b and c, species-specific S_T and its standard deviation (in brackets)
11 across all sites in three periods and its difference between 1999-2013 and 1980-1994. The colour
12 scale indicates magnitude of S_T . AG, *Alnus glutinosa*; BP, *Betula pendula*; AH, *Aesculus*
13 *hippocastanum*; FS, *Fagus sylvatica*; TC, *Tilia cordata*; QR, *Quercus robur*; FE, *Fraxinus*
14 *excelsior*. The number of sites for each species are in brackets under the species name. (d) The
15 distribution of the proportion and corresponding days (e) of the encroachment of phenology dates
16 into the preseason temperature that the preseason was determined on the period 1980-2013. The
17 proportion was defined as the difference of the mean leaf unfolding dates (diff MSOS) between
18 the period 1999-2013 and 1980-2013 (which is the end date of the preseason temperature that
19 was used to calculate the S_T) divided by the preseason length in days. The mean values and its
20 standard deviation (in brackets) are provided for each and all species.**

21 **Extended Data Figure 4. The distribution of partial correlation coefficients between
22 preseason temperature and leaf unfolding dates over the time period 1980- 2013.** The mean
23 (and standard deviation: STD) of the correlation coefficients across all species and sites are
24 provided. The percentages of negative correlations and statistically significant negative
25 correlations (Neg(Sig)) are also provided.

26 **Extended Data Figure 5. Changes of apparent temperature sensitivity of leaf unfolding (S_T ,
27 **advances in days per degree Celsius warming) determined by different methods.** The S_T
28 were analyzed in two 10-year periods (a), were calculated using the reduced major axis (RMA)**

1 regression (b), or were calculated based on another climate forcing dataset (CRU-NCEP v5, c).
2 Species-specific S_T and its standard deviation (in brackets) across all sites in three periods and the
3 difference two study periods are provided. The colour scale indicates magnitude of S_T . AG, alder
4 (*Alnus glutinosa*); BP, silver birch (*Betula pendula*); AH, horse chestnut (*Aesculus*
5 *hippocastanum*); FS, beech (*Fagus sylvatica*); TC, lime (*Tilia cordata*); QR, oak (*Quercus*
6 *robur*); FE, ash (*Fraxinus excelsior*). The number under the species name is the number of sites.
7 The histograms show the distribution of S_T across all species and sites in two different periods
8 and the mean S_T and standard deviations (in brackets). The asterisk indicates a significant
9 difference of S_T between the two periods at $P<0.05$.

10 **Extended Data Figure 6. Changes of apparent temperature sensitivity of leaf unfolding (S_T ,
11 advances in days per degree Celsius warming) over time.** Same as Fig. 1c, but temporal
12 change of S_T with 10-year moving windows from 1980 to 2013. The S_T was calculated using
13 simple linear regression. The black line indicates the average across all species, and the grey area
14 indicates one standard deviation either side of the mean. The dotted line indicates the linear
15 regression.

16 **Extended Data Figure 7. The differences in climatology over the preseason.** The fluctuations
17 in mean daily temperature (left panels) and diurnal variation temperature ($T_{max} - T_{min}$, right
18 panels) over the preseason across all sites during the time period 1980-1994 and 1999-2013 in
19 three MAT groups, i.e. (top panels) 6- 8°C, (middle panels) 8-10°C and (bottom panels) 10-12°C.
20 The preseason was determined over the period 1980-2013.

21 **Extended Data Figure 8. Spatial difference in apparent temperature sensitivity of leaf
22 unfolding (S_T , advances in days per degree Celsius warming) reduction.** The difference of S_T
23 for each species and across all species studied between two time periods, 1999-2014 and 1980-
24 1994, at different latitudes (bin: 0.5°) and chilling conditions (bin: two chilling days). The colour
25 scales indicate the differences of S_T between the two periods.

26 **Extended Data Figure 9. Changes in chilling accumulation and modeled correlation
27 between chilling and apparent temperature sensitivity of leaf unfolding (S_T , advances in**

1 **days per degree Celsius warming).** (a) Chilling accumulation for each and all species with 15-
2 year moving windows from 1980 to 2013. The chilling accumulation was calculated as chilling
3 days when daily temperature was between 0 and 5 °C from 1 November to the average date of
4 leaf unfolding. The black line indicates the average across all species, and the grey area indicates
5 one standard deviation either side of the mean. The dotted line indicates the linear regression. (b)
6 Same as Fig. 2b, but chilling accumulation was calculated as chilling days when daily
7 temperature was below 5°C from 1 November to the average date of leaf unfolding. The asterisks
8 indicate significant differences at $P<0.05$. (c) The modelled (Unified model) S_T under different
9 artificial winter warming conditions. The temperature in winter, defined as the period from the 1
10 November to 31 January, was warmed by +1 °C to +5 °C over the period 1980-2013. The points
11 with most chilling days indicate the real winter temperatures, and each of the other points
12 indicate one winter warming treatment. The lines indicate simple linear regressions.

13 **Extended Data Figure 10. Changes in apparent temperature sensitivity of leaf unfolding**
14 **(S_T , advances in days per degree Celsius warming) between years with more or less chilling.**
15 S_T for years with (a) less chilling and (b) more chilling with a 20-year moving window for 1980-
16 2013. For each 20-year series, we divided the 20 years into two groups based on the mean
17 chilling accumulation (Chilling was accumulated when daily temperature within the temperature
18 range between 0°C and 5°C from 1st November to the day of leaf unfolding). The 10 years with
19 chilling higher than the overall mean were defined as more chilling, and the other 10 years were
20 defined as less chilling. The black lines indicate the average across all species, and the grey area
21 indicates one standard deviation either side of the mean. The dotted lines are the linear
22 regressions. (c) Chilling accumulation for years with less chilling (red line) and more chilling
23 (blue line) with a 20-year moving window for 1980-2013. (d) The mean radiation sum over the
24 preseason for years with less chilling (red line) and more chilling (blue line) with a 20-year
25 moving window for 1980-2013. The preseason was determined over the period 1980-2013.

1 Supplementary information

To test the hypothesis that the observed decline in S_T is in fact a response to the declining chilling, we applied three commonly used chilling-based phenology models, i.e. the Sequential, Parallel and Unified models, to simulate the leaf unfolding dates. We then calculated the S_T using the same method as for the observations. We chose a simulated annealing method to fit the models based on the observation over the period 1980-2013. The details of these three models are described below. In the models, the effects of the forcing and chilling temperatures are accounted for by calculating (daily) rates of forcing (R_f) and chilling (R_c), which are functions of the daily air temperature (T). These functions differ between models. R_f and R_c determine the rates of change of the states of forcing (S_f) and chilling (S_c), respectively:

$$13 \quad S_f(D) = \sum_{t=t_{1f}}^D R_f(T) \quad (1)$$

$$S_c(D) = \sum_{t=t_{l_c}}^D R_c(T) \quad (2)$$

where t_{lf} and t_{lc} are the initial days of the forcing and chilling periods, respectively, and D is the day of the year. Leaf unfolding is triggered when S_f reaches a forcing threshold F^* , whereas in the Sequential and the Parallel models, the start of quiescence (the forcing period) is triggered when S_c reaches the chilling threshold C^* .

19 if $S_f(D) \geq F^*$ then leaf unfolding induction is completed (3)

$$if \quad S_c(D) \geq C^* \quad \text{then dormancy is completed} \quad (4)$$

22 Sequential model (*SM*)^{32,33}

23 *SM* starts to accumulate warmth units when a sufficient amount of chilling has occurred (Eq.
 24 4). In *SM*, we fixed t_{1c} on 1 November. As in the previous applications of *SM*, we defined R_c
 25 as a triangular function of $T^{32,33}$:

$$R_c(D) = \begin{cases} 0 & \text{if } T(D) \leq T_{\min} \\ \frac{T - T_{\min}}{T_{\text{opt}} - T_{\min}} & \text{if } T_{\min} < T(D) \leq T_{\text{opt}} \\ \frac{T - T_{\max}}{T_{\text{opt}} - T_{\max}} & \text{if } T_{\text{opt}} < T(D) \leq T_{\max} \\ 0 & \text{if } T \geq (D)T_{\max} \end{cases} \quad (5)$$

where T_{\min} , T_{\max} and T_{opt} are the minimum, maximum and optimum temperature for the chilling period. R_f is calculated with a similar sigmoid function as:

$$R_f(D) = \begin{cases} 0 & \text{if } S_c < C^* \\ \frac{a}{1 + e^{-b(T-c)}} & \text{if } S_c \geq C^* \end{cases} \quad (6)$$

Parallel model (PM)^{32,33,34}

PM assumes that forcing temperature can affect leaf unfolding even during the chilling. As for *SM*, we fixed t_{1c} and t_{1f} on 1 November. R_c is calculated as in *SM*, whereas R_f is calculated with the following equation, a modification of Eq. 6 of *SM*:

$$R_f(D) = \begin{cases} 0 & \text{if } D < t_0 \\ k \frac{a}{1 + e^{-b(T-c)}} & \text{if } D \geq t_0 \end{cases} \quad \text{and} \quad k = \begin{cases} K_m + \frac{1 - K_m}{C^*} S_c & \text{if } S_c < C^* \\ 1 & \text{if } S_c \geq C^* \end{cases} \quad (7)$$

where K_m is a model parameter. *PM* has one more parameter (K_m) than *SM*.

11

Unified model(UM)³⁵

UM combines features of the other models and merges the equations for R_c and R_f into one sigmoid equation:

$$\frac{1}{1 + e^{a(T-c)^2 + b(T-c)}} = \begin{cases} R_c(D) & \text{if } a = C_a \text{ and } b = C_b \text{ and } c = C_c \\ R_f(D) & \text{if } a = 0 \text{ and } b = F_b \text{ and } c = F_c \end{cases} \quad (8)$$

where C_a , C_b and C_c are chilling-rate parameters and F_b and F_c are forcing-rate parameters. In *UM*, t_{1c} is set to be 1 September. The forcing units start to accumulate when a sufficient amount of chilling has occurred (C^*), and F^* is calculated with an exponential function of R_c from t_{1c} to t_{2c} :

$$F^*(D) = \omega^* e^{-k \sum_{t_{1c}}^{t_{2c}} R_c} \quad (9)$$

1 where k , w and t_{2c} are model parameters.

2 **Parameter estimation**

3 All three models were fitted using observed leaf unfolding dates for each site and species for
4 the period 1980-2013, for a total of 5,472 (sites*species) parameter estimates. Parameters
5 were adjusted by minimizing the root mean square error (RMSE; Eq. 10) between observed
6 and modelled leaf unfolding dates:

$$RMSE = \sqrt{\frac{\sum_{i=1}^n (X_{obs,i} - X_{mod,i})^2}{n}} \quad (10)$$

7 where $X_{obs,i}$ is the observed value, $X_{mod,i}$ is the modelled value of the observation i and n is the
8 number of observations. Following the study of Chuine *et al*³⁶, we calibrated the models
9 using a simulated annealing method. The simulated annealing refers to thermodynamic
10 principles where the objective function, here the RMSE, is considered as an energy function
11 of a cooling and crystallizing molten metal. An artificial temperature is introduced and
12 gradually lowered until it reaches a global minimum. At each iteration, the algorithm
13 explores the range of possible states of the system by changing parameter values according to
14 a generalized Metropolis algorithm acceptance probability. Simulated annealing methods are
15 less affected by local minima than gradient methods³⁷, but the number of local minima of the
16 RMSE function of phenological models is high. We thus performed thousands of global
17 searches with few iterations and random initial parameters followed by a global search with
18 more iterations and starting at the best result yet obtained for each optimization³⁵. The range
19 of variation for each parameter was prescribed according to previously published results of
20 model optimization^{35,36,38}.

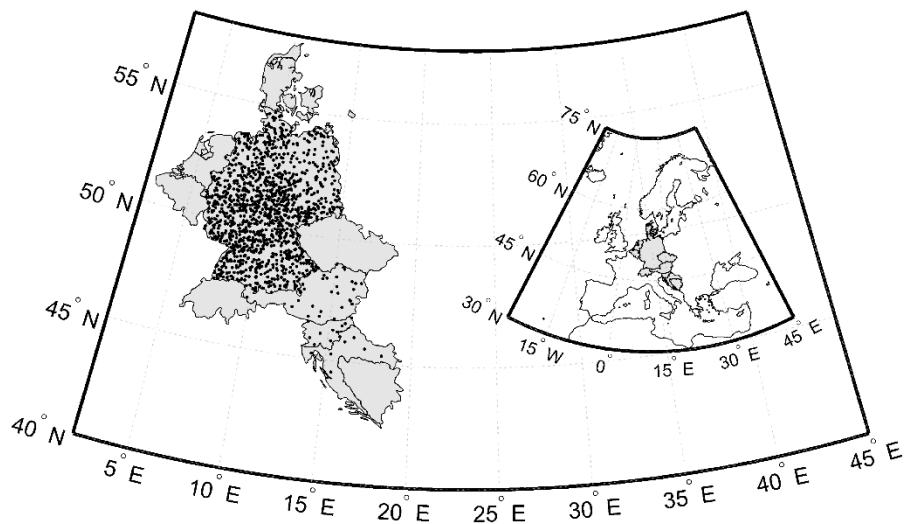
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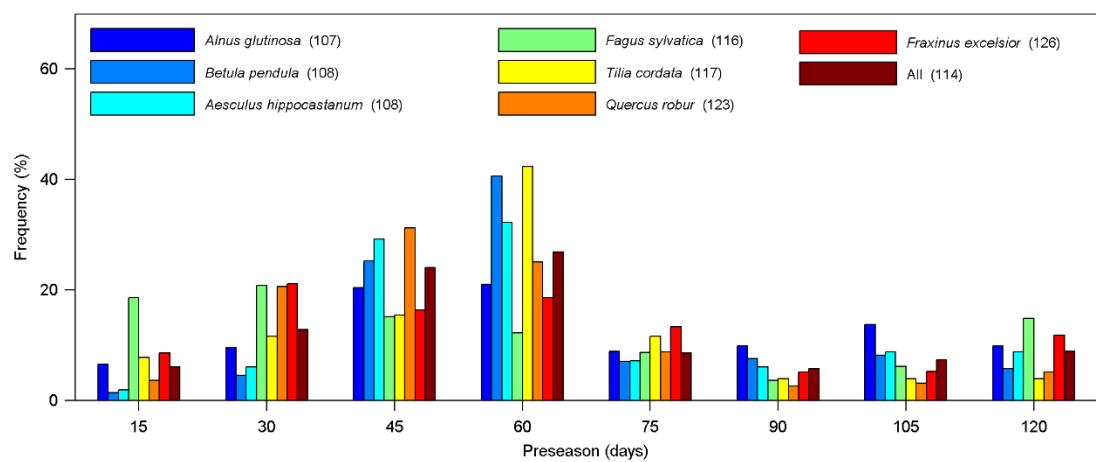
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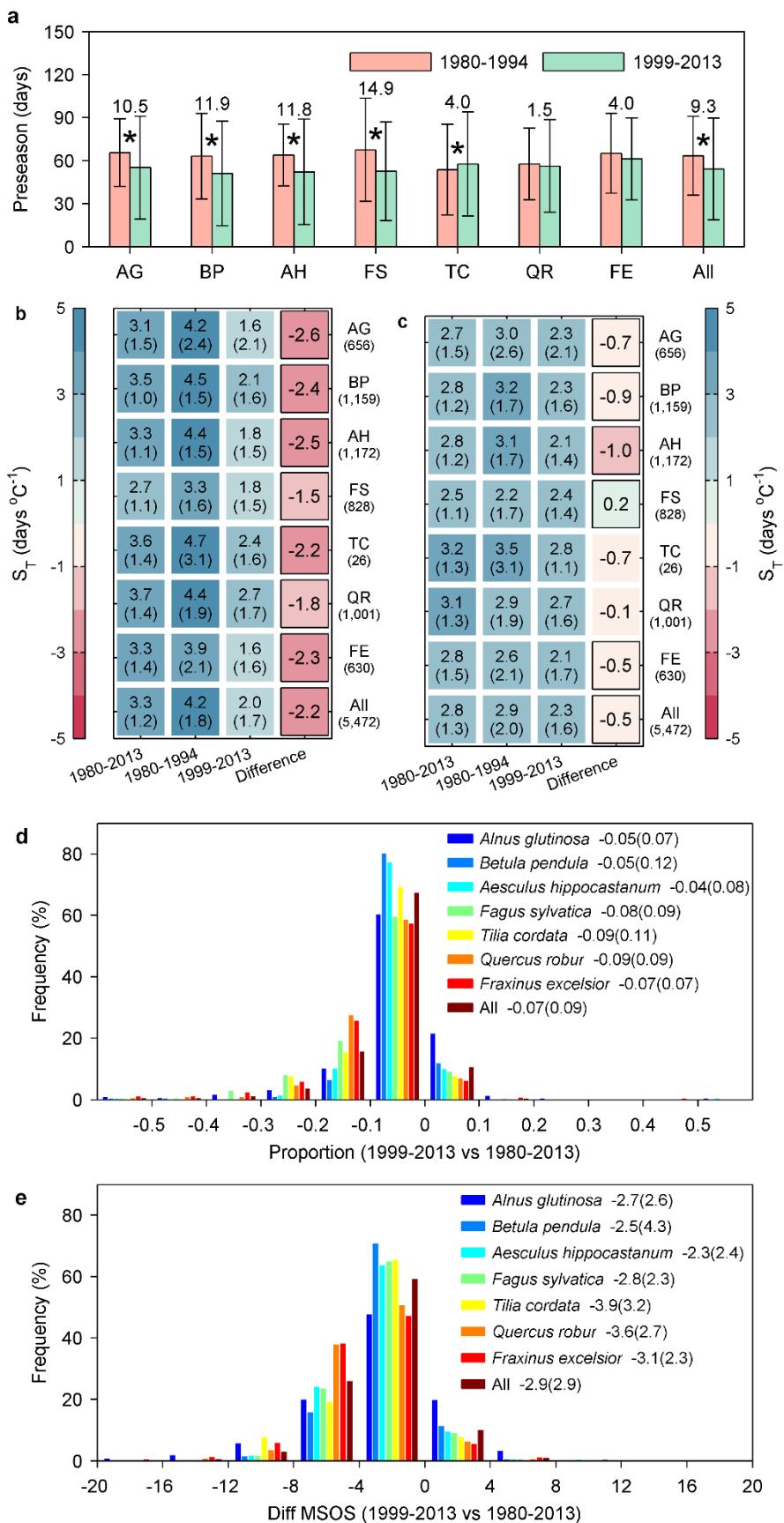
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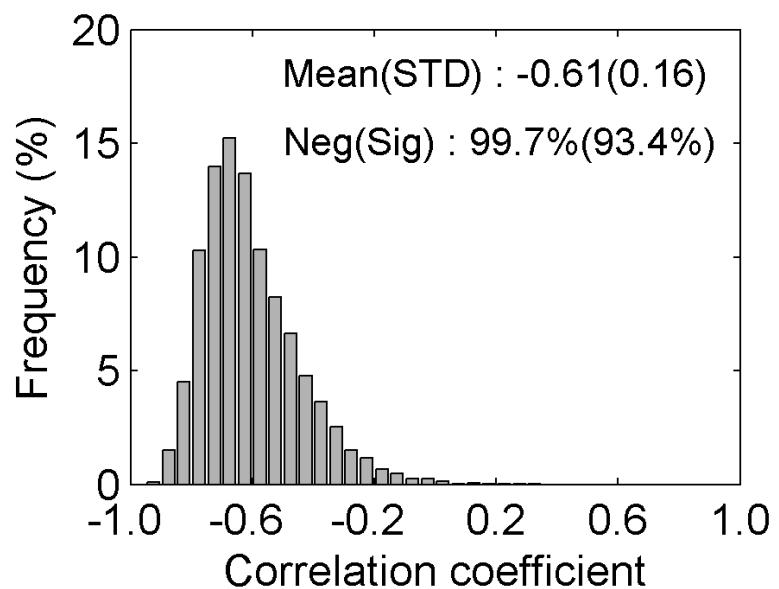
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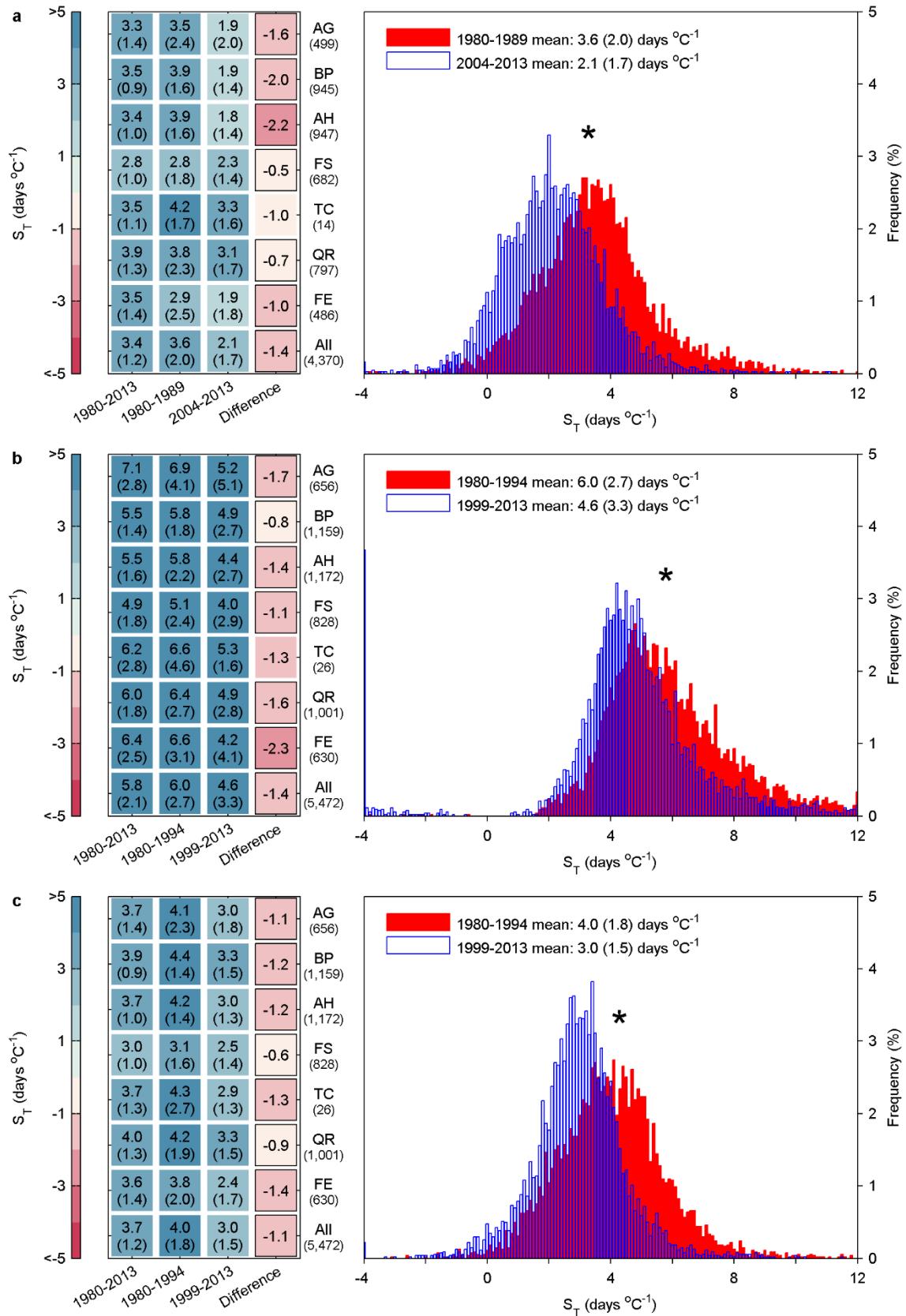
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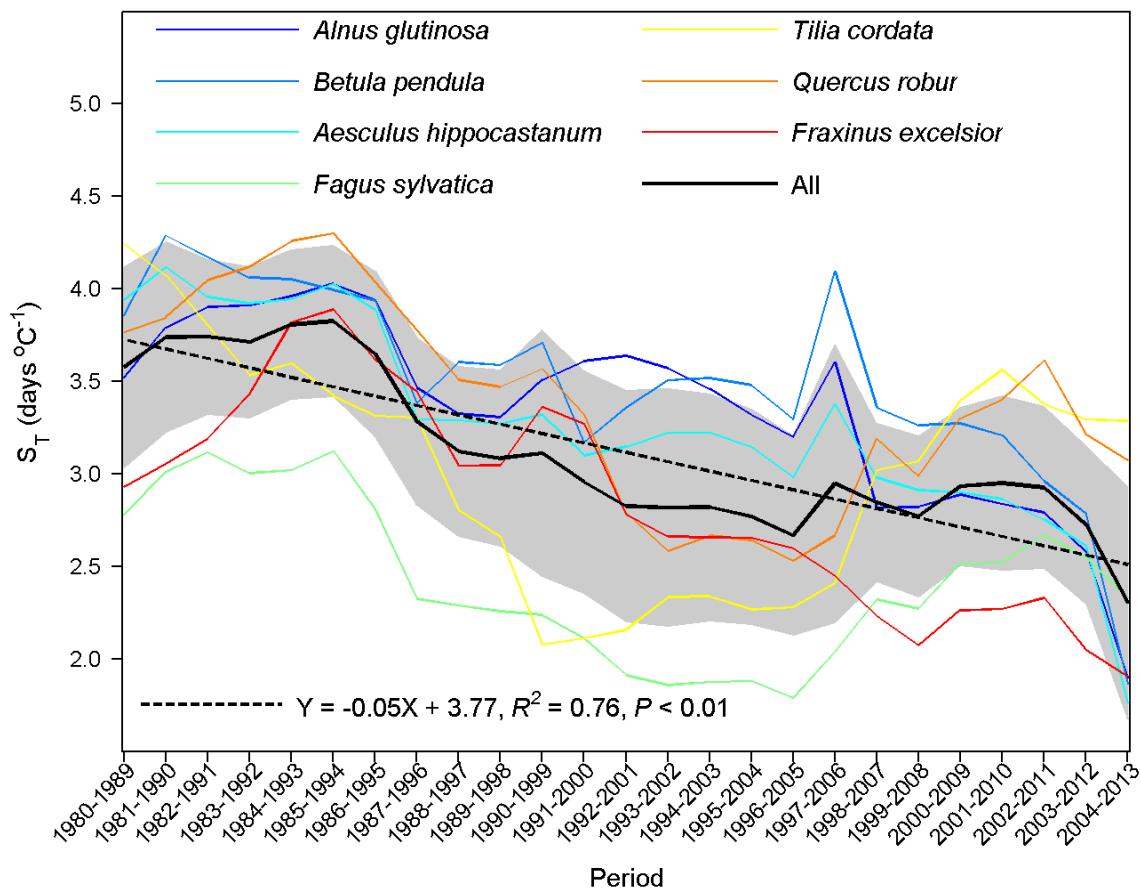
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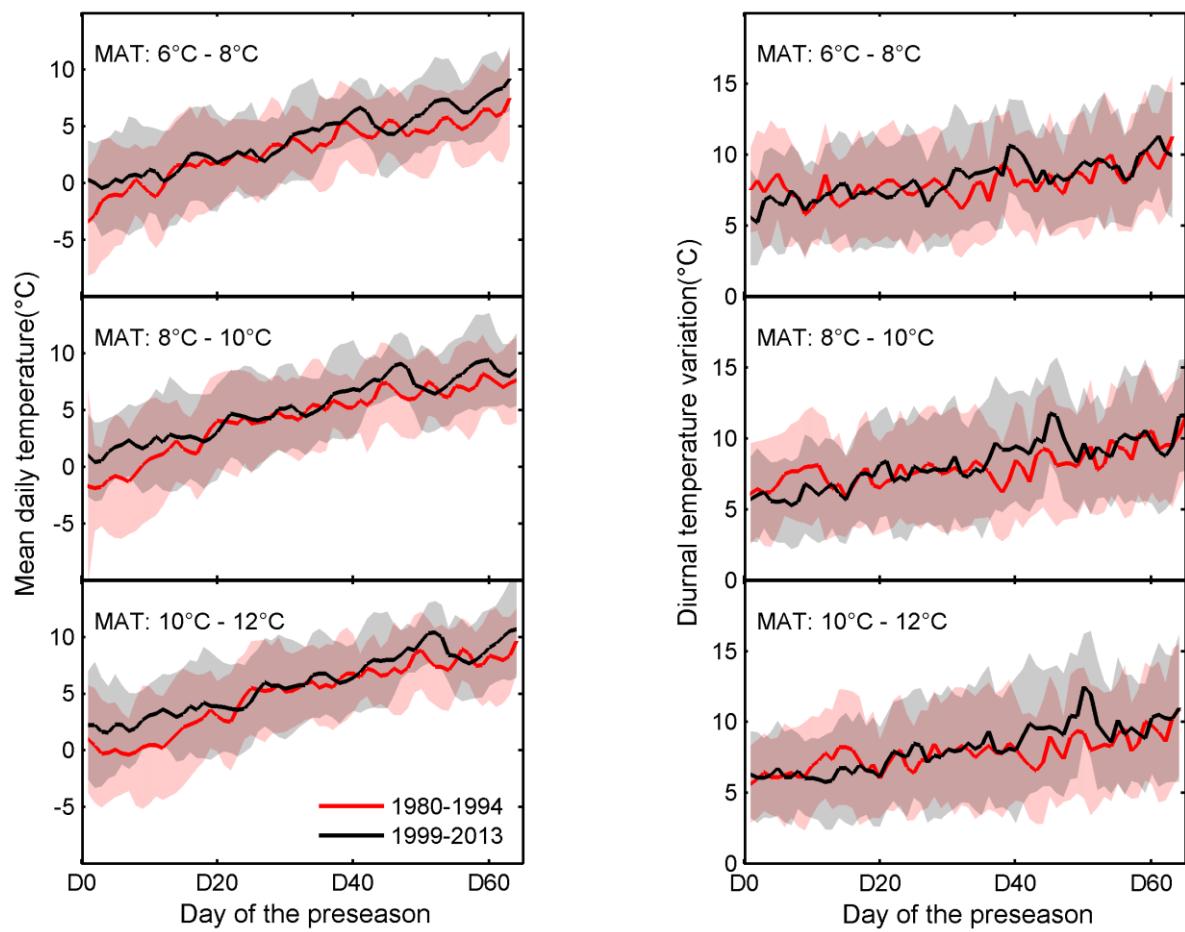
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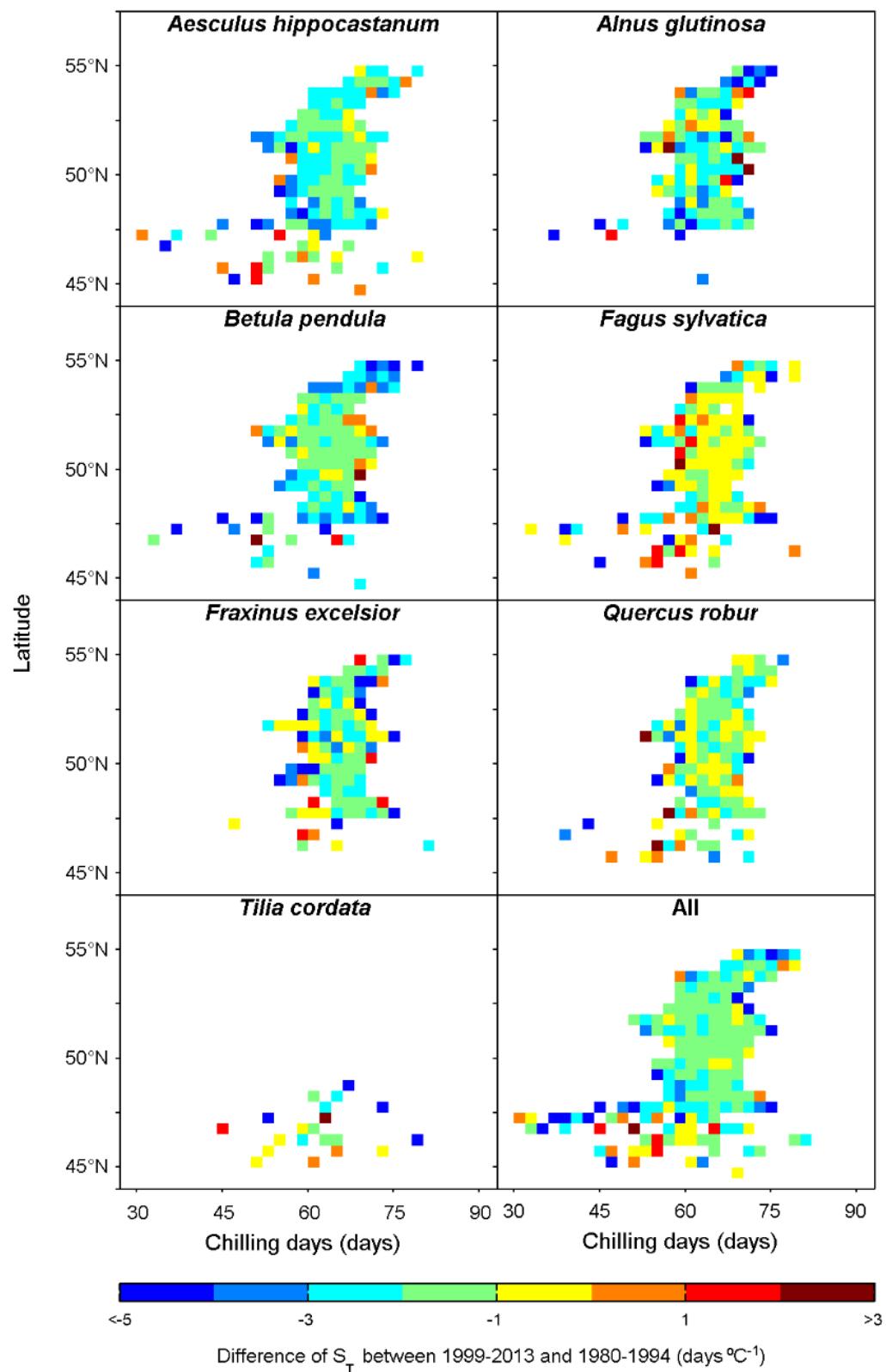
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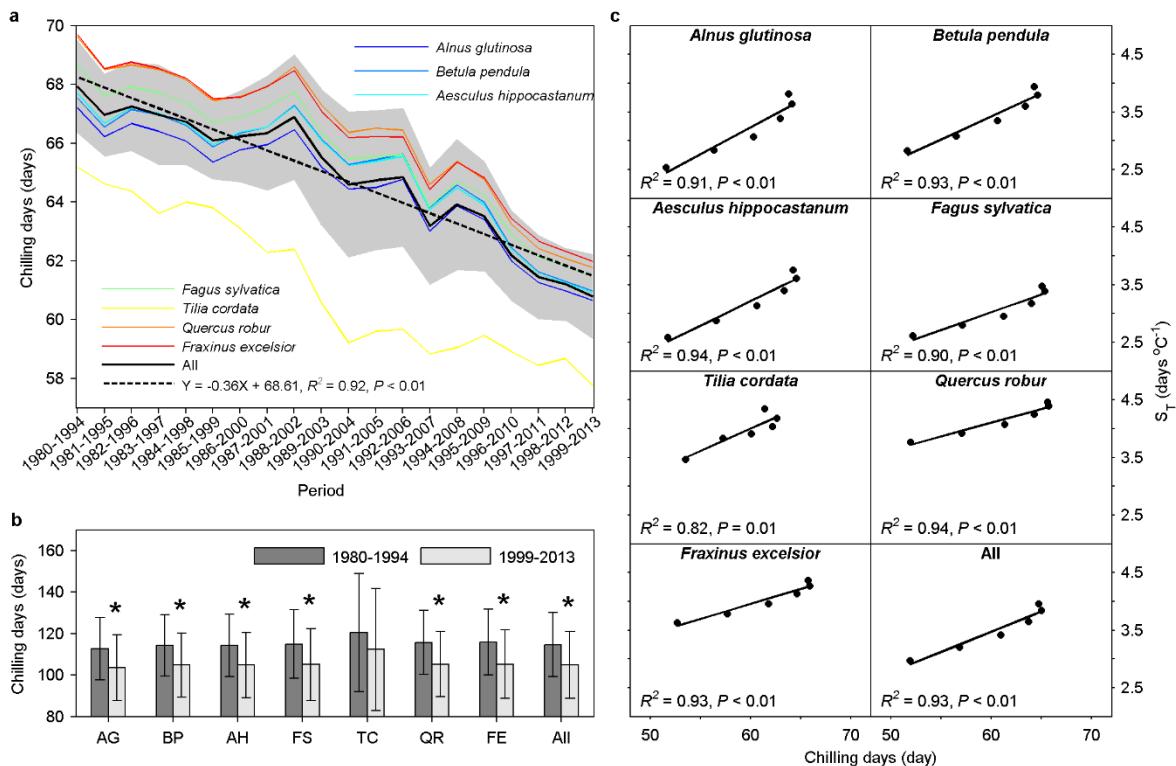
Extended Data Figure 7.



Extended Data Figure 8.



Extended Data Figure 9.



Extended Data Figure 10.

