Declining global warming effects on the phenology of spring leaf unfolding

Yongshuo H Fu[1,2], Hongfang Zhao[1], Shilong Piao[1,3,4], Marc Peaucelle[5], Shushi Peng[1,5], Guiyun Zhou[6], Philippe Ciais[5], Mengtian Huang[1], Annette Menzel[7,8], Josep Peñuelas[9,10], Yang Song[11], Yann Vitasse[12,13,14], Zhenzhong Zeng[1], Ivan A Janssens[2]

[1] Sino-French Institute for Earth System Science, College of Urban and Environmental Sciences, Peking University, Beijing 100871, China

[2] Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Wilrijk, Belgium

[3] Key Laboratory of Alpine Ecology and Biodiversity, Institute of Tibetan Plateau Research, Chinese Academy of Sciences, Beijing 100085, China

[4] Center for Excellence in Tibetan Earth Science, Chinese Academy of Sciences, Beijing 100085, China

[5] Laboratoire des Sciences du Climat et de l'Environnement, CEA CNRS UVSQ, Gif-sur-Yvette, France

[6] School of Resources and Environment, University of Electronic Science and Technology of China, Chengdu, China

[7] Ecoclimatology, Technische Universität München, Freising, Germany

[8] Technische Universität München, Institute for Advanced Study, Lichtenbergstraße 2a, 85748 Garching, Germany

[9] CREAF, Cerdanyola del Vallès, Barcelona 08193, Catalonia, Spain

[10] CSIC, Global Ecology Unit CREAF -CSIC-UAB, Cerdanyola del Vallès, Barcelona 11 08193, Catalonia, Spain

[11] Department of Atmospheric Sciences, University of Illinois, Urbana, IL 61801, USA

[12] University of Neuchatel, Institute of Geography, Neuchatel, Switzerland

[13] WSL Swiss Federal Institute for Forest, Snow and Landscape Research, Neuchatel, Switzerland

[14] WSL Institute for Snow and Avalanche Research SLF, Group Mountain Ecosystems, Davos, Switzerland

Revised manuscript for *Nature*

August 12, 2015

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 ±**

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 balances[2], the long-term distribution of tree species[9], and plant-animal interactions[10]. 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 increase[13], 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 increases[7]. 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 warmed[13], 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 0.25º (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

with previous studies[1,4], the timing of leaf unfolding substantially advanced in all species for 1980-2013, with an average advancing rate of 3.4 ± 1.2 days $°C^{-1}$ 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 ± 1.8 days $°C^{-1}$ during 1980-1994 to 2.3 ± 1.6 days $°C^{-1}$ during 1999-2013 (t=-37.3, df=5473, 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 $°C^{-1}$), while S_T decreased only slightly (but still significantly) in *Fagus sylvatica* (-0.9 days $°C^{-1}$) (Fig. 1a). Similar results were also obtained using a fixed preseason length determined either in the time period 1980-1994 or in 1999-2013 (Extended Data Fig. 3b and 3c). The declining S_T could, however, also have been an artifact resulting from the 'encroachment' of leaf unfolding dates into the preseason 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 and 3e). Because the time scale of the analysis could affect the estimates of S_T [19], we also calculated S_T using 10-year intervals (instead of 15 years) and found consistent results, i.e., 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 $°C^{-1}$ 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 significant change in the response of leaf unfolding to the ongoing climate warming in all studied tree species in Central Europe.

Since 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, and (3) reduced duration and/or sum of cold temperatures during dormancy, a 'lost chilling' mechanism.

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 temperature[20]. 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 damage[21]. 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 trees[21]. To

18   overcome this risk during warm springs, many species have evolved a protective mechanism

19   related to photoperiod[22], 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 photoperiod[23]. 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 age[17], successional niche[23] (although there is some

30   contradictory evidence[8]), xylem anatomy[24], or chilling conditions[8]. 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 spring[25]. 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 cycling[12]. 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 springs[29], 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

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 0.25º spatial resolution (approximately 25 km)[18]. We also applied another climate forcing dataset (CRU-NCEP v5, with spatial resolution of 0.5º and temporal resolution of 6h, http://dods.extra.cea.fr/data/p529viov/cruncep/), and returned very similar results (Extended Data Fig. 5c).

Analysis. The relevant period for leaf unfolding is several months prior to the phenological event[1], 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 preseason for each species at each site[30]. The optimal preseason 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 preseason for two 15-year periods (e.g., 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 preseason 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, i.e. 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

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 requirement[31] 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   $$CD_{req}(t) = \sum_{t_0}^{t_{LF}} 1 \quad if \quad 0 \le T_t \le 5$$

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°C[24], and included all temperatures below this threshold.

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

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.

Reference

1   Menzel, A. *et al.* European phenological response to climate change matches the warming pattern. *Global Change Biol.* **12**, 1969-1976 (2006).

2   Myneni, R. C., Keeling, C. D., Tucker, C. J., Asrar, G. & Nemani, R. R. Increased plant growth in the northern high latitudes from 1981 to 1991. *Nature* **386**, 698-702 (1997).

3   Peñuelas, J. & Filella, I. Responses to a warming world. *Science* **294**, 793-795 (2001).

4   Fu, Y. S. H. *et al.* Recent spring phenology shifts in western Central Europe based on multiscale observations. *Global Ecol. Biogeogr.* **23**, 1255-1263 (2014).

5   Yu, H. Y., Luedeling, E. & Xu, J. C. Winter and spring warming result in delayed spring phenology on the Tibetan Plateau. *Proc. Natl. Acad. Sci. U.S.A* **107**, 22151-22156 (2010).

6   Chuine, I., Morin, X. & Bugmann, H. Warming, photoperiods, and tree phenology. *Science* **329**, 277-278 (2010).

7   Fu, Y. S. H., Campioli, M., Deckmyn, G. & Janssens, I. A. Sensitivity of leaf unfolding to experimental warming in three temperate tree species. *Agric. For. Meteorol.* **181**, 125-132 (2013).

8   Laube, J. *et al.* Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biol.* **20**, 170-182 (2014).

9   Chuine, I. Why does phenology drive species distribution? *Philos. Trans. R. Soc. London, Ser. B* **365**, 3149-3160 (2010).

10   Zohner, C. M. & Renner, S. S. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecol. Lett.* **17**, 1016-1025 (2014).

11   Peñuelas, J., Rutishauser, T. & Filella, I. Phenology feedbacks on climate change. *Science* **324**, 887-888 (2009).

12   Richardson, A. D. *et al.* Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agric. For. Meteorol.* **169**, 156-173 (2013).

13   IPCC. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Field, C.B., V.R. Barros, D.J. Dokken, K.J.*

Mach, M.D. Mastrandrea, T.E. Bilir, M. Chatterjee, K.L. Ebi, Y.O. Estrada, R.C. Genova, B. Girma, E.S. Kissel, A.N. Levy, S. MacCracken, P.R. Mastrandrea, and L.L. White (eds.)]. (Cambridge University Press, 2014).

14   Piao, S. *et al.* Leaf onset in the northern hemisphere triggered by daytime temperature. *Nat. Commun.* **6**, 6911 (2015).

15   Way, D. A. & Montgomery, R. A. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant Cell Environ.* **38**, 1725-1736 (2014).

16   Wolkovich, E. M. *et al.* Warming experiments underpredict plant phenological responses to climate change. *Nature* **485**, 494-497 (2012).

17   Vitasse, Y. Ontogenic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytol.* **198**, 149-155 (2013).

18   Beer, C. *et al.* Harmonized European long-term climate data for assessing the effect of changing temporal variability on land-atmosphere CO_2 fluxes. *J. Clim.* **27**, 4815–4834 (2014).

19   Badeck, F. W. *et al.* Responses of spring phenology to climate change. *New Phytol.* **162**, 295-309 (2004).

20   Wang, T. *et al.* The influence of local spring temperature variance on temperature sensitivity of spring phenology. *Global Change Biol.* **20**, 1473-1480 (2014).

21   Vitasse, Y., Lenz, A. & Körner, C. The interaction between freezing tolerance and phenology in temperate deciduous trees. *Front. Plant Sci.* **5**, 541 (2014).

22   Körner, C. & Basler, D. Phenology under global warming. *Science* **327**, 1461-1462 (2010).

23   Basler, D. & Körner, C. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agric. For. Meteorol.* **165**, 73-81 (2012).

24   Hunter, A. F. & Lechowicz, M. J. Predicting the timing of budburst in temperate trees. *J. Appl. Ecol.* **29**, 597-604 (1992).

25   Harrington, C. A., Gould, P. J. & St Clair, J. B. Modeling the effects of winter environment on dormancy release of Douglas-fir. *Forest Ecol. Manag.* **259**, 798-808 (2010).

26   Kimball, J. S. *et al*. Satellite radar remote sensing of seasonal growing seasons for boreal and sub-alpine evergreen forests. *Remote Sens. Environ* **90**, 243-258 (2004).

27   Piao, S. *et al*. Growing season extension and its impact on terrestrial carbon cycle in the Northern Hemisphere over the past 2 decades. *Glob. Biogeochem. Cycles* **21**, GB3018 (2007).

28   White, M. A., Running, S. W. & Thornton, P. E. The impact of growing-season length variability on carbon assimilation and evapotranspiration over 88 years in the eastern US deciduous forest. *Int. J. Biometeorol* **42**, 139-145 (1999).

29   Rahmstorf, S. & Coumou, D. Increase of extreme events in a warming world. *Proc. Natl. Acad. Sci. U.S.A* **108**, 17905-17909 (2011).

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. U.S.A* **111**, 7355-7360 (2014).

31   Coville, F. V. The influence of cold in stimulating the growth of plants. *Proc. Natl. Acad. Sci. U.S.A* **6**, 434-435 (1920).

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

Acknowledgments

1 manuscript. The authors gratefully acknowledge all members of the PEP725 project for providing

2 the phenological data.

3

Author contributions

Author Information

12

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

Figure 2. Changes of chilling and spring temperature variation (Tstd) **between 1980-1994 and 1999-2013.** Species-specific Tstd (a) and chilling accumulation (b) across all sites over two periods, 1980-1994 and 1999-2013. The Tstd was calculated as the standard deviation of mean spring temperature during the preseason over these two periods. The preseason 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 and 5 °C from 1 November to the average date of leaf unfolding. The asterisks indicate significant differences at P<0.05.

10

Figure 3. Changes of modeled apparent temperature sensitivity of leaf unfolding (S_T, advances in days per degree Celsius warming). As in Fig. 1a, panels a-c show the modelled species-specific S_T, including the standard deviations (in brackets), across all sites during three periods and its difference between 1999-2013 and 1980-1994. (a) Sequential model, (b) Parallel model and (c) Unified model. As in Fig. 1c, panels d-f show the modelled temporal change of S_T for each and all species across all sites with a 15-year moving window from 1980 to 2013. (d) Sequential model, (e) Parallel model and (f) Unified model. The model performance is provided in (g). The S_T was determined using the preseason fixed at the time period 1980-2013 and using ordinary least squares linear regression. The colour scale indicates magnitude of S_T. RMSE, 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.

24

Extended Data Figure Legends:

Extended Data Figure 1. The distribution of the sites. The data were obtained from the Pan 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)

regression (b), or were calculated based on another climate forcing dataset (CRU-NCEP v5, c). Species-specific S_T and its standard deviation (in brackets) across all sites in three periods and the difference two study periods are provided. The colour scale indicates 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*). 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 standard deviations (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 (S_T, advances in days per degree Celsius warming) 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 standard deviation 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 panels) and diurnal variation temperature (Tmax – Tmin, right panels) over the preseason across all sites during the time period 1980-1994 and 1999-2013 in three MAT groups, i.e. (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 (S_T, advances in days per degree Celsius warming) 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 modeled correlation between chilling and apparent temperature sensitivity of leaf unfolding (S_T, advances in

days per degree Celsius warming). (a) Chilling accumulation for each and 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 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 standard deviation 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℃ to +5℃ 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 (S_T, advances in days per degree Celsius warming) between years with more or less chilling.** S_T for years with (a) less chilling and (b) more chilling 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 1st 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 standard deviation 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 preseason for years with less chilling (red line) and more chilling (blue line) with a 20-year moving window for 1980-2013. The preseason was determined over the period 1980-2013.

1   **Supplementary information**

2

3   To test the hypothesis that the observed decline in S_T is in fact a response to the declining

4   chilling, we applied three commonly used chilling-based phenology models, i.e. the

5   Sequential, Parallel and Unified models, to simulate the leaf unfolding dates. We then

6   calculated the S_T using the same method as for the observations. We chose a simulated

7   annealing method to fit the models based on the observation over the period 1980-2013. The

8   details of these three models are described below. In the models, the effects of the forcing and

9   chilling temperatures are accounted for by calculating (daily) rates of forcing (R_f) and chilling

10   (R_c), which are functions of the daily air temperature (T). These functions differ between

11   models. R_f and R_c determine the rates of change of the states of forcing (S_f) and chilling (S_c),

12   respectively:

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

14
$$S_c(D) = \sum_{t=t_{1c}}^{D} R_c(T) \tag{2}$$

15   where t_{1f} and t_{1c} are the initial days of the forcing and chilling periods, respectively, and D is

16   the day of the year. Leaf unfolding is triggered when S_f reaches a forcing threshold F^*,

17   whereas in the Sequential and the Parallel models, the start of quiescence (the forcing period)

18   is triggered when S_c reaches the chilling threshold C^*.

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

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

21

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]:

1

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

2   where T_{min}, T_{max} and T_{opt} are the minimum, maximum and optimum temperature for the

3   chilling period. R_f is calculated with a similar sigmoid function as:

4

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

5   ***Parallel model (PM)*** [32,33,34]

6   *PM* assumes that forcing temperature can affect leaf unfolding even during the chilling. As

7   for SM, we fixed t_{1c} and t_{1f} on 1 November. R_c is calculated as in *SM*, whereas R_f is calculated

8   with the following equation, a modification of Eq. 6 of *SM*:

9

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

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

11

12   ***Unified model(UM)*** [35]

13   *UM* combines features of the other models and merges the equations for R_c and R_f into one

14   sigmoid equation:

15

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

16   where C_a, C_b and C_c are chilling-rate parameters and F_b and F_c are forcing-rate parameters. In

17   *UM*, t_{1c} is set to be 1 September. The forcing units start to accumulate when a sufficient

18   amount of chilling has occurred (C^*), and F^* is calculated with an exponential function of R_c

19   from t_{1c} to t_{2c}:

20

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

2

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

Parameter estimation

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

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

where $X_{obs,i}$ is the observed value, $X_{mod,i}$ is the modelled value of the observation i and n is the number of observations. Following the study of Chuine *et al*[36], we calibrated the models using a simulated annealling method. The simulated annealling refers to thermodynamic principles where the objective function, here the RMSE, is considered as an energy function of a cooling and crystallizing molten metal. An artificial temperature is introduced and gradually lowered until it reaches a global minimum. At each iteration, the algorithm explores the range of possible states of the system by changing parameter values according to a generalized Metropolis algorithm acceptance probability. Simulated annealling methods are less affected by local minima than gradient methods[37], but the number of local minima of the RMSE function of phenological models is high. We thus performed thousands of global searches with few iterations and random initial parameters followed by a global search with more iterations and starting at the best result yet obtained for each optimization[35]. The range of variation for each parameter was prescribed according to previously published results of model optimization[35,36,38].


References:

32   Hänninen, H., Modelling bud dormancy release in trees from cool and temperate regions. *Acta For. Fenn* **213**, 1- 47 (1990).

33   Kramer, K., Selecting a model to predict the onset of growth of Fagus-Sylvatica. *J. Appl. Ecol.* **31**, 172-181 (1994).

34   Landsberg, J.J., Apple fruit bud development and growth - analysis and an empirical model. *Ann. Bot.* **38**, 1013-1023 (1974).

35   Chuine, I., A unified model for budburst of trees. *J. Theor. Biol.* **207**, 337–47 (2000).

36   Chuine, I., Cour, P. and Rousseau. D. D., Fitting models predicting dates of flowering of temperate-zone trees using simulated annealing. *Plant Cell Environ* **21**, 455–66 (1998).

37   Tsallis, C., & Stariolo, D.A., Generalized simulated annealing. *Physica A* **406**, 395-406 (1996).

38   Linkosalo, T, Lappalainen, H.K. and Hari, P., A Comparison of phenological models of leaf bud burst and flowering of boreal trees using independent observations. *Tree Physiol.* **28**, 1873–82 (2008).
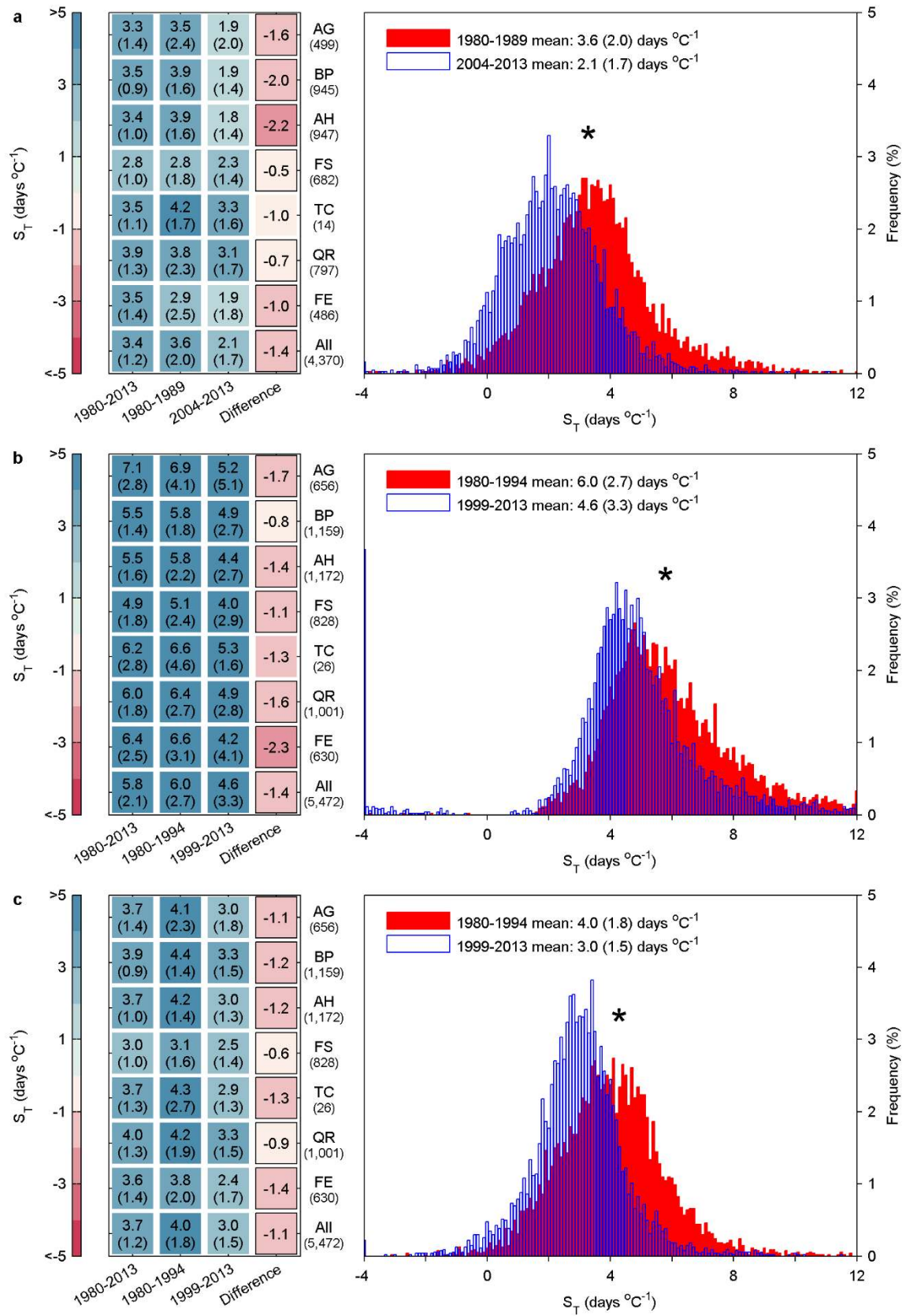
Extended Data Figure 1.
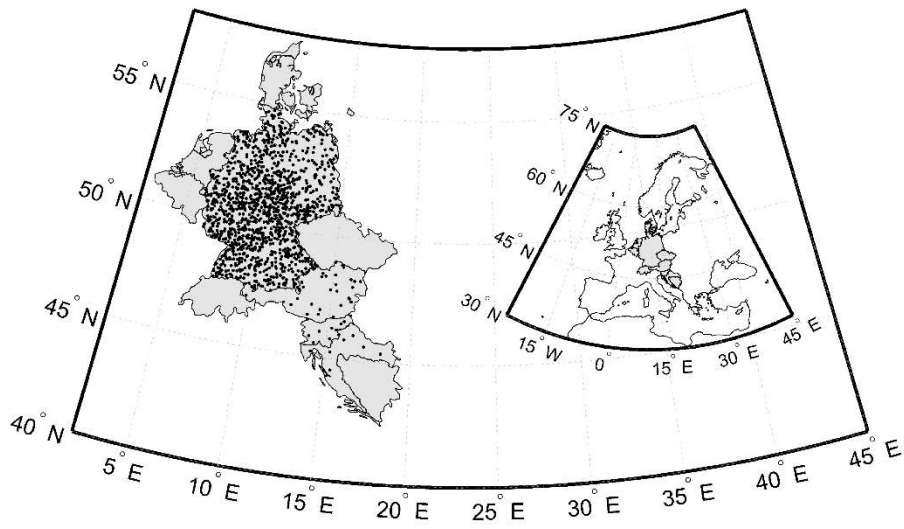
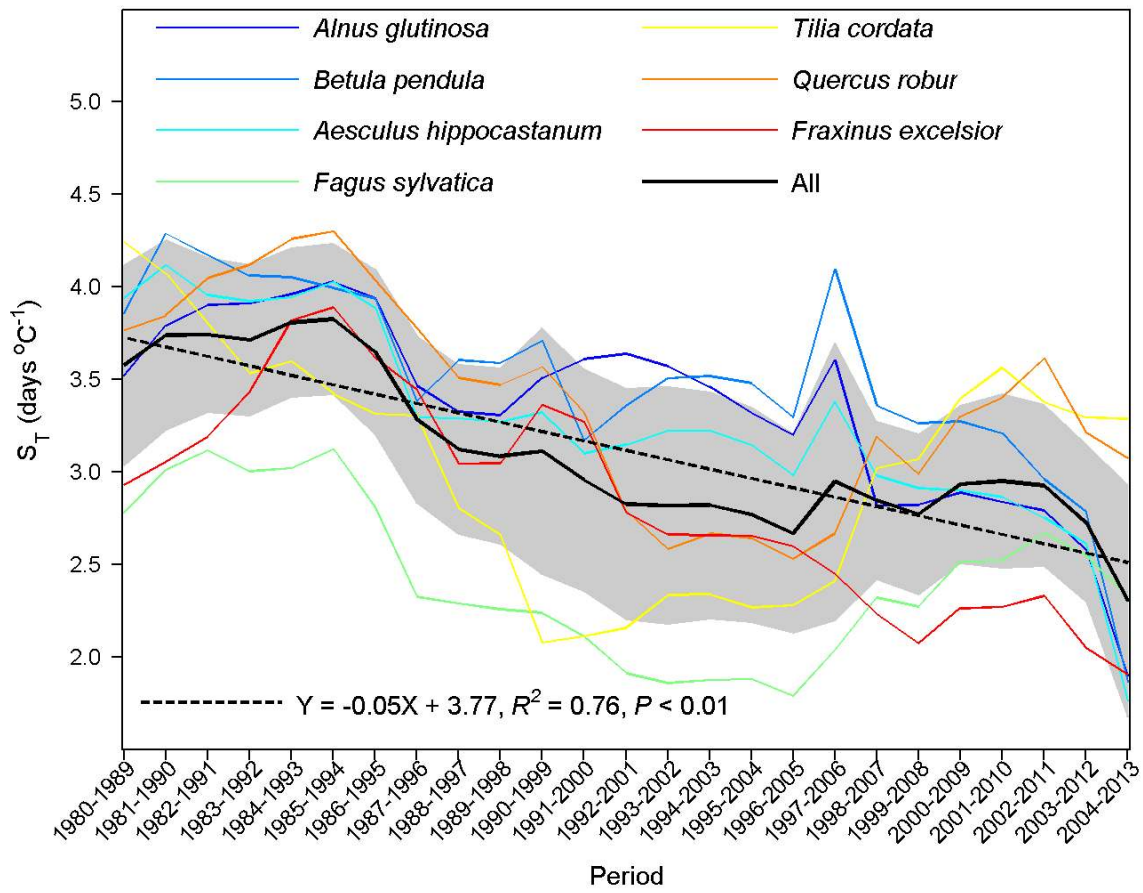**Extended Data Figure 2.**
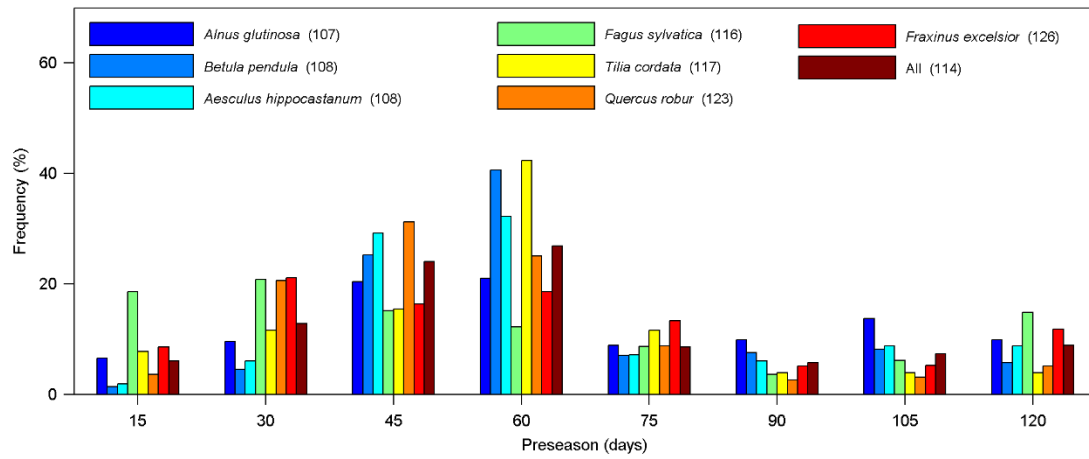
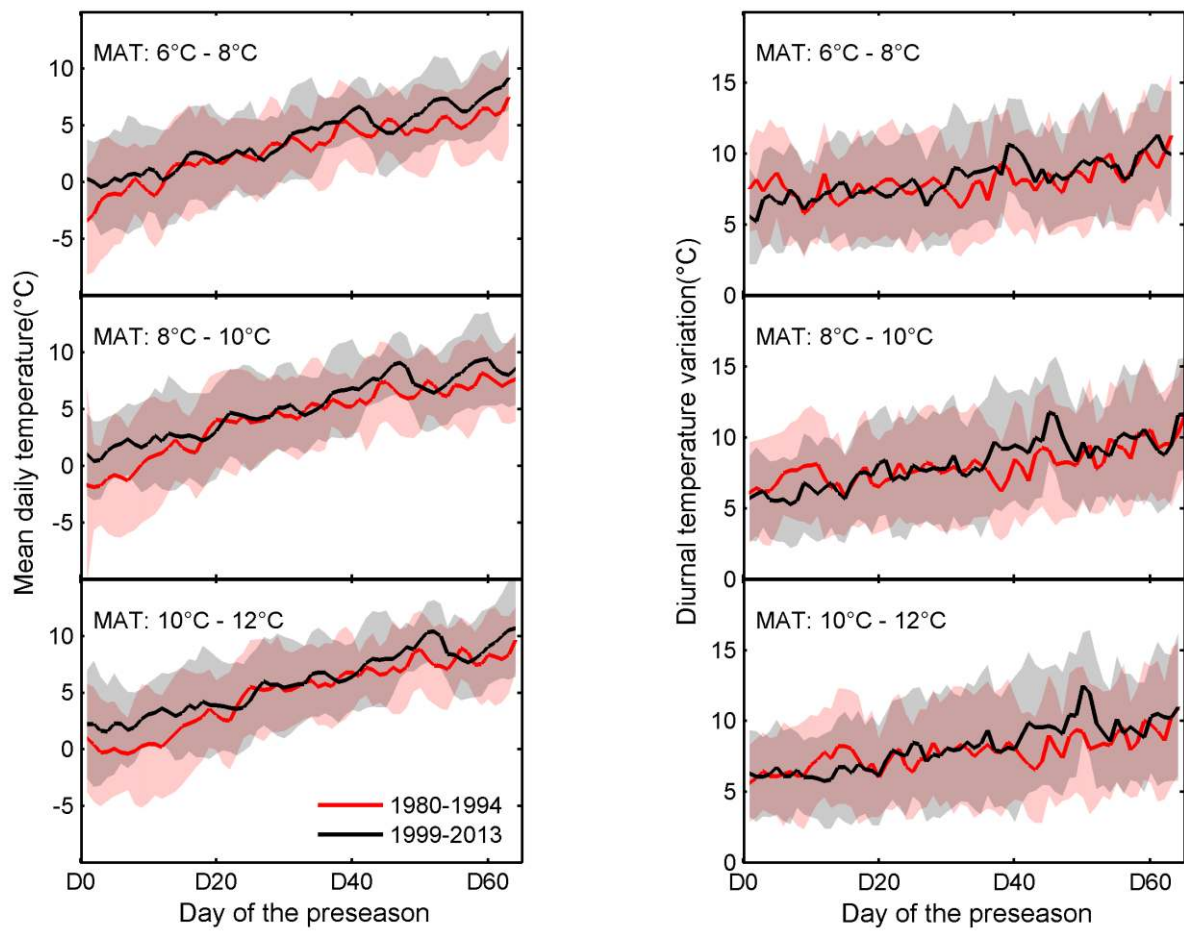**Extended Data Figure 3.**
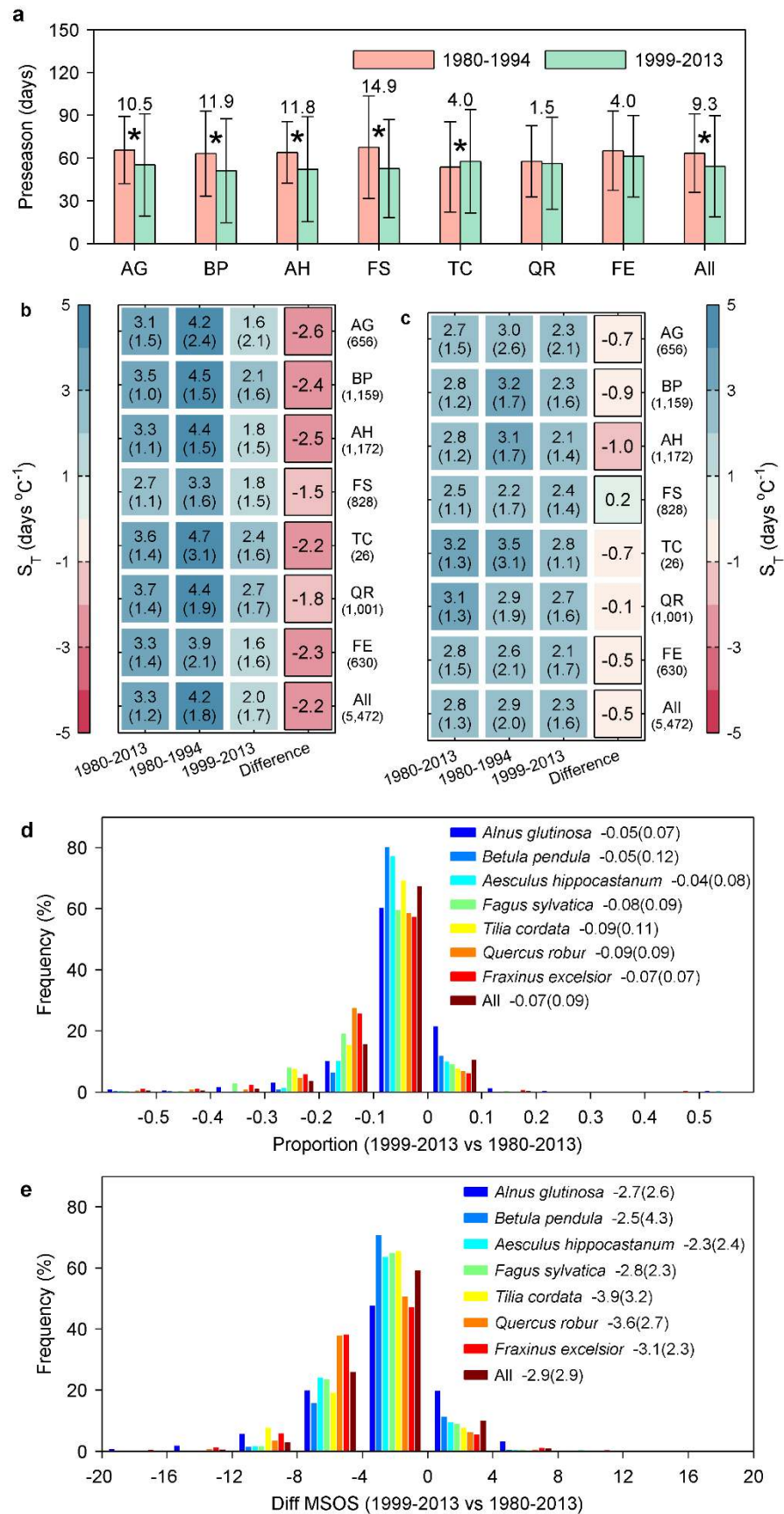
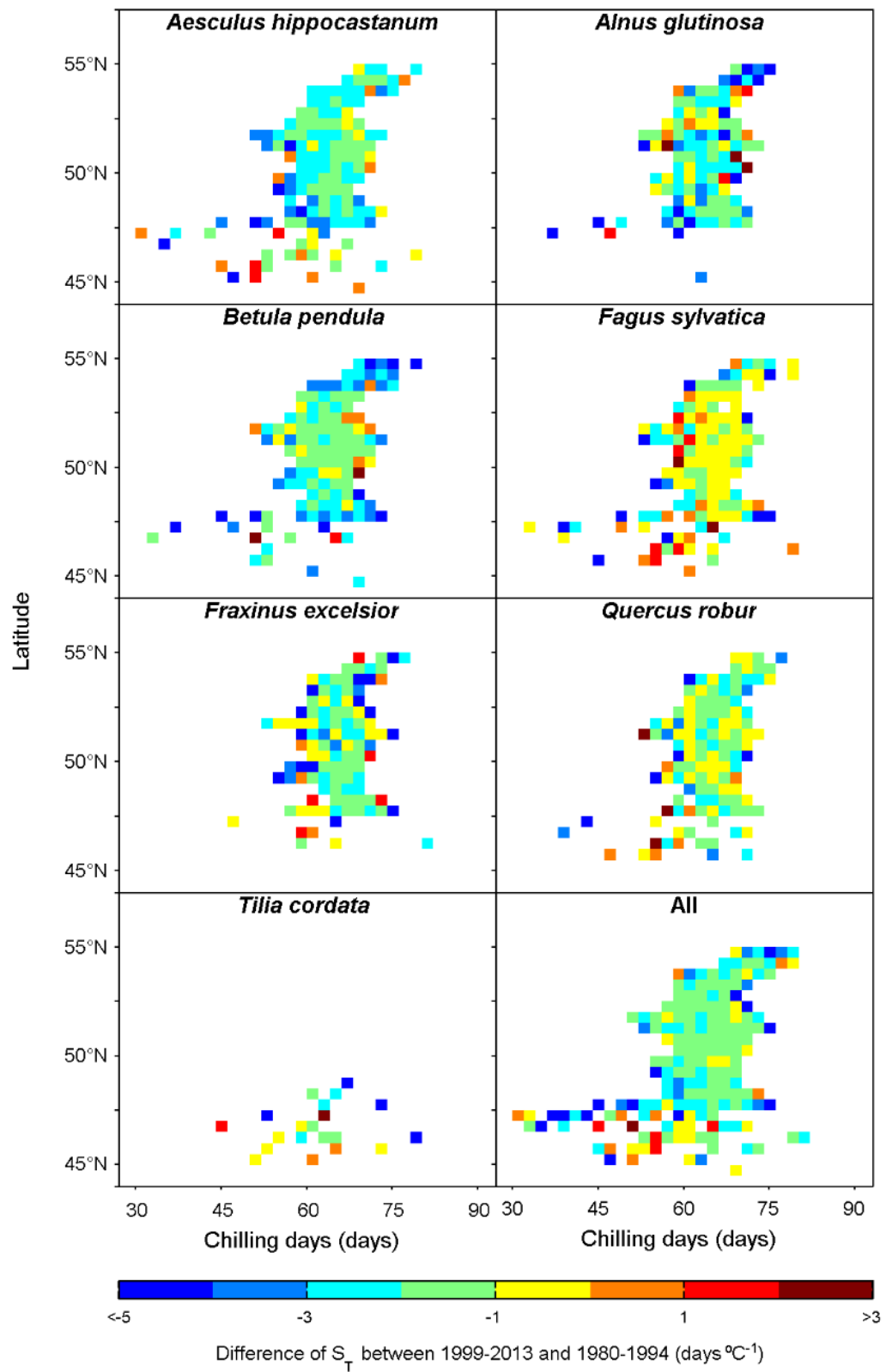**Extended Data Figure 4**.
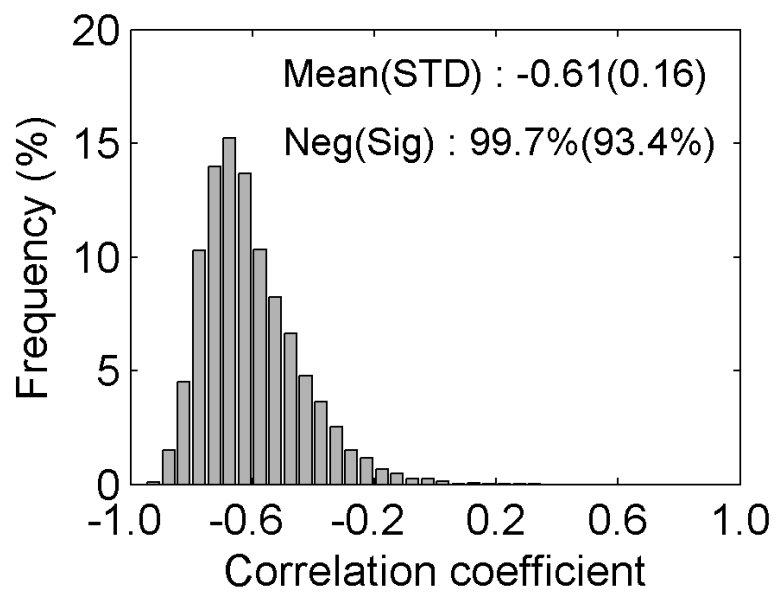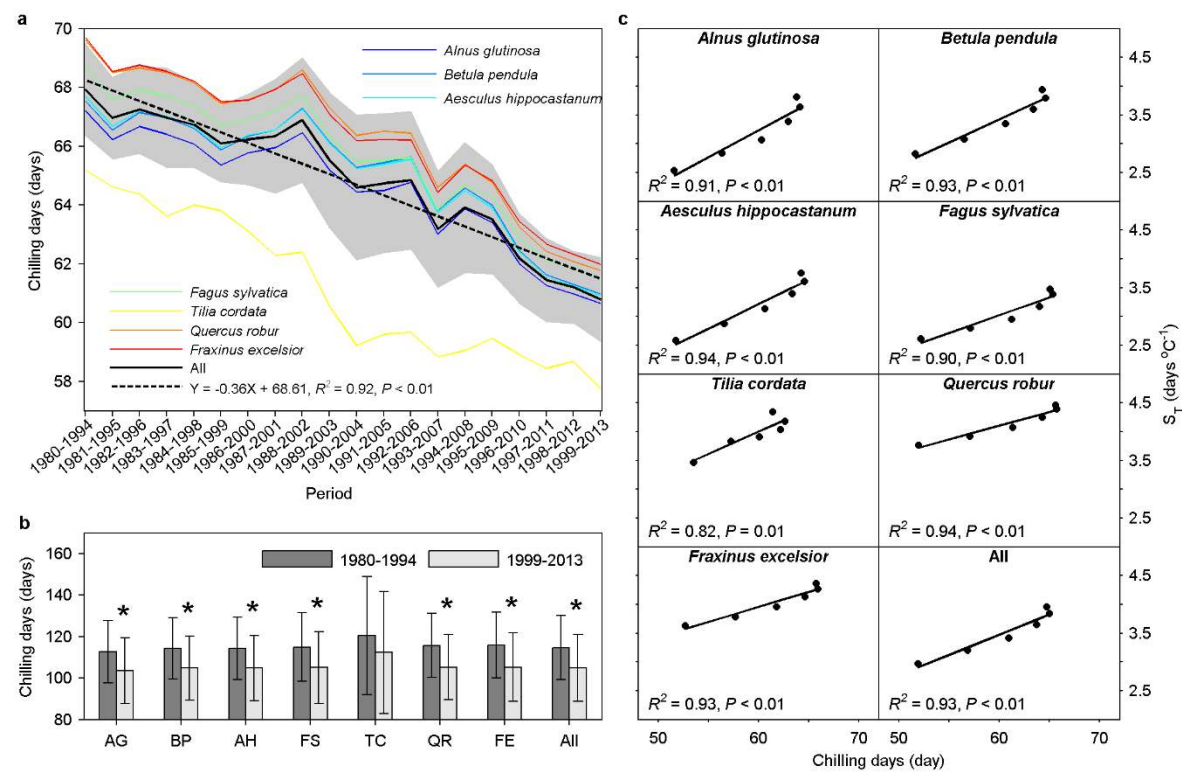
Extended Data Figure 5.

Extended Data Figure 6.

Extended Data Figure 7.

Extended Data Figure 8.

Difference of S_T between 1999-2013 and 1980-1994 (days ºC^{-1})

Extended Data Figure 9.

Extended Data Figure 10.