

Reduced geographical variability in spring phenology of temperate trees with recent warming

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ABSTRACT

The occurrence of species-specific phenological timing among populations over broad geographical areas may have converged or diverged with recent climatic warming. The changes in spatial geographical variability of phenological timing may affect the degree of species overlap, and thus have profound ecological consequences in the context of global change. The potential converging or diverging has been little explored, although advancements of spring phenology due to climate warming have been observed worldwide in the last decades. Here we addressed this question through analyzing temporal changes in the geographical variability for 22 spring phenological events (both leaf-out and flowering phenology) of 16 temperate tree species in Europe. We found that the species-specific geographical variability of spring phenological timing decreased during 1980–2013, indicating that phenological differences among populations over a large geographical area decreased. The reduced geographical variability is mainly due to the fact that populations in cold sites had higher advancement rates and exhibited stronger responses to elevated temperature than those in warm sites. Warming-induced convergence of spring phenology in temperate trees over a large geographical area may affect the activities of other species in the food chain through trophic mismatch, and may ultimately affect the ecosystem carbon and nutrient cycles that are driven through functioning of the food chain.

1. Introduction

The last three decades is likely the warmest 30-year period during the last 1400 years in the history of the Northern Hemisphere (IPCC, 2014). Global average surface temperatures have risen by 0.2 °C per decade from 1975 to 2005 and they are predicted to continue to rise (Hansen et al., 2006). Plant phenological events, such as budburst, leaf unfolding and flowering, are important indicators of global warming (Menzel et al., 2006a). In recent decades, advances of spring phenological events with elevated temperature have been reported extensively (Cleland et al., 2007; Menzel and Fabian, 1999; Parmesan and Yohe, 2003; Root et al., 2003; Sherry et al., 2007). Furthermore, species which track climate change by adjusting phenology tend to increase their performance, as indicated by biomass, percent cover, and individual growth (Cleland et al., 2012).

Air temperature has been identified as the primary environmental factor affecting spring phenology in plants (Menzel et al., 2006a). It has a dual role in regulating the spring phenology of temperate trees

(Hänninen, 2016). Long-term exposure to relatively high temperatures (“forcing”) is required for the invisible anatomic development in the buds that leads to the visible phenological events, such as budburst. However, since the study of Coville (1920) it has been known that long-term exposure to low chilling temperatures is required in many tree species for rest break, that is, removing the growth arresting physiological conditions in the dormant buds during autumn and winter (for other references, see Hänninen (2016)). Thus, in addition to the well-known advancing of spring phenology, by reducing chilling climatic warming may have a lower impact on the advance, or sometimes even cause delayed spring phenology in temperate trees (Ford et al., 2016; Murray et al., 1989), thus complicating any inferences about the effects of climatic warming in natural conditions. Photoperiod (day length) does not change with warming climate, but it can nevertheless limit the ability of trees to respond to climate warming (Way and Montgomery, 2015). Furthermore, the photoperiodic responses of spring phenology are species-specific (Basler and Körner, 2012). A recent study even found that species from high latitudes with long winters leafed out

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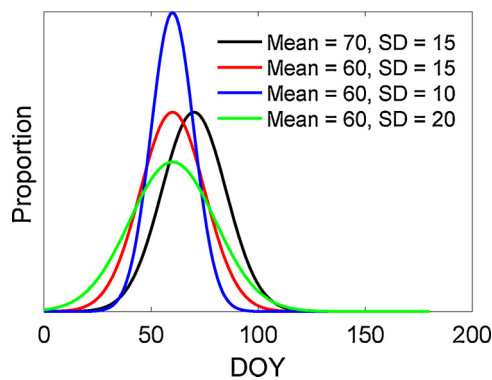


Fig. 1. A hypothetical example of the effect of climatic warming on the flowering time and its variability over a large geographical area. The vertical axis shows the proportion of populations, out of all populations in the geographical area, having their peak flowering time on the day of year (DOY) indicated by the horizontal axis. The black curve represents the current situation, and the three colored curves are three cases of advanced phenological timing caused by climatic warming. For details, see text. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

independently of photoperiod (Zohner et al., 2016).

Determined by the environmental factors and the genetic structure of the tree population, the phenological timing in a given tree species may differ significantly among populations (Beuker, 1994). Populations in warm regions are likely to have earlier phenological timing than those in cold regions. In addition, the advancement rates in response to elevated temperatures may vary among populations (Parmesan, 2007; Schwartz et al., 2006), and this may alter the degree of differences in the phenological timing among populations. In this way, climatic warming may affect not only the phenological timing at each geographical location, but also the magnitude of its variability over the large geographical area. Here we take a hypothetical example of shifted distributions of flowering time to demonstrate the potential consequences of the changes in geographical variability (Fig. 1). Under climate warming, the current flowering dates (black curve, mean DOY = 70) are assumed to be advanced by ten days, to the average DOY = 60. Despite the same average advancing by ten days, the duration of flowering season over the geographical area may be shortened (blue curve), prolonged (green curve), or it may have stayed unaltered (red curve).

Both advances in mean phenological timing and changes in its geographical variability may affect the degree of species overlap in phenological timing over geographical areas. This may have profound consequences on ecological processes. The convergence or divergence of phenological events in one species is not only critical for its own growth and reproduction, but it may also affect the survival of other species in the food web (Post and Forchhammer, 2008; Saino et al., 2011; Thomas et al., 2004) through both direct and indirect interactions (Ma and Kazanci, 2013). A trophic mismatch related to these changes has been reported in all major ecosystems of the world (Edwards and Richardson, 2004; Memmott et al., 2007). For example, temporal mismatches between plants and their pollinators could reduce seed set in plants and reduce food availability to the pollinators. Ultimately, this may lead to the extinction of both the pollinator and the plant species involved in the interaction (Memmott et al., 2007). The changes in geographical variability, through affecting the temporal overlap between species, may aggravate the trophic mismatch (Hegland et al., 2009; Rafferty et al., 2015), and thus affect the carbon cycles and nutrient cycles that rely on the transfer of mass and energy through the food chain (Edwards and Richardson, 2004; Richardson et al., 2010). Therefore, it is critical to better understand how and to what extent the geographical variability in plant phenology may change under climate

warming.

Previous research has mainly focused on the overall advancement of the spring phenological timing, but less on the potential changes in its geographical variability. Although there are a few related studies (Menzel et al., 2006b; Post et al., 2008), no agreement on the changes in geographical variability has been reached yet and the reasons for the altered variability remain poorly understood. In recent decades, there has been growing evidence that high altitudes and latitudes (cold areas) experience more rapid warming than low altitudes and latitudes (IPCC, 2014; Pepin et al., 2015). The uneven warming may cause more dramatic advances of spring phenology in cold than in warm areas. Additionally, Fu et al. (2015) recently showed that spring phenological response of trees to temperature rise has declined during the last three decades. This decline in sensitivity of spring phenology is probably partly due to reduced chilling in warm years, although the possible constraining effect of photoperiod cannot be excluded (Fu et al., 2015). Similarly, the reduced chilling may also restrict the further advance of already early phenological timings in warm areas. We expect to retrieve this pattern of decreasing sensitivity from cold to warm regions, which may ultimately shorten the difference between late phenological timing in cold regions and early timing in warm areas. Thus, we hypothesize that the advances of spring phenological timing over time have been accompanied by the decrease in its geographical variability.

To address this hypothesis, we examined comprehensive long-term phenological records across Europe provided by the Pan European Phenology (PEP) network (www.pep725.eu) (Templ et al., 2018). Our aim was to examine the changes in geographical variability in spring phenology during the period 1980–2013, which is characterized by the strongest warming being recorded until today. To further explore the underlying mechanisms behind varying geographical variability in phenology, we investigated how the changes in preseason temperature, phenological timing, and chilling accumulation varied among sites representing different temperature conditions.

2. Materials and methods

2.1. Phenological data and climate data

The phenology dataset used in the study was obtained from the Pan European Phenology network (PEP, www.pep725.eu), which provides an open access to *in situ* phenology records across Europe (Templ et al., 2018). The PEP phenology dataset, contributed by both researchers and citizen scientists, includes multiple phenophases for a variety of plant species. The phenological timing was recorded as the day of year (DOY). Selection of the data was based on the following criteria: (i) The selected sites cover at minimum 25 years' observations during 1980–2013. Selecting sites with long-term phenological records guaranteed that there were a similar number of sites each year and the geographical distribution of the sites did not vary significantly among years. Fig. S1 shows that the geographical distribution of sites where first flowering dates for *Tilia platyphyllos* were recorded was similar over the years. The yearly distributions of the sites for each of the other 21 phenophases were also similar during the studied period, but are not shown due to the large number of figures involved. (ii) The selected phenological events include at least 100 observation sites. This ensured there was enough data each year to compute the geographical variability. The locations of all 1415 selected phenological observation sites are shown in Fig. 2. The geographical distribution of observation sites for each phenological event is provided in Fig. S2. Most of the phenological sites are located in Germany. A total of 22 phenological events (5 phenophases in 16 temperate tree species) were included in the study. There are 3 conifer and 13 broadleaf species (3 ring-, 1 semi-ring- and 9 diffuse-porous species), and 8 wind- and 8 insect-pollinated species included in the study. Summary statistics of the phenological events are provided in Table 1. In total, 510,506 phenological observations were included in this study.

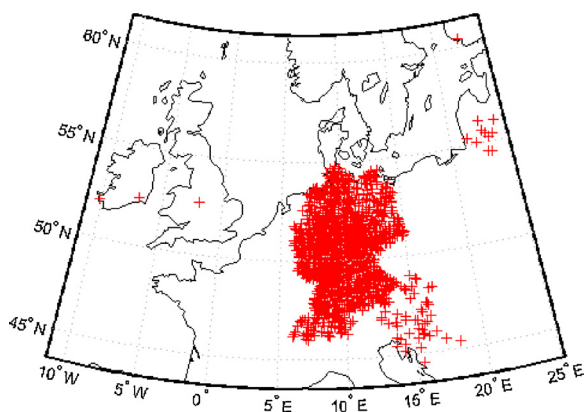


Fig. 2. Locations of the in situ phenological observation sites.

We used temperature data from a gridded climate dataset E-OBS from the EU-FP6 project ENSEMBLES (<http://ensembles-eu.metoffice.com>) and the ECA&D project (<http://www.ecad.eu>) (Haylock et al., 2008). E-OBS provides daily temperature data in Europe, with a spatial resolution of 0.25°. The mean altitude for the climate grid cell is provided as well. To accurately capture temperature variation in each phenological observation site, the temperature data were adjusted using the elevation difference between the site and the climate grid cell. The adjustment was based on a temperature lapse rate of 6.4 °C/km (Olsson and Jönsson, 2014).

2.2. Changes in geographical variability in phenological timing over the years 1980–2013

For each phenological event in Table 1, a linear mixed effects model, including phenological site as a random variable, was employed to compute the long-term shifting rate of the phenological timing (days/year):

$$y_{ij} = \alpha + \beta x_{ij} + a_j + \varepsilon_{ij} \quad (1)$$

Table 1

The 22 phenological events in 16 tree species addressed in the study. BBCH code: 10 (first leaves separated), 11 (leaf unfolding), 60 (first flowering), 65 (full flowering), and 69 (end of flowering). 22 phenological events are ordered according to their overall mean DOY (day of year), which is computed for each phenological event as the mean of the phenological timing across all years and all sites.

Index	Name	Common name	Functional group	Pollination	BBCH code	#observations	#years	#sites	Overall mean DOY
1	<i>Alnus glutinosa</i>	European alder	Broadleaf	Wind	60	19461	34	639	70
2	<i>Larix decidua</i>	European larch	Conifer	Wind	10	26534	34	858	104
3	<i>Prunus spinosa</i>	Blackthorn	Broadleaf	Insect	60	25057	34	811	105
4	<i>Acer platanoides</i>	Norway maple	Broadleaf	Insect	60	18739	33	627	106
5	<i>Alnus glutinosa</i>	European alder	Broadleaf	Wind	11	18996	34	623	107
6	<i>Betula pendula</i>	Silver birch	Broadleaf	Wind	11	36425	34	1171	108
7	<i>Aesculus hippocastanum</i>	Chestnut	Broadleaf	Insect	11	36485	34	1171	108
8	<i>Fraxinus excelsior</i>	Ash	Broadleaf ^a	Wind	60	15627	34	521	114
9	<i>Fagus sylvatica</i>	European beech	Broadleaf	Wind	11	25485	34	822	116
10	<i>Prunus cerasus</i>	Sour cherry	Broadleaf	Insect	60	22564	31	775	117
11	<i>Prunus cerasus</i>	Sour cherry	Broadleaf	Insect	65	15175	31	523	121
12	<i>Quercus robur</i>	English oak	Broadleaf ^a	Wind	11	30123	34	981	123
13	<i>Picea abies</i>	Norway spruce	Conifer	Wind	10	32140	34	1045	126
14	<i>Fraxinus excelsior</i>	Ash	Broadleaf ^a	Wind	11	18699	34	613	126
15	<i>Aesculus hippocastanum</i>	Chestnut	Broadleaf	Insect	60	36258	34	1170	128
16	<i>Syringa vulgaris</i>	Lilac	Broadleaf ^b	Insect	60	38632	34	1245	128
17	<i>Pinus sylvestris</i>	Scots pine	Conifer	Wind	10	21530	31	749	130
18	<i>Prunus cerasus</i>	Sour cherry	Broadleaf	Insect	69	14351	31	494	130
19	<i>Sorbus aucuparia</i>	Rowan	Broadleaf	Insect	60	23762	34	775	132
20	<i>Pinus sylvestris</i>	Scots pine	Conifer	Wind	60	13484	31	470	138
21	<i>Robinia pseudoacacia</i>	Black locust	Broadleaf ^a	Insect	60	20979	34	698	149
22	<i>Tilia platyphyllos</i>	Largeleaf linden	Broadleaf	Insect	60	22771	31	795	173

Note: For broadleaf species.

^a Denotes ring-porous species.

^b Denotes semi-ring-porous species, and the others are diffuse-porous species.

where y_{ij} is the phenological timing (DOY) in year i at the site j , x_{ij} is the year i at the site j , α is the intercept with the y -axis, β is the shifting rate, a_j is the random effect of site j , and ε_{ij} is the error term.

For each phenological event, a simple linear regression analysis was performed to examine the changes in geographical variability in phenological timing over the period examined. Geographical variability was calculated as the standard deviation (SD) of the phenological timing across all sites for each year. SD is an indication of the dispersion of data that does not depend on the sample size. A low geographical variability, indicated by a small SD, indicates a high degree of synchrony of the phenological timing among the sites. As an alternative metric, the interquartile range (IQR) was also used to quantify the geographical variability.

An independent t -test was used to compare whether there exist statistically significant differences in the rate of change of the geographical variability between flowering (BBCH = 60, 65 and 69) and leaf budburst (BBCH = 10 and 11), between broadleaf and conifer tree species, between ring- and diffuse-porous tree species, and between wind-pollinated and insect-pollinated tree species.

2.3. Changes in preseason temperature in relation to site temperature

For a given phenological event and site, the optimal preseason was first defined as the period before the mean phenological timing over years for which the correlation between phenological timing and temperature is highest during the study period (Fu et al., 2015). The optimal preseason length varied from 15 to 120 days (with 15-day steps), with 60 days having the highest frequency (Fig. S3), which is in agreement with Fu et al. (2015). Accordingly, the preseason temperature at each site was calculated as the average of the daily mean temperatures during the 60 days before the mean phenological timing over the years.

For each phenological event, the rate of preseason temperature change at each phenological site was computed as the slope of the linear regression of preseason temperature against calendar year. Then simple linear regression analysis was applied to examine how the differences in the rate of preseason temperature change were related to the

site temperature. Site temperature was calculated for each observation site as the average of annual mean temperatures across all years providing phenological observations for the site.

2.4. Changes in phenological timing in relation to site temperature

To explore the potential explanations for changes in the geographical variability in phenological timing over the years, we examined for each phenological event (Table 1) how the differences in three phenological indices among sites were related to site temperature: For each phenological site and event, 1) the mean phenological timing was determined as the average of the phenological timing across all years providing observations; 2) the shifting rate of the phenological timing was determined as the slope of the linear regression of the phenological timing against calendar year; and 3) the temperature sensitivity of the phenological timing was determined as the slope of the linear regression of the phenological timing against pre-season temperature (for calculation of pre-season temperature, see the previous section). Then, simple linear regression analyses were applied to separately examine how the differences in 1) the mean phenological timing, 2) the shifting rate of the phenological timing, and 3) the temperature sensitivity of the phenological timing were related to the site temperature.

2.5. Changes in chilling accumulation in relation to site temperature

To further explore the reasons behind varying temperature sensitivity of phenology among populations, we examined how the decrease over time in chilling accumulation varied among sites. Accumulated chilling was computed as the number of days with daily mean air temperature within the range between 0 °C and 5 °C, counted from 1st November in the previous year to the phenological onset date (Coville, 1920; Fu et al., 2015).

For each phenological event, the rate of change of chilling accumulation over the years at each phenological site was computed as the slope of the linear regression of accumulated chilling against calendar year. Then simple linear regression analysis was applied to examine how the differences in the rate of decrease of chilling accumulation were related to the site temperature.

In all data analyses, residuals from regressions were tested to confirm normality. All data analyses were conducted using R (R Development Core Team, 2015).

3. Results

3.1. Changes in geographical variability in phenological timing over the years 1980–2013

We found that all 22 spring phenological events advanced during 1980–2013, with shifting rates varying from -0.55 to -0.27 days/year (Fig. 3). Delayed phenological timing was not observed in the present data. Comparing the shifting rates among different phenophases, *t*-test showed flowering events (BBCH = 60, 65 and 69) had higher (more negative) advancement rates than leaf budburst events (BBCH = 10 and 11) (difference = -0.09 days/year, $p = 0.02$).

The geographical variability varied among phenological events and exhibited large year-to-year fluctuations during 1980–2013 (Figs. 4 & S4). Except one (first flowering dates of *Sorbus aucuparia*), all other phenological events show a decreasing geographical variability during the studied period, although the trends of 9 events were not statistically significant at $p = 0.05$ (Figs. 4, S4 & S5). An additional analysis based on IQR also shows that the geographical variability of phenological timing declined during the studied period (Fig. S5), indicating that our finding is robust. Events 1 and 18 have the highest decreasing rates of the geographical variability (Fig. 5). Scatter plots of these events show that the decline in geographical variability is a consistent trend, which is not

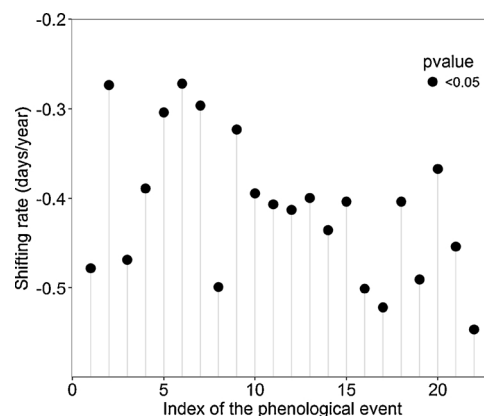


Fig. 3. Shifting rate of phenological timing of 22 phenological events of 16 tree species in Europe during 1980–2013 (for the indices of the events, see Table 1). Negative values of the shifting rate indicate a trend towards earlier phenological timing during 1980–2013.

caused by any particular deviating years (Fig. 4). The declining geographical variability indicates that the timing of events during spring became more compressed over large geographical areas during the last three decades. *t*-tests showed that there were no significant differences in the rates of decrease of geographical variability between phenological event categories, or types of species: flowering vs leaf budburst events ($p = 0.36$), broadleaf vs conifer species ($p = 0.24$), ring- vs diffuse-porous species ($p = 0.73$) and wind-pollinated vs insect-pollinated species ($p = 0.36$).

3.2. Changes in pre-season temperature in relation to site temperature

Site temperature across the whole study area varied from 3.0 to 14.0 °C, with an average of 9.1 °C (Fig. S6). The negative slope (-0.003 °C/year/°C) of pre-season temperature change in relation to site temperature for the event 4 (flowering date of *Acer platanoides*) indicates that the warming rate during the pre-season of flowering of *Acer platanoides* declined from cold to warm sites (Fig. 6a). Out of the 22 events, 20 show a negative slope, indicating that the warming rate was commonly larger in cold than in warm sites (Fig. 6b). The strong warming in cold sites may trigger fast advancements of spring phenological timing in these sites, while the weak warming in warm sites may have a lower impact on the advance.

3.3. Changes in phenological timing in relation to site temperature

To explore the underlying mechanisms behind the decreasing geographical variability in phenological timing, we examined how the differences among sites in three phenological variables were related to the site temperature (Fig. 7). The site temperature effect is quantified as the slope of a linear regression relating the particular variable on the site temperature. The phenological timing was earlier in populations at warm than in those at cold sites (Fig. 7a). However, compared with the populations at the cold sites, the phenological timing advanced at a lower rate (Fig. 7b) and with a lower temperature sensitivity (Fig. 7c) in the populations at the warm sites. In all, then, the differences between the warm sites with early and the cold sites with late phenological timing decreased during 1980–2013.

3.4. Changes in chilling accumulation in relation to site temperature

To further explore the reasons behind the varying sensitivity to elevated temperature among populations at different phenological sites, we examined how the rate of decrease of chilling accumulation during 1980–2013 was related to the site temperature. The negative slope

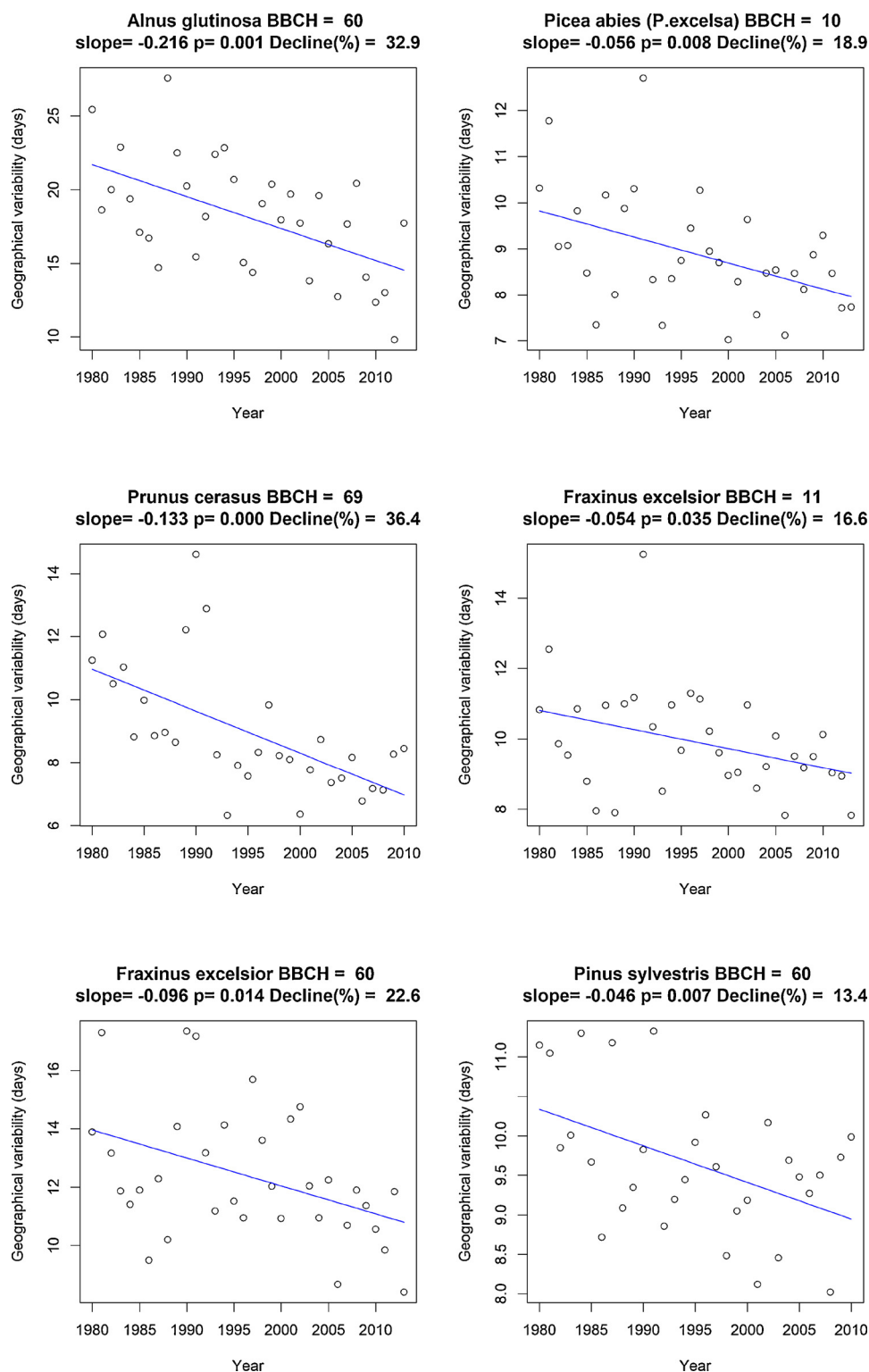


Fig. 4. Geographical variability of phenological timing for six phenological events in Europe during 1980–2013. The rates are shown for the three events having the largest and for other three events having the smallest significant rates of change indicated by the fitted slopes. The geographical variability was calculated as the standard deviation (SD, days) of the phenological timing over the sites for each year. Corresponding graphs for the other 16 phenological events are presented in Fig. S4.

(-0.072 days/year/ $^{\circ}\text{C}$) of decrease of chilling accumulation in relation to site temperature for event 4 (flowering date of *Acer platanoides*) indicates that the rate of decrease of chilling accumulation was higher (more negative) at warm than at cold sites (Fig. 8a). Out of the 22 events, 21 have a negative slope, indicating that the finding with

flowering date of *Acer platanoides* can be generalized to other species and phenological events (Fig. 8b). Higher reduction rate of chilling accumulation in warm sites may constrain the advance of phenological timing, or even cause a delayed spring phenology, at these sites.

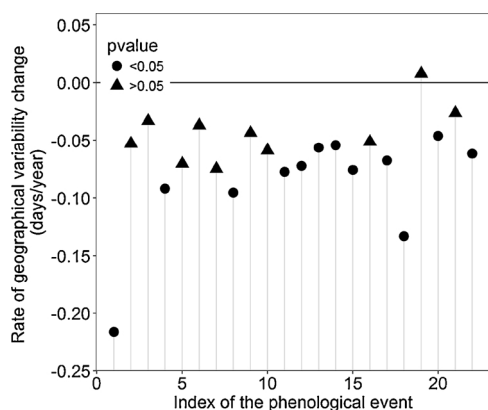


Fig. 5. Changes in geographical variability of phenological timing for 22 phenological events in Europe during 1980–2013 (for the indices of the events, see Table 1). Negative values indicate a decreasing geographical variability over the period 1980–2013.

4. Discussion

A proper understanding of plant phenological responses to climate warming is critical to assessing and predicting their ecological consequences in the context of global change. In this study, we, for the first time, found that the advancements of spring phenology of temperate trees were accompanied by a reduction in the geographical (or between-site) variability of the phenological timing over broad spatial scale. The percent of the reduction of geographical variability ranged from 8.2% to 36.4%, with an average decline of 14.5%. The decreasing rates show no significant differences between functional or phylogenetic groups: flowering vs leaf budburst events, broadleaf vs conifer tree species, ring- vs diffuse-porous tree species, or wind-pollinated vs insect-pollinated tree species. The majority of studied sites are located between 45°N and 55°N and between 5°E and 15°E, and the nearest sites are about 10 km away from each other. Although sites in Ireland, UK and Finland are very far away from the bulk of the sites, which mostly locate in Germany, analysis based on Germany data only shows very similar results (Fig. S7), indicating that our finding is solid and robust, regardless whether the far-away sites were considered, or not.

Reduced geographical variability in phenological timing shows that more phenological events are happening over large geographical areas in a shorter time span, indicating a compressed green-up period and a shortened flowering season in spring. This geographical synchrony in spring phenological timing may increase the damage caused by large-scale drought, frost, ice, snow, etc., as these large-scale events could affect many more populations with increasingly closer phenological timing than before. In a broader ecological context, the decreased

variability may reduce the overlap between species with trophic interactions, which, together with asynchronous advances in their mean phenological timing, may disrupt feeding interactions and lead to trophic mismatch. Thus, the spatial compression of plant phenology may affect the activities of other species in the food chain (e.g., pollinators, herbivores, insectivores, etc.), especially that of herbivores which explore resources over large geographical distances (Menzel et al., 2006b; Post et al., 2008). Migrants may move along the altitude or latitude in spring to explore resources whose availability varies seasonally at the stopover sites. A compressing green-up or flowering season may reduce the number of days when food is available. For example, hummingbirds move from south to the northern breeding grounds in the spring. Due to the faster phenological advancement in the northern breeding ground, hummingbirds may arrive at the northern breeding grounds after the appearance of seasonal resources and thus their nesting success is reduced (McKinney et al., 2012). Another study found that the offspring production of female caribou (*Rangifer tarandus*) was reduced as the geographical variability in plant phenological timing declined (Post et al., 2008).

The reduced geographical variability is a consequence of the different phenological changes among populations growing at sites with different temperature conditions. Due to the spatial difference in climate warming (Fig. 6), populations in cold sites experienced more dramatic warming and thus tended to have faster advancing rates in phenological timing than those in warm sites. Additionally, populations in cold sites exhibited stronger responses to increasing pre-season temperature than populations in warm sites, which is contradictory to Menzel et al. (2006a)'s finding. Our finding on the different sensitivities to temperature among populations is in agreement with Fu et al. (2015)'s finding that the response of leaf unfolding to climate warming has recently decreased in warm years. The subtle difference is that we found the decreasing trend in temperature sensitivity from cold to warm sites, whereas Fu et al. (2015) found a similar declining temperature sensitivity from cold to warm years. Fu et al. (2015) suggested that the reduced sensitivity in warmer years is likely to be partly attributable to the reduced chilling caused by the warming. Similarly, our results also suggest that the strong reduction of chilling accumulation at the warm sites is the limiting factor that restricted further advance of the already early phenophases at the warm sites (Fig. 8); and thus led to the declining temperature sensitivity at these sites (Fig. 7c). We also tried an alternative approach of calculating the temperature sensitivity based on varying pre-season length at different sites, and found similar results (Fig. S8), indicating that the results are robust regardless of the methods used. In addition to the strong reduction of chilling accumulation, short photoperiod related to the early phenological timing may also constrain the warming response of spring phenology in warm sites. Although the photoperiodic effect on phenological timing cannot be revealed with *in situ* phenological records, we cannot exclude the

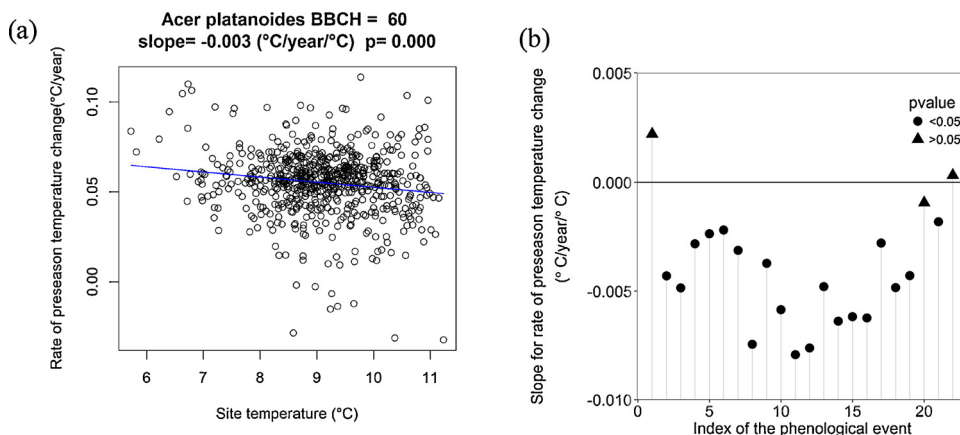


Fig. 6. Changes in pre-season temperature in relation to site temperature at phenological observation sites in Europe during 1980–2013. (a) Scatter plot of the rate of pre-season temperature change in relation to site temperature for flowering date of *Acer platanoides* (phenological event 4). Negative slope indicates a declining warming rate from cold to warm sites. (b) Changes in pre-season temperature in relation to site temperature for 22 phenological events (for the indices of the events, see Table 1). Vertical axis represents the slope of a linear regression relating the rate of pre-season temperature rise on the site temperature (for an example, see the a-panel). The site temperature was computed as the average of the annual mean temperatures across all years providing phenological observations.

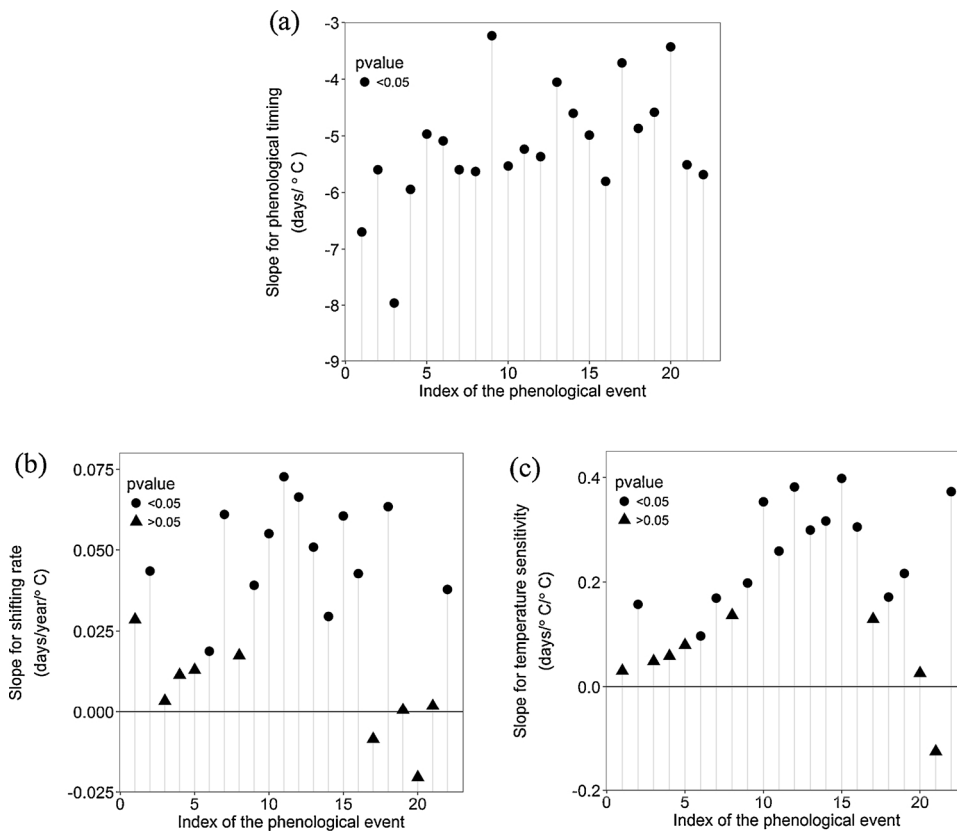


Fig. 7. Effect of site temperature on the phenological timing of 22 phenological events in Europe during 1980–2013 (for the indices of the events, see Table 1). In each panel, the site temperature effect is presented as the slope of a linear regression relating the particular variable on the site temperature. The site temperature was computed as the average of the annual mean temperatures across all years providing phenological observations. (a) Effect of the site temperature on the mean phenological timing. Negative slope values indicate earlier phenological timing at warmer sites. (b) Effect of the site temperature on the shifting rate of the phenological timing during 1980–2013. Positive slope values indicate smaller (less negative) shifting rates at warmer sites. (c) Effect of the site temperature on the temperature sensitivity of the phenological timing during 1980–2013. Positive slope values indicate smaller (less negative) temperature sensitivities at warmer sites.

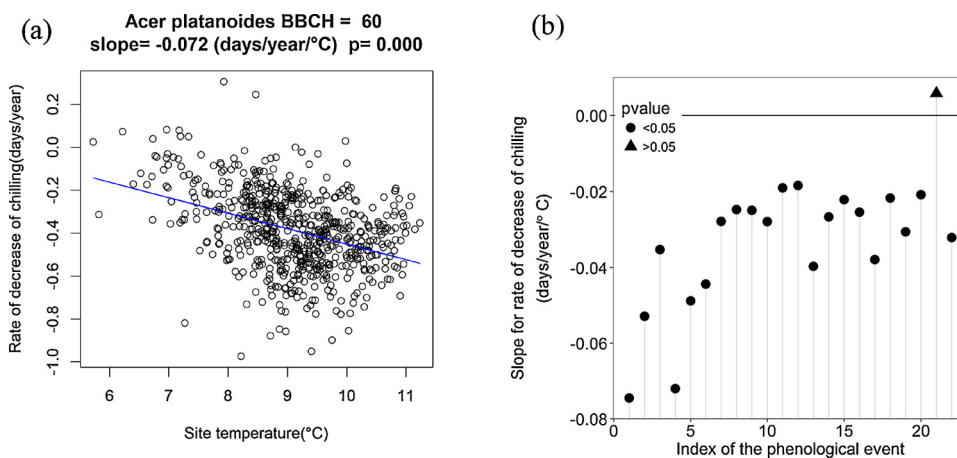


Fig. 8. Effect of site temperature on the rate of decrease of chilling accumulation at phenological observation sites in Europe during 1980–2013. (a) Scatter plot of the rate of decrease of chilling accumulation in relation to site temperature for flowering date of *Acer platanoides* (phenological event 4). The negative slope indicates that the rate of decrease of chilling accumulation was larger (more negative) at warm than at cold sites. (b) Changes of chilling accumulation in relation to site temperature for all 22 phenological events (for the indices of the events, see Table 1). Vertical axis represents the slope of a linear regression relating the rate of decrease of chilling accumulation on the site temperature (for an example, see the a-panel). The site temperature was computed as the average of the annual mean

temperatures across all years providing phenological observations.

photoperiod as a factor causing the slow advancements of spring phenological events observed in the present study in warm sites.

Contrary to our findings, utilizing phenology data from Germany National Weather Service, Menzel et al. (2006b) found that the geographical variability of spring events was greater in warmer years (represented as earlier phenological timing) that had fast plant development. The discrepancy between the results of these two studies is probably due to the different periods studied. Menzel et al. (2006b) analyzed phenology data from 1950 to 2002, while we focused on the period 1980–2013 characterized by the strongest warming. Based on climate dataset E-OBS, the spring temperatures in our studied area even declined slightly during 1950–1980, with the rates varying from -0.07 to -0.003 °C per decade. According to the PEP phenology dataset, in addition to advancing, also delay of spring phenological timing was observed during 1950–1980 (Fig. S9). Analyzing the overall trend during 1950–2002 with linear models may thus fail to uncover the

trends that only exist during the more recent shorter period with strong warming.

Utilizing the phenological dataset used also in the present study, Wang et al. (2016) found that the inter-specific variability in phenological timing decreased in years and/or in areas with rapid within-spring warming. Combined with our findings addressing variability in phenological timing within species, the findings of Wang et al. (2016) addressing the corresponding variability among species project a compressed start of the growing season at the regional level under climate warming.

Our finding of geographical convergence in spring phenology with recent warming highlights the effects of climate warming on plant phenology at a regional level. This deepens our understanding of how phenology responds to climate change. The phenological responses may in turn have crucial implications at broader ecological scales. Trophic mismatch due to the reduced geographical variability and

asynchronous advancements may eventually lead to food web disruptions and therefore affect the ecosystem carbon and nutrient cycles that are mediated by the food chain. The converging phenological development during spring may also be one of the mechanisms how climate warming causes profound changes in species distribution and co-evolution in the temperate terrestrial ecosystems.

Competing interests

The authors declare no competing interests.

Data accessibility statement

All phenology data used in this study are openly available at Pan European Phenology (PEP) network (www.pep725.eu). Climate data are freely accessible at the ECA&D (<http://www.ecad.eu>)

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:<https://doi.org/10.1016/j.agrformet.2018.04.012>.

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