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Uniforming spring phenology under non-uniform climate warming across latitude in China

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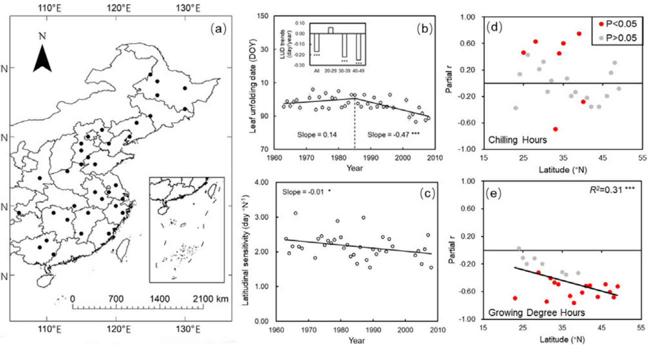
HIGHLIGHTS

- LUD of tree species was advanced at middle and high latitudes in central east China.
- The latitudinal sensitivity of LUD (S_{lat}, days per °N) was declined during 1963–2008.
- Growing Degree Hours instead of Chilling Hours played a critical role in this process.

GRAPHICAL ABSTRACT



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ABSTRACT

Temperature is the primary factor controlling plant phenology. As temperature changes with latitude, leaf phenology in spring always shows a significant latitudinal pattern. However, under asymmetric warming at the low and high latitudes, the variability of the spring leaf phenology with latitude is becoming unclear. Based on the 23,094 observations of the leaf unfolding date (LUD) for woody species located in eastern China within latitudes 23–49°N, we analyzed the variability of LUD and its latitudinal sensitivity (S_{lat}, days $°N^{-1}$, expressed in delayed days per degree in latitude) during 1963–2008. The results showed an earlier LUD at the mid- (-2.2 days decade^{-1}) and high (-2.5 days decade^{-1}) latitude regions, while a stable LUD at the low-latitude regions during 1963–2008. However, the temperature sensitivity of LUD (S_T, days $°C^{-1}$, expressed in advanced days per degree in temperature) remained stable across the latitudes although a slight decreasing trend from 1963 to 2008. As a result, the non-uniform optimal preseason warming with latitude (T_{lat}, °C $°N^{-1}$, expressed in the increase of temperature per degree in latitude) decreased S_{lat} from 2.38 (days $°N^{-1}$) in 1963 to 1.55 (days $°N^{-1}$) in 2008. Further analyses indicated that the Growing Degree Hours (GDH) played a critical role in these processes, although the Chilling Hours (CH) showed significant variability after 1991. Our results provide evidence that the change in the balance of CH and GDH across latitude induced declining S_{lat} over the last 40 years in eastern China. Furthermore, it may continue under the future climate warming scenarios and ultimately has important consequences on the structure and function of ecosystems.

1. Introduction

The phenology of leaf unfolding (LUD) is one of the most important and sensitive indicators of climate change impacts on ecological

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systems (Schwartz, 1998; Menzel and Fabian, 1999). Many environmental factors have been shown to affect phenological change, such as temperature (Peñuelas et al., 2002; Cleland et al., 2007), precipitation (Reich, 1995; Shen et al., 2011; Shen et al., 2015), and radiation (Doughty and Goulden, 2008; Bradley et al., 2011). Among these variables, the temperature is considered as one of the most important factors (Schwartz et al., 2006; Li et al., 2018). Substantial earlier LUD has been observed as a response of plants to climate warming in most Northern Hemisphere regions (Wang et al., 2015a; Ge et al., 2014; Fu et al., 2015). Climate warming is predicted to further increase, however, future changes in spring phenology and its consequent feedbacks remains debated (Estrella et al., 2009; Chen et al., 2018; Piao et al., 2019).

Numerous studies have observed an advanced LUD matching warming trends in recent decades (Menzel et al., 2006; Fu et al., 2014), as phenology is so sensitive to temperature changes. For example, Keenan et al. (2014) have found that the spring phenology of plants in temperate forests was advanced under global warming in 1989–2012. The relationship of LUD with temperature can be expressed by temperature sensitivity (S_T, days $°C^{-1}$), which includes the dates of phenological events observed in different years or sites (Menzel, 2005; Estrella et al., 2009; Fu et al., 2014). However, a weakening phenology response to global warming has also been reported in recent years (Pope et al., 2013; Rutishauser et al., 2008; Fu et al., 2013). For example, due to the warming trend in the past few decades, a declined S_T of spring phenology was observed in seven tree species of Europe during 1980–2013 (Fu et al., 2015). Besides, plant phenology shows strong classification differences under climate change (Root et al., 2003; Parmesan, 2007; Ge et al., 2015). Mo et al. (2017) observed a lower S_T of trees and shrubs than that of herbs based on a meta-analysis, which is consistent with the filed observation of Root et al. (2003) in China. Therefore, further investigation and research are required to explore the underlying mechanism of changing leaf phenology, especially at the species level, under future warming scenarios (Fu et al., 2015; Piao et al., 2019).

Furthermore, an improved understanding of S_T across different regions can lead to a more reliable projection of phenology change for future climate change (Piao et al., 2011; Wang et al., 2014). As early as 1918, Hopkins' bioclimatic law has suggested that spring advances one day for every 15 minutes (quarter degree) of latitude northward, which was determined by the change in temperature (Hopkins, 1918).

The latitudinal changes of spring phenology, representing plant adaptability and distribution (Vitasse et al., 2018), have been proven to be a key role in regulating ecosystem functions and controlling the carbon fluxes between biosphere and atmosphere (Piao et al., 2015; Mo et al., 2017). However, under the trend of global warming, the rates of temperature change at different latitudes are not synchronized (IPCC, 2014; Plummer et al., 2006; Donat and Alexander, 2012). Growing evidence has shown that temperature at northern latitudes is increasing more pronounced in winter than spring (Anderegg and Diffenbaugh, 2015; Xia et al., 2015). Since the leaf unfolding process is generally influenced by both winter chilling (i.e., Chilling hours) and spring forcing (i.e., Growing degree hours) (Chuine et al., 1998; Chuine, 2000), we are not clear whether the Hopkins' bioclimatic law, which was proposed 100 years ago, is still valid. Therefore, considering the observed pattern of temperature and the variability of S_T, we hypothesize a different trend of LUD with latitude (S_{lat}, expressed as delayed days per degree in latitude; days $°N^{-1}$) under further warming. Based on the current research, the following hypotheses are generated (Fig. 1). If LUD is unchanged (mode1), advanced (mode 2), or delayed (mode 3) by the same magnitude at the high- and low- latitudes, then the S_{lat} will not be changed. However, if the LUD is delayed at the low-latitudes but advanced at the high-latitudes (mode 4), or the LUD is advanced less (mode 5) or delayed more (mode 6) at the low-latitudes, the S_{lat} will be decreased. On the contrary, if the LUD is advanced at the low-latitude regions but delayed at the high-latitudes (mode 7), or the LUD is advanced more (mode 8) or delayed less (mode 9) at the low-latitudes, the S_{lat} will be increased.

To test these hypotheses, we used phenological records of woody species LUD at 37 sites in eastern China during 1963–2008 to quantify the long-term trend of S_{lat}. By analyzing phenological records and long-term temperature data, we further attempt to clarify the mechanisms that cause phenological changes along latitudes.

2. Materials and methods

2.1. Data collection

Phenological data of species leaf unfolding was extracted from the National Earth System Science Data Center network (http://www.

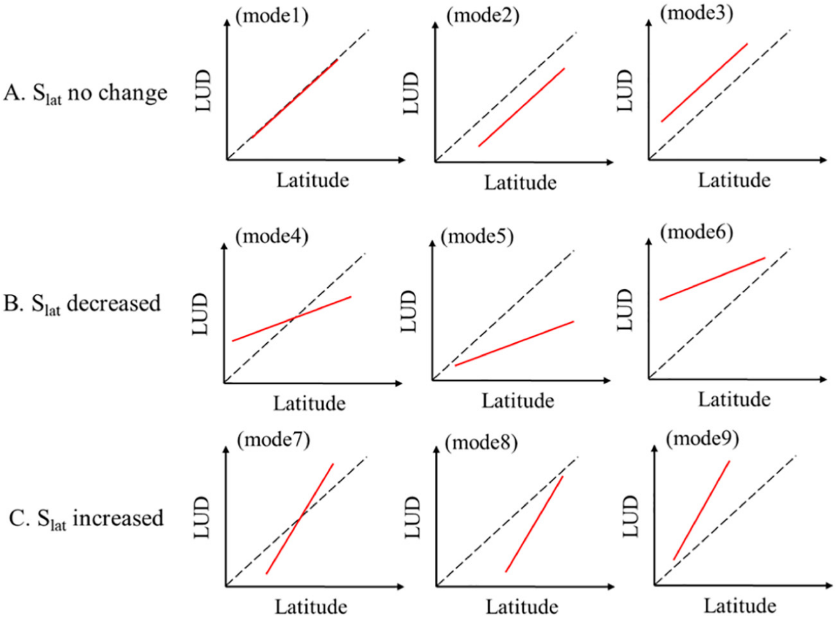

Fig. 1. The diagrams of our hypotheses in this study. Nine modes of the LUD across latitude (S_{lat}, days $°N^{-1}$) including were shown. The dashed line and red solid line represents the control and hypothesized S_{lat}, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

geodata.cn). This original set of phenological records includes 44 long-term observation sites in eastern China, with latitudes from 23°N to 49°N. The objective of these phenological records is to analyze the long-term climate change and biological response to changes in environmental factors. Therefore, each station is selected according to the principles of strong statistical representativeness, long observation time, and continuous observations. All the selected woody species are local representative plants, middle-age, normal development. Phenological observations were conducted weekly by the same phenology monitoring protocol. To reveal the responses of various plant types, we searched studies or online (http://cn.bing.com/com/; http://frps.eflora.cn/) to complete species classification, including life forms (trees, shrubs, and lianas) and other plant functional groups (deciduous vs evergreen trees, and broad-leaf vs coniferous-leaf trees).

LUD was defined as the date when 50% of the leaves or needles are unfolded (Wan and Liu, 1979), which the timing of spring leaf unfolding is expressed as the day of the year (DOY). The altitudes of these sites are ranged from 2 m to 1378.5 m, with a mean value of 538 m. To eliminate the influence of altitude, 37 sites with elevations between 0 and 450 m were finally selected (Fig. 2; Table S1). Among them, 10 stations with low latitude (<29 °N), 18 stations with middle latitude (30–39 °N), and 9 stations with high latitude (>40 °N) were listed as the low-, mid-, and high- latitudes, respectively, to do further analysis. Additionally, we used the interquartile ranges method (IQRs) to exclude some deviating observations. The records that are more than 1.5 × IQR above the third quartile or below the first quartile (Chen et al., 2018) were excluded in this study. Therefore, nearly 1% of observations (314 numbers) were excluded across all the sites with no site or species bias (Fig. S1). The information of outliers was shown in Table S2.

Climatic data (daily temperature, precipitation, and radiation) were collected from the database of China Earth Exchange Station Climatic Data Day Value Dataset (http://data.cma.cn) by the location of the study site. All the climatic data was from the nearest stations (e.g. a distance from 110 m to 236.5 m) according to the phenology sites.

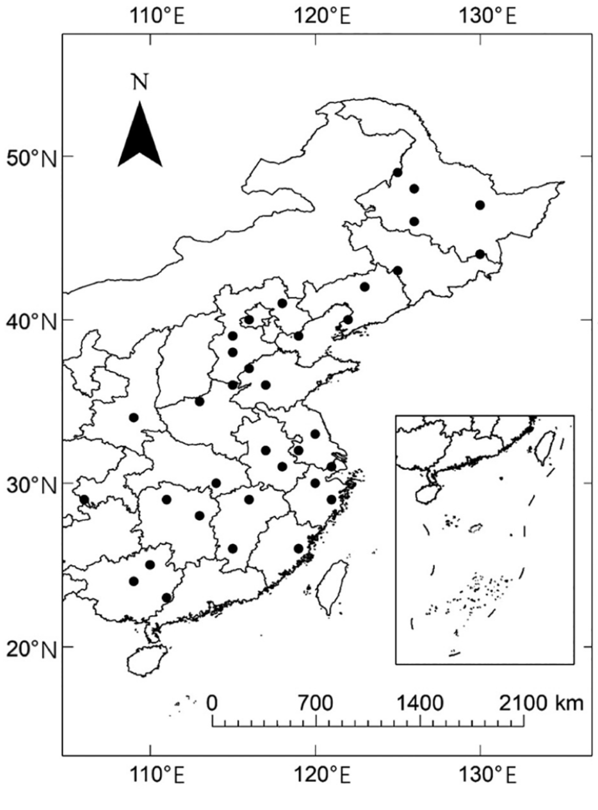

Fig. 2. The distribution of 37 observation sites in this study.

2.2. Data analysis

The chilling period of plants refers to the minimum period of leaf unfolding after the cold weather, while spring forcing refers to the heat accumulation of plants in spring, both of which are important for the trigger of plant phenology (Ruiz et al., 2007; Alburquerque et al., 2008). Therefore, Chilling Hours (CH, referred to as chilling) and Growing Degree Hours (GDH, referred to as spring forcing) of different species at each site were calculated in this study. CH was calculated as the accumulated hours (0 to 5 °C) from November 1st (the starting day for CH in the northern hemisphere; Fu et al., 2015; Zohner and Renner, 2014) to April 7th (the averaged LUD of all sites in this study). GDH was calculated as the accumulated hours (above 5 °C) from February 1st (Chen et al., 2018; Vitasse et al., 2018) to April 7th. The “chillR” package (Luedeling et al., 2013) of R (Team, 2013) were used to calculate CH and GDH.

Preliminary analyses showed that no significant trend of precipitation in spring and winter was found during the period of 1963–2008 (Fig. S2). Besides, the daily mean, maximum, and minimum temperature in these two seasons showed synchronized variations at both the temporal and spatial scales (Fig. S3). Therefore, this study mainly analyzed the influence of daily mean temperature on the latitude model of the LUD.

Phenological events observed in different years or at different locations are always associated with the mean temperature during a period of several weeks when preceding the event (Estrella et al., 2009; Menzel, 2005; Menzel et al., 2006). The definition of optimal preseason is often used to represent the period whose mean temperature is most related to phenological dates (Fu et al., 2015). In this study, the length of optimal preseason for each species is estimated by LUD and partial correlation analysis was used for each species at each site to remove the covariate effects of precipitation and radiation. Briefly, we compared partial correlation coefficients (*partial r*) between the average LUD of each species at each site and the daily mean temperature of each species in the 15–120 days before leaf unfolding using a time step of 15-day, 30-day, 45-day and so on (15 days, 30 days, 45 days, etc. before LUD of each species at each site). Optimal preseason temperature (OPT) was estimated by the average air temperature in the corresponding period for each species at each site when *partial r* was highest by the step of 15-day (Fu et al., 2015).

The trend of OPT across the latitude (T_{lat}, °C °N^{-1}) was calculated as follows.

$$T_{lat} = \frac{OPT}{Lat} \tag{1}$$

where OPT is the daily mean temperature in optimal preseason (°C). Lat is the latitude (°N) of each site.

S_T was first calculated by the linear regression of the corresponding LUD with OPT for each species at each site by Eq. (2), and then averaged for each life form or all species at each site.

$$S_T = \frac{LUD}{OPT} \tag{2}$$

Yearly LUD of each species at each site was calculated by the mean LUD of each species at each site. The trend of LUD with latitude (S_{lat}, days °N^{-1}) can be expressed by the below equation.

$$S_{lat} = \frac{LUD}{Lat} \tag{3}$$

where LUD is the average of yearly LUD during a period at each site. Lat is the latitude (°N) of each site.

We first obtained the temporal variability of S_T by using a moving window of 20 years. Then, we used the "lme4" (Bates et al., 2014) package of R (Team, 2013) to estimate the trends of CH, GDH, OPT, LUD, T_{lat},

S_T, and S_{lat} over time. Segment breakpoints were also calculated by piecewise regression with 2 linear segments of OriginPro 2016 software (OriginLab Corp., Northampton, MA, U.S.A.). Using "ggm" (Giovanni et al., 2020) package of R (Team, 2013), partial correlation analyses were carried out to estimate the effects of CH and GDH on LUD at the temporal and spatial scales. Since the temporal LUD across all sites shows segment breakpoint at 1985 (Fig. 3d), we also compared the spatial pattern of S_T and partial correlation of LUD with CH and GDH in 1963–1983 and 1988–2008.

3. Results

3.1. The temporal and spatial variability of temperature

During 1963–2008, the daily mean temperature in optimal preseason (OPT, °C) of all sites showed an increasing trend (0.04 °C yr^{-1}), especially after 1993 (0.18 °C yr^{-1}, $P < 0.001$; Fig. 3a), mainly due to a significant increase at the mid-latitude regions (0.05 °C yr^{-1}, $P < 0.001$; insert panel of Fig. 3a). As the asymmetric warming at different latitudes, a decreasing trend of OPT across latitude was shown from 1963 to 2008, with a significant rate of −0.02 °C $°N^{-1}$ yr^{-1} ($P < 0.01$; Fig. 4a; Table S3).

Chilling hours (CH) showed an increase before 1991 (4.46 h yr^{-1}, $P < 0.001$), but a decrease after then (6.94 h yr^{-1}, $P < 0.001$), with no significant trend in 1963–2008 (Fig. 3b). A Significant change of CH during 1963–2008 was only found at mid-latitudes (2.09 h yr^{-1}, $P < 0.01$; insert panel of Fig. 3b). Growing degree hours (GDH) increased significantly by a rate of 54.00 h yr^{-1} at all site from 1963 to 2008 ($P < 0.001$; insert panel of Fig. 3c), mainly due to the rapid increase (119.40 h yr^{-1}, $P < 0.001$) after 1985 (Fig. 3c). Similar increased trends were found at all latitudes from 1963 to 2008 (insert panel of Fig. 3c).

3.2. The temporal and spatial variability of the leaf unfolding date (LUD)

The analysis results showed that LUD (a negative value indicates advancement) was averagely advanced by −0.17 days yr^{-1} at all site from 1963 to 2008 ($P < 0.001$), which was mainly attributed to the great advance after 1985 (−0.47 days yr^{-1}, $P < 0.001$; Fig. 3d). Therefore, an advance of nearly 8 days (−0.17 days yr^{-1} × 45 years) was found in LUD for all sites.

Across increasing latitude, LUD was slow down with a negative slope of 0.01 days $°N^{-1}$ in the period of 1963–2008 ($P < 0.001$; Fig. 4c). This was mainly attributed to the advance of LUD at the higher latitudes (>30 °N; −0.22 ~ −0.25 days yr^{-1}, $P < 0.001$) with no change at the lower latitudes (<30 °N; 0.05 days yr^{-1}, $P > 0.05$) in this period (insert panel of Fig. 3d). Therefore, the S_{lat} was statistically decreased from 2.38 days $°N^{-1}$ in 1963 to 1.55 days $°N^{-1}$ in 2008 (Table S2), with a rate of −0.01 days $°N^{-1}$ yr^{-1} ($P < 0.05$; Fig. 4c).

3.3. The dependence of LUD upon temperature

During 1963–2008, the yearly LUD at most sites showed significant relationships with OPT (Table S3). The temperature sensitive of LUD referring to OPT (S_T) of all sites was -4.62 ± 0.13 days $°C^{-1}$ during

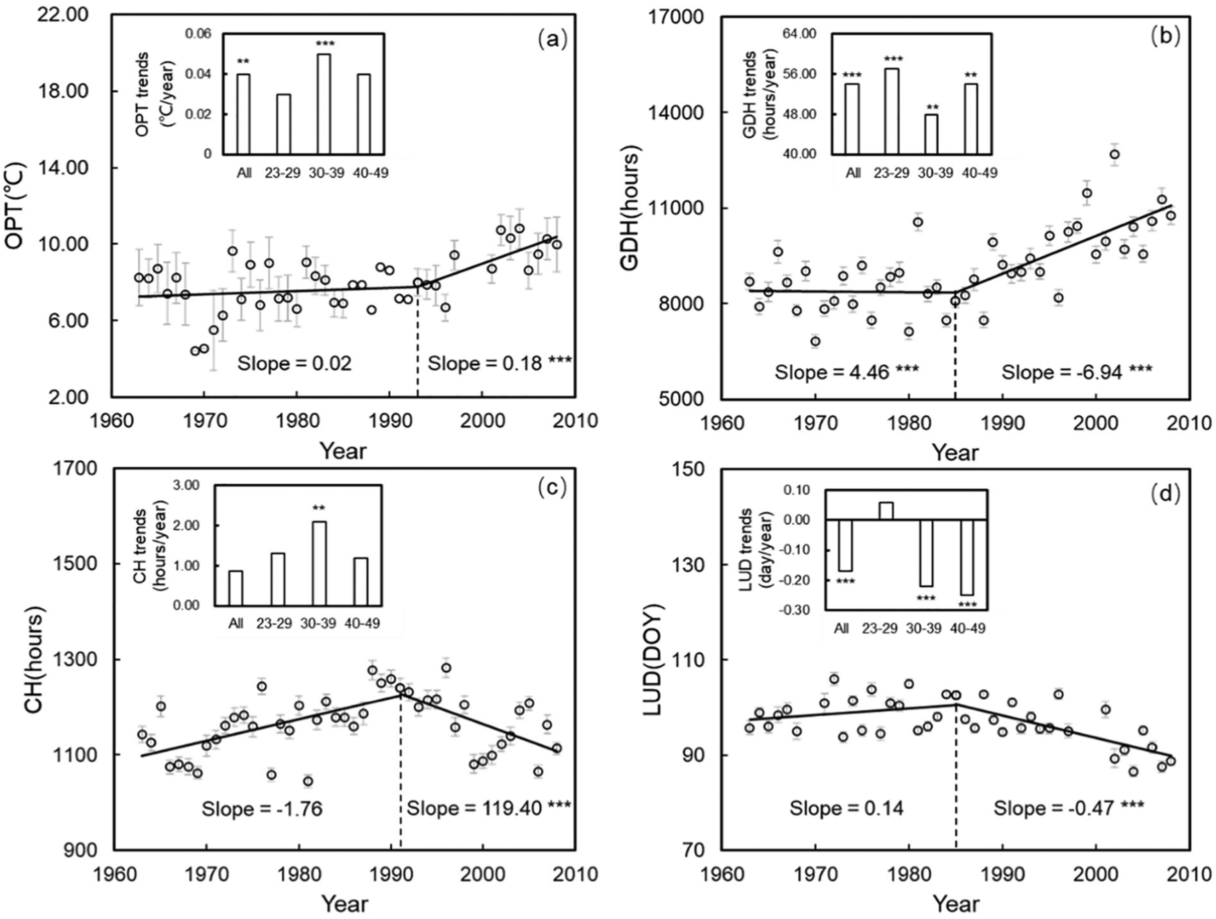

Fig. 3. Temporal variability of the optimal preseason temperature (OPT, °C; a), Chilling Hours (CH, hours; b), Growing Degree Hours (GDH, hours; c) and leaf unfolding dates (LUD, DOY; d) at all sites from 1963 to 2008. The dashed lines show the segment breakpoints, and the insert panels represent the variability rates for different latitude gradients (all sites, 23–29°N, 30–39°N, 40–49°N) during 1963–2008, respectively. ** and *** indicate significance levels of $P < 0.01$ and $P < 0.001$, respectively.

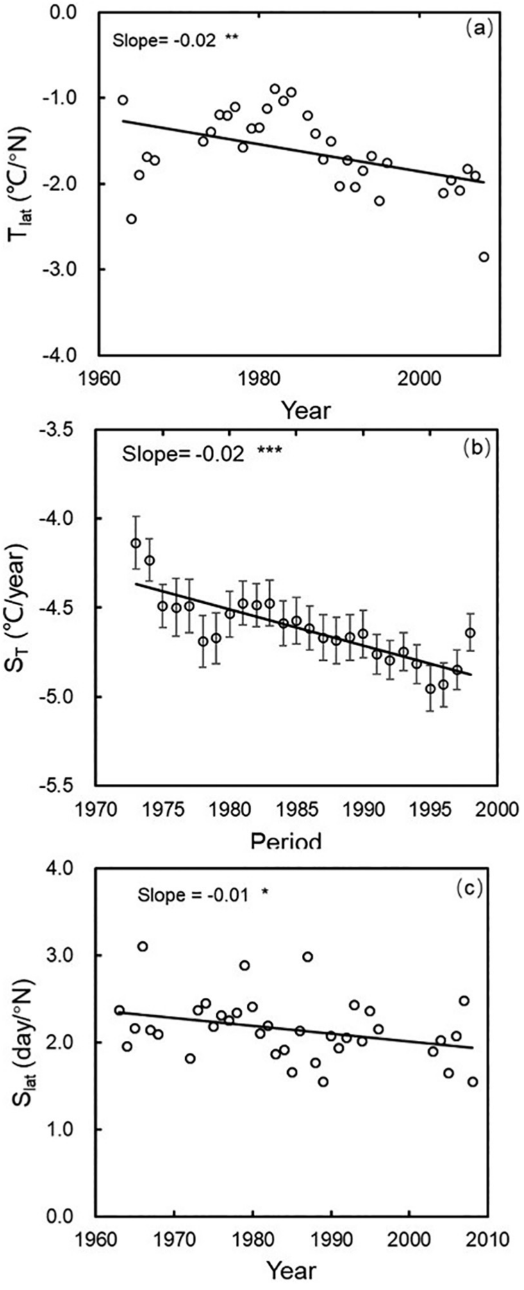

Fig. 4. The temporal trends of latitudinal sensitivity of OPT (T_{lat}, °C $°N^{-1}$; a), the temperature sensitivity of LUD (S_T, days $°C^{-1}$; b), and latitudinal sensitivity of LUD (S_{lat}, days $°N^{-1}$, c). The temporal S_T was obtained by using a moving window of 20 years. *, ** and *** indicate significance levels of $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

1963–2008. No significant difference was found in the averaged S_T between 1963 and 1983 (-4.14 ± 0.15 days $°C^{-1}$) and 1988–2008 (-4.64 ± 0.10 days $°C^{-1}$). However, a decreasing trend of all sites was shown when using a 20-year moving window (slope = −0.02, $P < 0.001$; Fig. 5b), especially in the high-latitudes (latitude >30 °N; Table S4). The analysis of the S_T across life forms suggested a wide range of S_T among life forms independent of latitude (Fig. 5b). It also showed that most life forms had no significant differences in S_T between 1963–1983 and 1988–2008, except deciduous broad-leaf trees (DBT) at higher latitudes (latitude >30 °N, Fig. 5c). Therefore, the slope of S_T of all species or life forms with latitude decreased but did not change significantly from 1963 to 1983 to 1988–2008 ($P > 0.05$, Fig. 5, Table S3).

Across all the sites, LUD showed no significant relationship with CH but a negative relationship with GDH (−0.005 day $hours^{-1}$, $P < 0.001$; Fig. 6a and b). The analysis of partial correlation showed that the importance of GDH (partial correlation coefficient, *partial r*) increased with increasing latitude ($R^2 = 0.31$, $P < 0.001$; Fig. 6d), but no obvious trend was found in CH (Fig. 6c). At the temporal scale, a significant partial correlation of LUD with CH was only found at low-latitudes in 1963–2008 (Pearson's r = 0.43, $P < 0.001$; Table 1). However, the effect of GDH on LUD was significant in all latitudes at any period when excluding the impact of CH, except at low-latitudes during 1963–1983 and 1963–2008 (Table 1).

4. Discussion

4.1. Changes in the spring phenology over time

Since plant growth and development require a certain temperature threshold and thermal accumulation, the most significant effect of global warming on vegetation is to advance its spring phenology, especially in the high latitudes of the Northern Hemisphere (Wolfe et al., 2005; Dai et al., 2013; Ge et al., 2015). However, controversial results have also reported no significant response or even a delay (Sherry et al., 2007; Dorji et al., 2013; Zhang et al., 2015). In this study, synchronizing with the increasing mean annual temperature, the LUD of forests species in eastern China (Altitude <450 m) has been substantially advanced by 8 days from 1963 to 2008, with its S_T of -4.62 ± 0.13 days $°C^{-1}$ during the whole period (hereafter, a negative value indicates advancement). Further analysis showed that there is a wide range of S_T across life forms independent of latitudes. Generally, the S_T of deciduous broad-leaf trees (DBT) and lianas are always higher than other life forms (Fig. 5).

S_T showed no significant change when compared to the period of 1963–1983 with that of 1988–2008. However, the 20-year moving window from 1963 to 2008 indicated that a significant decrease in S_T by an average of −0.02 days $°C^{-1}$ yr^{-1} for all sites, especially in higher latitudes (Latitude >30 °N; Fig. 4). Our result is in contrast to the results of Fu et al. (2015), which demonstrated a declining warming effect on the spring phenology of European tree species. Three hypotheses were proposed in their research for this reduction: a reduced chilling, and increased spring temperature, and photoperiodic limitations overriding temperature controls. In our study, the LUD always showed a synchronous change with GDH from 1963 to 2008, while no significant trend was found in CH for all sites (Table 1). It indicates that the ‘chilling’ is not important in the response of phenology to warming in this process or other mechanisms, e.g. spring forcing, may have a role that neutralized the effect of ‘chilling’. More studies are required to further investigate the mechanisms underlying the changes in spring phenology at the temporal scale. Our findings highlight a warmer winter and spring under future climatic scenario may accelerate the advancement of spring phenology, especially in higher latitudes.

4.2. Changes of the spring phenology with latitude

Understanding the long-term changes in spring phenology along spatial patterns (latitude, altitude, etc.) is critical to clarify and predict the responses of terrestrial ecosystems under climate warming. Based on long-term and large-scale transect observations, we found that the LUD was unchanged at the low-latitude regions (Latitude <30 °N), but advanced more than 10 days (−0.22 ~ −0.25 days yr^{-1} × 45 years) at the high-latitude regions (Latitude >30 °N; Altitude <450 m) from 1963 to 2008 (Fig. 3b). Consequently, consistent with mode 5 of our hypotheses, a decreasing S_{lat} with a rate of −0.1 days $°N^{-1}$ per decade was shown in eastern China during 1963–2008. Our results confirm more sensitive spring phenology at the colder locations (high latitude or altitude) than at the warmer locations (low latitude or altitude), consistent with previous studies (Jolly et al., 2005; Zhang et al., 2007; Vitasse et al.,

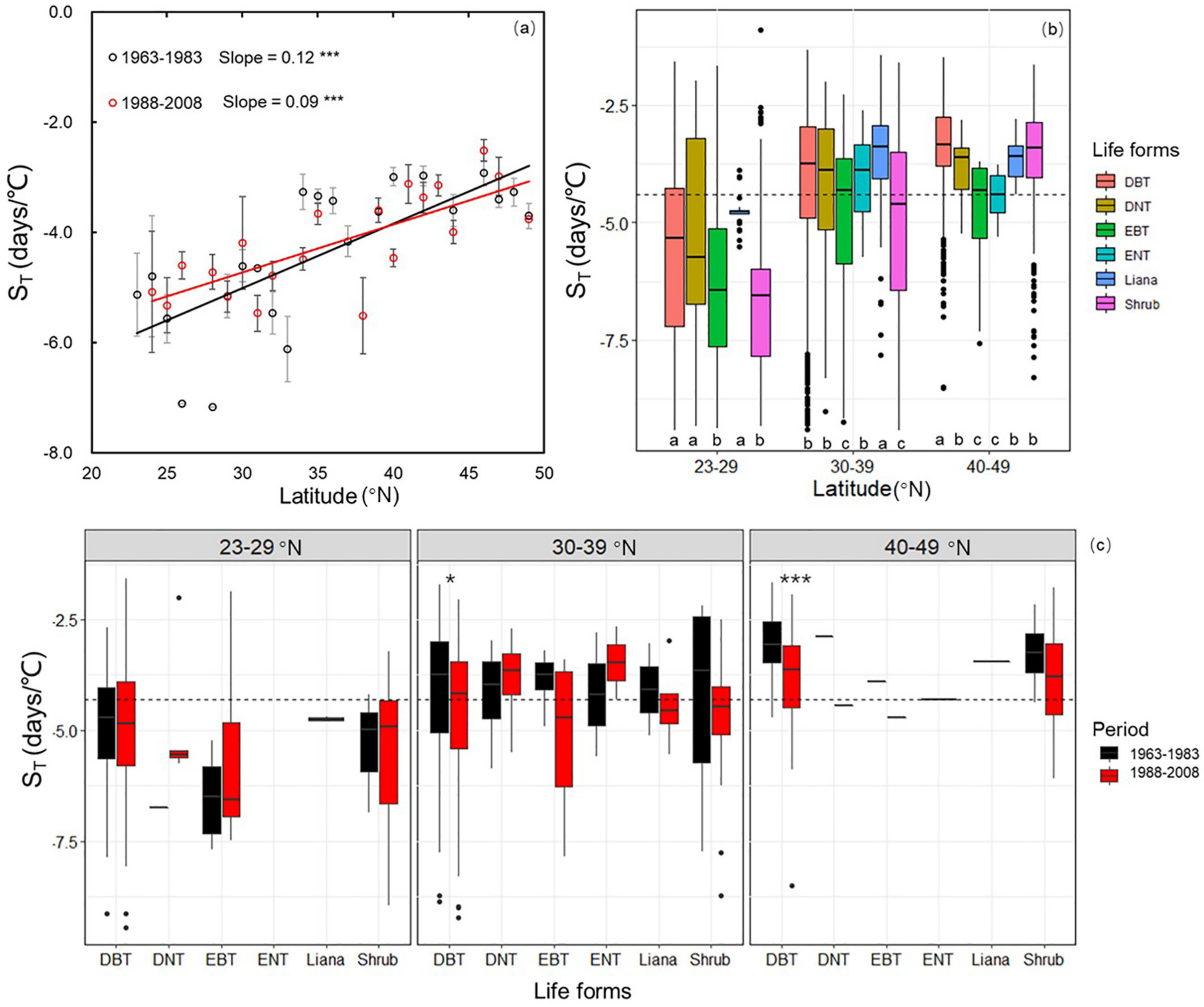

Fig. 5. The Spatial pattern of S_T for all species (a) and each life form (b and c) in 1963–1983 and 1988–2008. The black dotted line in panel b and c represents the mean S_T of all species, the lowercase letter in panel b represents if the difference among life forms is significant at different latitudes, which the same letter represents the difference is not significant, in verse significant ($\alpha = 0.01$). * and *** indicates significance levels of $P < 0.05$ and $P < 0.001$, respectively. DBT represents deciduous broad-leaf trees, DCT represents deciduous coniferous trees, EBT represents evergreen broad-leaf trees, and ECT represents evergreen coniferous trees.

2018). Furthermore, the declined difference in the LUD between low- and high- latitudes implies the patterns of spring phenology became less contrasted across the latitude gradient.

Winter cooling requirements must be met to release vegetation bud dormancy before greening, or else the genetic and physiological processes will be inhibited and consequently spring phenology will be delayed (Chuine et al., 1998; Kramer, 1994). Once sufficient chilling has accumulated, the bud enters the second phase of dormancy, during which sufficient warmth is required to initiate spring burst, referred to as spring forcing (Fu et al., 2013). Furthermore, an interaction influence has been found between spring forcing and winter chilling, which means more spring thermal accumulation will be required for insufficient previous chilling (Murray et al., 1989; Luedeling et al., 2009). However, as an asymptotic relationship is assumed to exist between the effect of spring forcing and chilling (Zhang et al., 2007; Fu et al., 2013), the importance of spring forcing will be greater with increasing chilling (i.e. latitude; Fig. 6d) and a threshold may exist for the regulation of chilling when the chilling is sufficient (Fig. 6c). In our study, CH showed obvious variabilities from 1963 to 2008, especially after 1985. However, no significant effects of CH on LUD were found for all sites or the three latitudes, except in low latitudes in 1963–1983 (*partial* $r = 0.42$, $P < 0.001$; Table 1). On the other hand, estimated by GDH, spring forcing in our study always has a positive effect on the advancement of leaf unfolding (Fig. 6b; Table 1). These findings suggested that warmer winter under current climate conditions seems to be still sufficient to ensure adequate chilling of woody species in eastern China. Therefore, the synchronous warmer temperatures in the spring offset or overcompensate the negative effect of the chilling, which finally induce an insignificant (Latitude <30°N) or positive effect (Latitude >30°N) on spring phenology.

To date, many studies have highlighted the key role of forced temperatures in the phenological responses of species to warming, however, declines in low temperatures may be more important in spring events (Atkinson et al., 2013; Funes et al., 2016). Our findings indicate that the ‘chilling’ could be one of the most important triggers for the onset of spring phenology, however, it may play less influence than spring forcing on the variability of LUD when it does not exceed the optimal range. Under the future warming scenarios, a stronger increase in

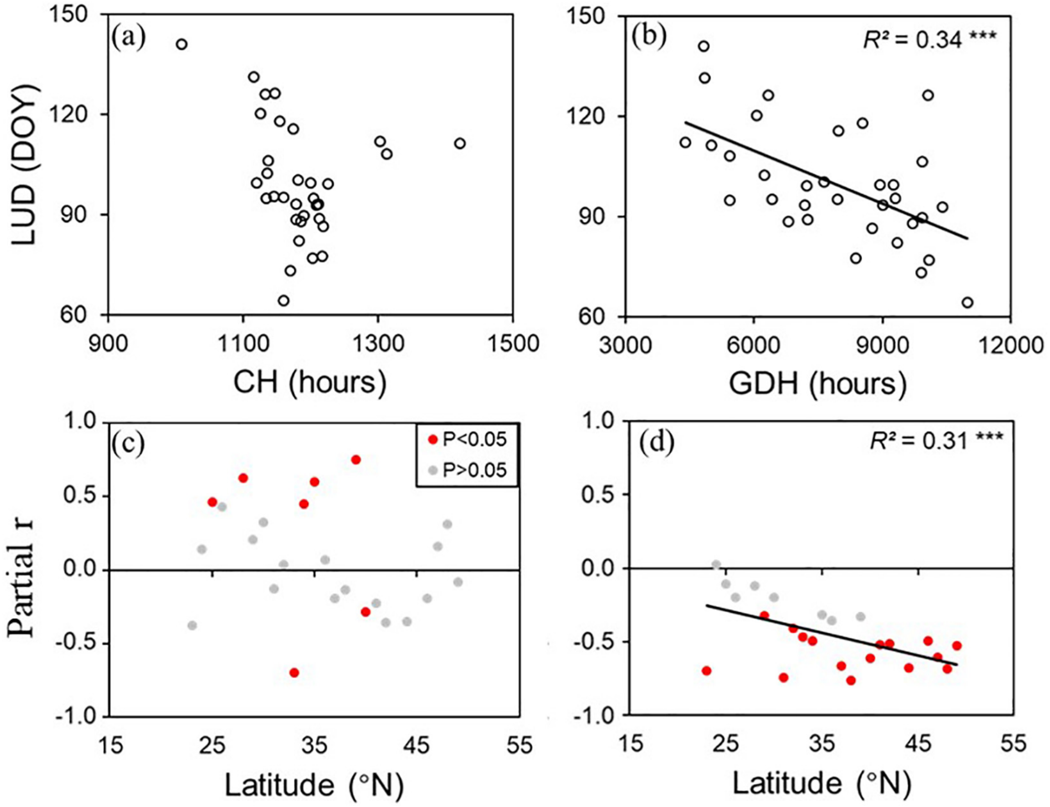

Fig. 6. The regression of LUD with CH (a) and GDH (b) at all sites, the partial correlation coefficient (*partial r*) of LUD with CH (c) and GDH (d) for each site during 1963–2008, respectively. *** indicate significance levels of $P < 0.001$.

winter than that in spring will alter the spring phenology patterns by reducing the chilling and increasing spring forcing effect. This change in the balance between chilling and forcing will lead to a shift in plant phenology and further have significant impacts on biogeochemical cycles and ecosystem functions and services (Yang et al., 2020).

4.3. Implications of uniform spring phenology across latitudes under climate warming

Our results suggest that warming temperature, especially in spring, advances LUD in mid- and high- latitudes but shows no effect in the low altitude in eastern China. This pattern is likely to continue in higher latitudes under future warming scenario as an increasing GDH is accompanied by a reducing but still sufficient CH. However, at the low latitude regions, the requirement of GDH will be rapidly increased when CH become insufficient to fulfilled vegetation chilling requirement. Then the plant has to delay LUD to accumulate sufficient cold. Nevertheless, LUD at high latitudes can be advanced by the continuously increasing GDH but the rate will slow down. The S_{lat} will then switch from mode 5 to mode 4 or even mode 6, determined by the trade-off between CH and GDH. These synchronized latitudinal patterns of spring phenology and temperature, consistent with previous studies (Dai et al., 2014; Wang et al., 2015b), suggest that the asymmetric warming in winter and spring across latitudes eventually induce a convergent phenological response of species under warming in China. In addition, numerous studies have observed that the change of spring phenology was affected by a variety of temperature indices (Shen et al., 2015) and different responses were shown in different regions (Piao et al., 2015; Cao et al., 2018). For example, Piao et al. (2015) found that daily maximum temperature has a greater influence on spring phenology in the north middle and high latitudes. However, Cao et al. (2018) indicated the influence of night temperature was more significant when modeling the spring phenology in Qinghai-Tibet Plateau. Although a synchronized pattern of the daily maximum and minimum temperature with the daily mean temperature at both the temporal and spatial scale in this study (Fig. S2), the asymmetric warming in the daytime and nighttime and their asymmetric effect on spring phenology also have been highlighted under future warming scenarios.

Furthermore, the analysis of life forms also supports the findings of more sensitive spring phenology at the higher latitudes than at the lower latitudes. However, there were no evergreen coniferous-leaf trees and lianas at the 23–29 °N latitudes, while no broad-deciduous-

Table 1
The partial correlation coefficient (*partial r*) of LUD with CH and GDH at different latitudes during 1963–1983, 1988–2008, and 1963–2008, respectively. The brackets represent condition variables, that is, the variables to be excluded. *, ** and *** indicate significance levels of $P < 0.05$, $P < 0.01$ and $P < 0.001$, respectively.

Latitude	LUD-CH(GDH)			LUD-GDH(CH)		
	1963–1983	1988–2008	1963–2008	1963–1983	1988–2008	1963–2008
23–29 °N	0.06	0.01	0.43**	−0.08	−0.59*	−0.25
30–39 °N	0.22	0.24	0.03	−0.68**	−0.77***	−0.87***
40–49 °N	0.01	0.04	−0.11	−0.71**	−0.74***	−0.86***
23–49 °N	0.20	−0.02	0.05	−0.12	−0.52*	−0.61***

shrub at the 40–49 °N latitudes. Therefore, only S_T of DBT showed a similar trend with mean S_T under recent warming across latitudes. This phenomenon may be caused by the insufficient database and inconsistent sample sizes, which is an unavoidable problem that we have to face in any big data analysis (Parmesan, 2007; Ge et al., 2015). For more reliable and comprehensive analysis of plant phenology, future databases should be built in a more uniform manner, including a well-matched species composition about life forms. On the other hand, the increasing variability in climate change leads to incomparability among different life forms to a certain extent. Trees and shrubs are much less dependent on temperature than lianas, as they can use and absorb sunlight for energy by more and larger leaves. Additionally, deciduous trees always require cold winter temperatures to break the natural dormancy and warm spring temperatures to initiate leaf unfolding (Chuine, 2000; Guo et al., 2019; Luedeling et al., 2013). Warm conditions in early spring can promote their satisfaction with heat demand, leading to early spring phenology (Murray et al., 1989; Gao et al., 2020). Therefore, large differences in responses among species with similar climatic trends were observed across latitudes, regions, and communities. The impacts of such reduction in the S_{lat} for life forms are largely unknown but may disrupt numerous plant-animal interactions (Menzel et al., 2006; Memmott et al., 2007). Long-term field observations are required to reveal complex interdependencies among species and predict the impact of climate change on the structure and function of terrestrial ecosystems in future warming scenarios.

5. Conclusion

To conclude, this study has explored an unchanged LUD in low-latitude regions but an advanced LUD in high-latitude regions in eastern China from 1963 to 2008. However, no significant difference was observed in the S_T along latitude at the temporal scale. Corresponding to mode 5 of our hypothesis, a decreasing S_{lat} was mainly triggered by the non-uniform change in spring temperature across latitude. This convergent response of spring phenology along latitude may deeply impact the structure and functioning of the terrestrial ecosystem. More attention should be paid to the underlying mechanisms and potential consequences of this phenomenon, especially under future warming scenarios.

CRediT authorship contribution statement

Wanying Cheng: Conceptualization, Methodology, Software, Formal analysis, Writing - original draft. **Zhao Li:** Data curation, Software, Writing - review & editing. **Liming Yan:** Supervision, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.scitotenv.2020.143177.

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