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Contrasting phenology responses to climate warming across the northern extra-tropics

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ABSTRACT

Climate warming has substantially advanced the timing of spring leaf-out of woody species at middle and high latitudes, albeit with large differences. Insights in the spatial variation of this climate warming response may therefore help to constrain future trends in leaf-out and its impact on energy, water and carbon balances at global scales. In this study, we used in situ phenology observations of 38 species from 2067 study sites, distributed across the northern hemisphere in China, Europe and the United States, to investigate the latitudinal patterns of spring leaf-out and its sensitivity (S_T , advance of leaf-out dates per degree of warming) and correlation (R_T , partial correlation coefficient) to temperature during the period 1980–2016. Across all species and sites, we found that S_T decreased significantly by $0.15 \pm 0.02 \text{ d } ^\circ\text{C}^{-1} \text{ } ^\circ\text{N}^{-1}$, and R_T increased by $0.02 \pm 0.001 \text{ } ^\circ\text{N}^{-1}$ (both at $P < 0.001$). The latitudinal patterns in R_T and S_T were explained by the differences in requirements of chilling and thermal forcing that evolved to maximize tree fitness under local climate, particularly climate predictability and summed precipitation during the pre-leaf-out season. Our results thus showed complicated spatial differences in leaf-out responses to ongoing climate warming and indicated that spatial differences in the interactions among environmental cues need to be embedded into large-scale phenology models to improve the simulation accuracy.

1. Introduction

Global warming has advanced the spring phenology of vegetation in the northern hemisphere by an average of 2–8 days per decade [1–3]. The warming is spatially heterogeneous which can contribute to non-uniform changes in spring phenology across regions [4, 5], and subsequently in terrestrial ecosystem carbon sinks [6–8]. The apparent temperature sensitivity of vegetation, measured as the advance of leaf-out dates per degree of warming during the period that determines spring leaf-out, has been widely used to quantify responses of leaf-out phenology to climate change [9, 10]. However, few studies have quantified spatial variations in the apparent temperature sensitivity, especially at mid and high latitudes in the northern hemisphere, where vegetation is exposed to rapid warming [11, 12].

Vegetation phenology responses to climate change are driven by multiple environmental factors, such as temperature, including winter cold temperatures (chilling) and spring warm temperatures (thermal forcing), photoperiod, and water availability [13–18]. The temperature has been identified as the predominant driver of forest phenology in spring, especially in temperate and boreal biomes [14, 19], but many recent studies also reported that other environmental factors can modify spatial variations in spring phenology [20, 21]. As such, spatial differences in the effects of warming on tree phenology can be expected. For example, spring phenology of temperate tree species has been shown to be more responsive to light than to temperature at lower latitudes [22, 23] and altitudes [24], and in oceanic climate regions [15]. Nevertheless, these spatial differences in temperature sensitivity and temperature correlation of spring phenology still require in-depth exploration.

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Table 1
Data sources.

Region (Number and proportion of sites)	Data source
Europe 41~68°N, -8.5~136.2°E (1992, 96%)	Pan European Phenology Network (PEP, http://www.pep725.eu/) and Chronicles of Nature (https://doi.org/10.1038/s41597-020-0376-z) [30] Gridded climatic dataset, with a spatial resolution of 0.25° [31] and Princeton climatic dataset, with a spatial resolution of 0.25° covering phenology sites in eastern Europe (http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/)
China 22~49°N, 101~130°E (23, 1%)	National Earth System Science Data Sharing Infrastructure, National Science & Technology Infrastructure of China (http://www.geodata.cn) [32–35] China Meteorological Data Sharing Service System (http://cdc.cma.gov.cn/cdc_en/home.dd)
North America 33~48°N, -123.5~62.1°E (52, 3%)	USA National Phenology Network (USA-NPN, https://www.usanpn.org/results/data) [36] Princeton climatic dataset, with a spatial resolution of 0.25° (http://hydrology.princeton.edu/data/pgf/v3/0.25deg/daily/)

Plants have evolved adaptive mechanisms to the long-term climate change [18], where spring phenology dates are determined by a trade-off between maximizing annual carbon and nutrient uptakes and reducing the risk of late frost damage [25, 26]. Most phenology studies have focused on single species [27–29] and there are few studies which have quantified interspecific differences in response mechanisms and adaptive capacity. This knowledge gap must be bridged by a comprehensive analysis of phenology data from multiple species at different locations to reach an understanding of the impacts of global change on the apparent temperature sensitivity of vegetation phenology across species. Here, we analyzed the spatial variability of spring leaf-out phenology and apparent temperature sensitivity and temperature correlation across 38 species at 2067 study sites (widely distributed across the northern hemisphere, including China, Europe, United States) to (1) quantify the spatial variation in spring leaf-out phenology as well as apparent temperature sensitivity and temperature correlation, and (2) reveal underlying mechanisms attributing to the spatial variations.

2. Material and methods

2.1. Datasets

Phenology datasets. Data for leaf-out of species were obtained from the Pan European Phenology Network (PEP), Chronicles of Nature database for Europe, National Earth System Science Data Sharing Infrastructure, National Science & Technology Infrastructure of China, and USA National Phenology Network (USA-NPN) for North America (Table 1). Leaf-out dates, recorded as day of year (DoY) and the date of first visible leaf stalk (BBCH 11 of the PEP dataset), were extracted for the 38 species. These selected species had been recorded at least 5 phenological sites and for a minimum of 15 years during the period 1980–2016. For each species, phenology data with $>2 \times \text{SD}$ variations among different sites were removed from the estimate of average response of vegetation to climate change. In total, 38 species from 2067 observation sites (i.e. 1992 sites distributes in Europe, which accounts for 96% of the total; 23 sites distributes in China, which accounts for 1% of the total; and 52 sites distributes in North America, which accounts for 3% of the total), comprising 12672 species-site combinations were used in this study (Table S1). The location of the selected phenological sites and sites density within each $2 \times 2^\circ$ cell are shown in Fig. S1.

Climatic datasets. Gridded daily climatic data, including average air temperature ($^\circ\text{C}$), precipitation (mm), and shortwave radiation ($\text{W}\cdot\text{m}^{-2}$), covering Europe and North America during the period 1980–2016 were collected, with a spatial resolution of 0.25° . To ensure high data quality for sites in China, we matched phenology sites to the closest meteorological station; on this basis, sunshine duration (hours) was used to account for the effect of solar radiation on leaf-out in China (Table S1).

2.2. Statistical analysis

We used temporal partial correlation analysis to quantify the relative importance of leaf-out phenology and daily climatic factors (average air

temperature, cumulative precipitation, and shortwave radiation or sunshine duration in China) during the optimal pre-season, the length of which was defined as the period prior to spring leaf-out (range: 15–180 d, with 15-d intervals). We selected the highest absolute partial correlation coefficient between leaf-out date and average air temperature (R_T), after controlling for the influence of precipitation and solar radiation (or sunshine duration) and the corresponding partial correlation coefficient between leaf-out date and pre-season precipitation was denoted as R_P . We used $1 \times \text{SD}$ of average temperature to evaluate variations in annual temperature (MAT_{SD}) and pre-season temperature ($\text{Preseason } T_{\text{SD}}$).

Apparent temperature sensitivity (S_T) was defined as the advance of spring leaf-out for 1°C of rising temperature, and determined by reduced major-axis (RMA) regression between leaf-out dates and average pre-season air temperature. The RMA regression method was applicable to data variables with errors that researchers cannot control [37].

Chilling requirement (CD_{req}) was defined as the number of days with non-freezing temperatures (generally between 0 and 5°C) during the period between the 1st November of the preceding year (t_0) and the average leaf-out date (LO), and calculated as Eq. (1) [9].

$$\text{CD}_{\text{req}} = \sum_{t_0}^{\text{LO}} 1 \text{ if } 0 \leq T_t \leq 5 \quad (1)$$

where T_t is the mean daily air temperature and LO is the average leaf-out date during the period 1980–2016 for each site.

Thermal forcing requirement (GDD_{req}) for leafing out corresponds to the sum of the mean air temperature above a temperature threshold from 1st January to the average leaf-out date. To ensure robustness, GDD_{req} was determined using the following three commonly used methods Eq. (2–4).

$$\text{GDD}_{\text{req}} = \sum_{t_0}^{\text{LO}} (T_t - 5) \text{ if } T_t \geq 5 \quad (2)$$

$$\text{GDD}_{\text{req}} = \sum_{t_0}^{\text{LO}} \begin{cases} 0 & \text{if } T_t < 5 \\ T_t - 5 & \text{if } 5 \leq T_t \leq 15 \\ 10 & \text{if } T_t > 15 \end{cases} \quad (3)$$

$$\text{GDD}_{\text{req}} = \sum_{t_0}^{\text{LO}} \begin{cases} 0 & \text{if } T_t < 0 \\ \frac{28.4}{1 + e^{-0.185(T_t - 18.4)}} & \text{if } T_t \geq 0 \end{cases} \quad (4)$$

where t_0 is the start date of the GDD_{req} calculation (fixed at 1st January), LO is the average leaf-out date during the period 1980–2016, and T_t is the mean daily air temperature. As the results obtained from Eq. (3) and Eq. (4) were similar to those derived by Eq. (2), we reported the results using Eq. (2) in the main text and the results of the other two functions Eq. (3 and 4) in Fig. S2.

We used simple linear regression analysis to estimate the relationship between a single explanatory variable (year and latitude) and a dependent variable (LO, S_T , R_T , MAT, T_{SD} , R_P , Std_{LO} , Psum, CD_{req} , and GDD_{req}).

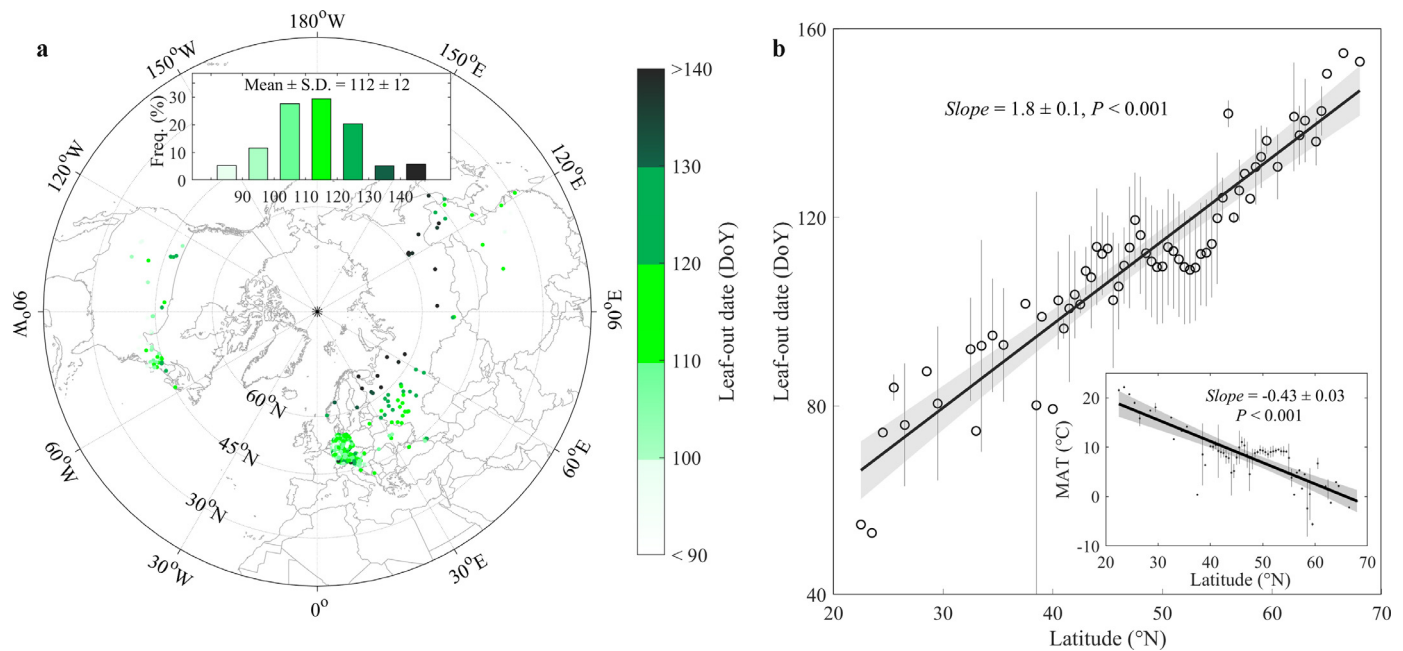


Fig. 1. Spatial pattern of tree leaf-out dates in the northern hemisphere. (a) Spatial and frequency (subpanel) distribution of leaf-out dates. (b) Linear regression analysis of latitudinal variation in leaf-out dates and latitudinal variation in mean annual temperature (MAT) (subpanel); data were averaged per $0.5^{\circ}\text{C}\cdot\text{N}^{-1}$, shaded areas represent 95% confidence intervals, and error bars are $1 \times \text{SD}$ of study site leaf-out date and MAT.

3. Results and discussion

3.1. Spatial variability in spring phenology

Across 38 species distributed over 2067 sites in the northern hemisphere, the average leaf-out date during the period 1980–2016 was day of year (DoY) 112 ± 12 (mean ± 1 SD; Fig. 1a). The spatial pattern of leaf-out date was highly heterogeneous (Fig. S3 and Table 1), with a trend towards later leaf-out at higher latitudes of $1.8 \pm 0.1 \text{ d } ^{\circ}\text{N}^{-1}$ ($P < 0.001$) that tracked mean annual temperature (MAT, Fig. 1b). In agreement with recent studies [24, 38], our results also indicated that global warming might have already altered the ‘Hopkins’ bioclimatic law’, which states that plant phenology is delayed by 4 days for each degree of increasing latitude [39].

3.2. Spatial variability and trends in apparent temperature sensitivity and temperature correlation

Large spatial heterogeneities were found in apparent temperature sensitivity (S_T , see Methods) of leaf-out, and also in a correlation between leaf-out and spring temperature (R_T , see Methods). More than 97% of individual trees across all species showed earlier leaf-out in warmer springs (Table S1), with a mean rate of $-4.8 \pm 2.6 \text{ d } ^{\circ}\text{C}^{-1}$ during the period 1980–2016 (Fig. 2a). After controlling for the confounding influences of precipitation and radiation (see Methods), we found strong negative partial correlations between leaf-out dates and spring temperature in more than 96% of individual trees across all species (average correlation coefficient = -0.58 ± 0.24 and $P < 0.05$ for $>83\%$ of site-species combination; Fig. 2b). We also found that S_T decreased markedly with increasing latitude, by $0.15 \pm 0.02 \text{ d } ^{\circ}\text{C}^{-1} \text{ } ^{\circ}\text{N}^{-1}$, R_T only increased by $0.02 \pm 0.001 \text{ } ^{\circ}\text{N}^{-1}$ across all species and sites ($P < 0.001$, Fig. 2c and d). However, only 26 and 13% of species showed significant trends in S_T ($P < 0.05$; range: $-0.17 \sim +3.61 \text{ d } ^{\circ}\text{C}^{-1} \text{ } ^{\circ}\text{N}^{-1}$) and R_T ($P < 0.05$; range: $-0.23 \sim +0.07 \text{ } ^{\circ}\text{N}^{-1}$), respectively (Table S1).

To understand the underlying drivers of these spatio-temporal responses to climate, we proposed two mutually non-exclusive hypotheses: (1) Based on the “optimum strategy hypothesis”, we expected that

the leaf-out strategy which maximizes tree fitness at higher latitudes is more conservative than at lower latitudes, as supported by the lower sensitivity to temperature increase but the stronger correlation with the temperature at high latitudes; (2) Under the “non-temperature dominant hypothesis”, plant growth at lower latitudes were found to be co-limited by photoperiod and/or water availability [17, 22], rather than temperature. Here, this hypothesis might link to the greater apparent temperature sensitivity and a weaker correlation with temperature found at low latitudes.

To test the “optimum strategy hypothesis”, we investigated the role of two possible mechanisms that may explain spatial differences in S_T . First, to minimize frost risk plants may respond to climate warming less in regions with higher levels of temperature variance, so that greater temperature variation is associated with lower sensitivity levels of spring phenology to temperature increase. Second, leaf-out dates may be largely dependent on a negative correlation between chilling requirement (CD_{req}) and thermal forcing requirement (GDD_{req}) at high latitudes [16], where higher CD_{req} or GDD_{req} lead to a longer period to fulfill these requirements and thus a lower S_T . To test the first mechanism, we analyzed the spatial distribution of annual and seasonal temperature variability that was defined as temperature variation during the year (MAT_{SD}) or during the period when temperature was statistically most relevant to leaf-out dates (Preseason T_{SD}); here, we determined the preseason as in Fu et al. [16] (see Methods). Preseason length was estimated for each species at each site to increase the precision of preseason windows according to site conditions [24, 40] (Fig. S4). In line with a previous study [41], preseason length decreased latitudinally by $1.0 \pm 0.3 \text{ d } ^{\circ}\text{N}^{-1}$ ($P < 0.001$, Fig. 3c). We did not find a significant trend of Preseason T_{SD} with latitudes (Fig. 3b), but there was an increase in MAT_{SD} with latitude at a rate of $0.09 \pm 0.02 \text{ } ^{\circ}\text{C } ^{\circ}\text{N}^{-1}$ ($P < 0.001$, Fig. 3a). These results indicate that greater annual variance in temperature (MAT_{SD}) associates with lower phenological S_T .

To test the second mechanism, we estimated the chilling requirement (CD_{req}) and forcing accumulation (GDD_{req}) for spring leaf-out for each species at each site (see Methods), and found that average CD_{req} and GDD_{req} during the period 1980–2016 across all sites and species were $109 \pm 11 \text{ d}$ and $140 \pm 62 \text{ } ^{\circ}\text{C d}$, respectively. CD_{req} in-

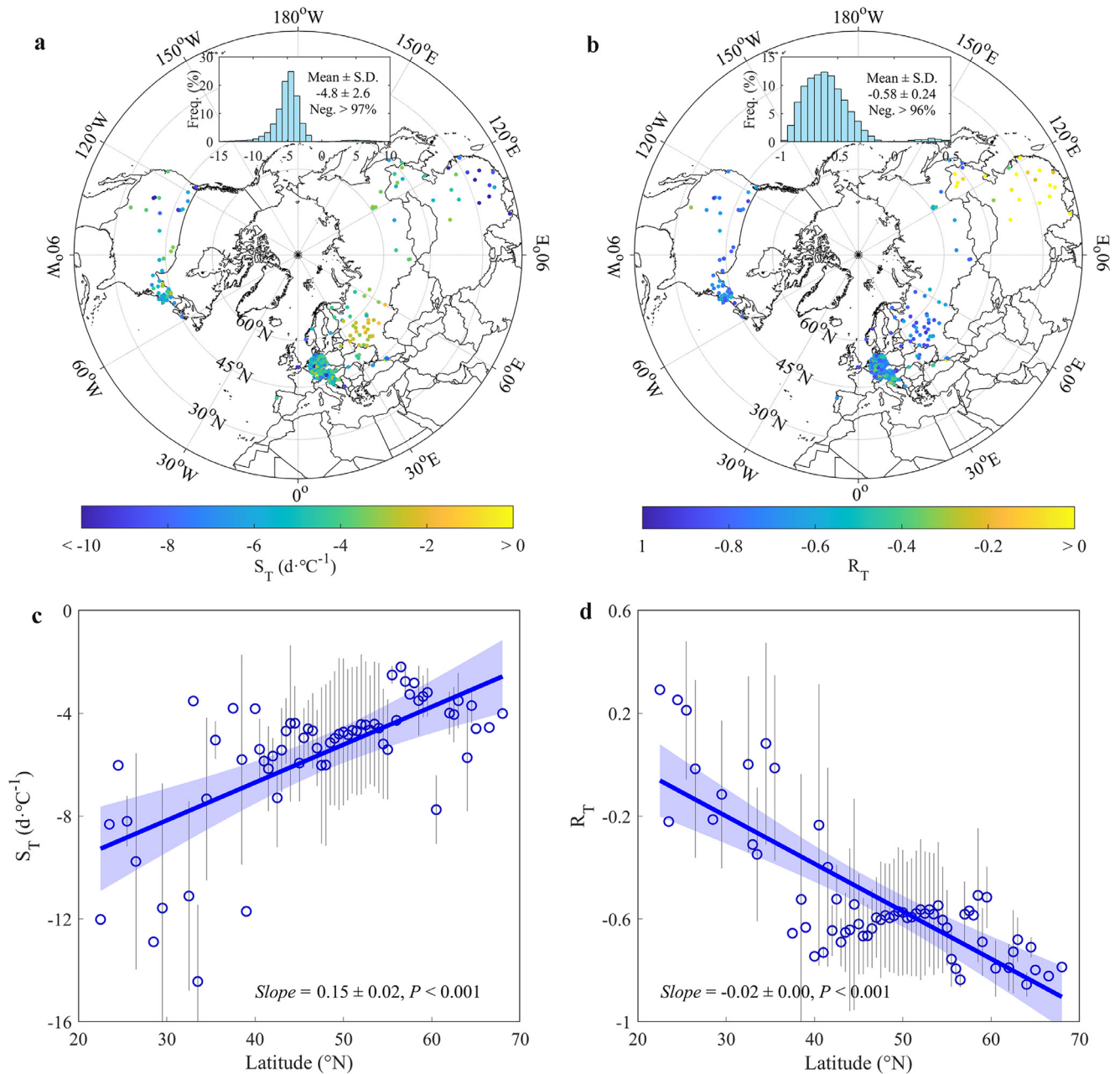


Fig. 2. Spatial patterns of apparent temperature sensitivity (S_T) of leaf-out and association with spring temperature (R_T). (a) and (b) Spatial distribution of S_T and R_T , respectively, and associated frequency distributions across sites and species (subpanels). (c) and (d) Linear regression analysis of latitudinal variation in S_T and R_T , respectively. All data were averaged per $0.5 \text{ } ^\circ C \cdot N^{-1}$. The shaded areas represent 95% confidence intervals and error bars are $1 \times SD$ of site data. S_T was defined as the advance of leaf-out date per $1^\circ C$ of rising air temperature and determined by reduced major-axis regression; R_T was determined by the partial correlation between leaf-out date and pre-season mean air temperature, after removing confounding effects of pre-season precipitation and radiation (see Methods).

creased with increasing latitude and the reverse was found for GDD_{req} (Fig. 3d). These results clearly indicate that plants at higher latitudes have greater chill tolerance and have lower thermal requirements to break dormancy. Over the study period, CD_{req} decreased at lower latitudes ($< 45^\circ N$), but increased at higher latitudes (Fig. 3e). Such contrasting temporal trends with latitude-dependent were, however, not observed in GDD_{req} , which remained unaltered along the latitudinal gradient (Fig. 3e). These findings indicate that the spatial difference in S_T is probably caused by the long-term ecological fitness responses of plants to local climate conditions by altering chilling and GDD requirements [18, 42, 43], and plants living in high latitudes tended to be characterized by conservative growth strategies [20, 44].

We found reductions in CD_{req} due to climate warming at lower latitudes, but no change in GDD_{req} (Fig. 3e). This might indicate the potential roles of other environmental factors in driving spring leaf-out at these lower latitudes compared to higher latitudes where effects of temperature may dominate [2, 19, 45]. These findings appear to support the second “non-temperature dominant hypothesis”. To further explore this hypothesis, we estimated the effects of photoperiod and water availability on spring phenology. Zohner et al. [22] provided an indirect approach to reveal photoperiod effects when direct evidence is limited. This indirect approach assumes that when leaf-out is strongly influenced by photoperiod, there is little variation in phenological dates; accordingly, we calculated the inter-annual variation in leaf-out dates as the SD of leaf-out dates during the study period (Std_{LO} , see Methods). This anal-

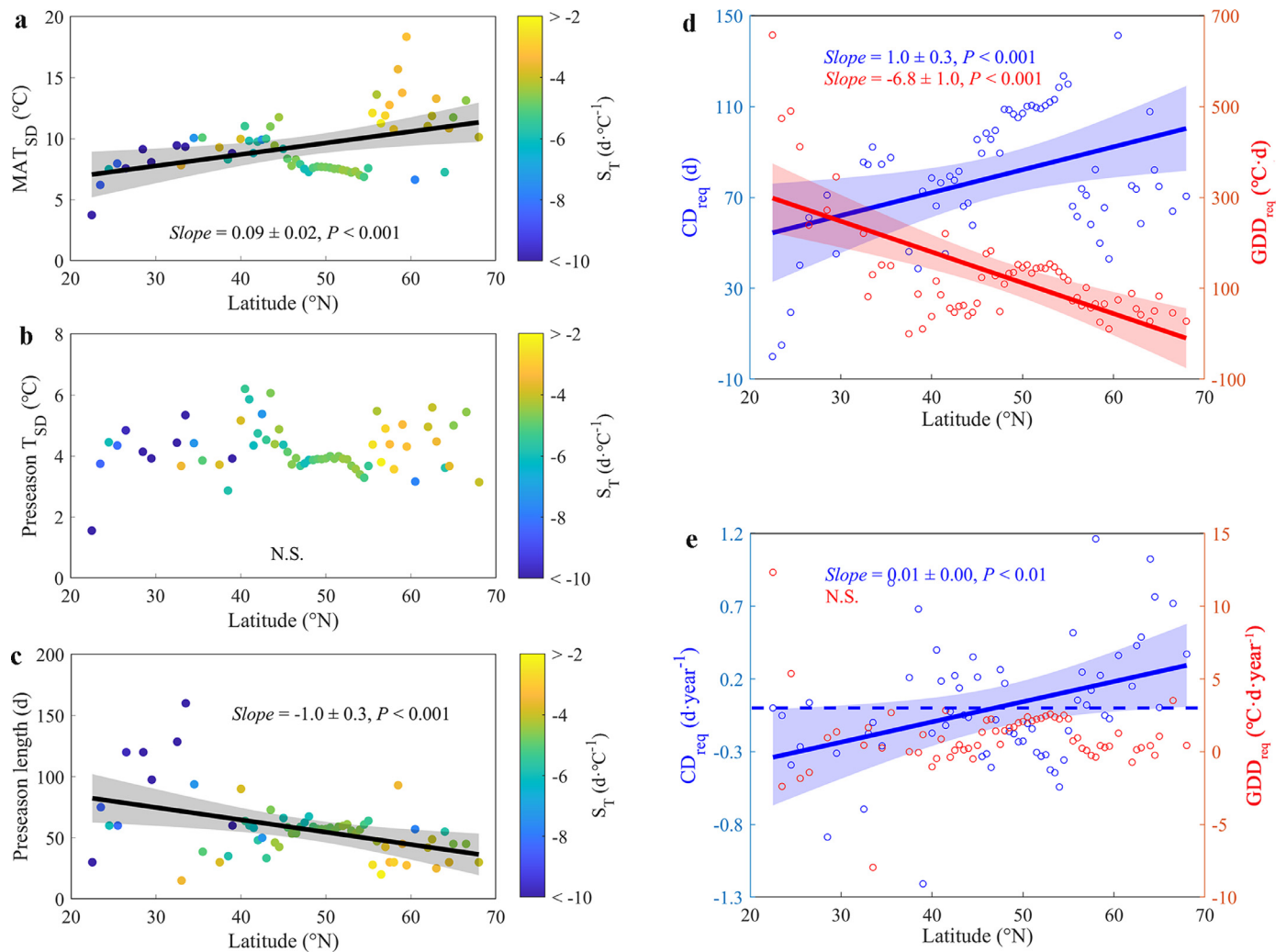


Fig. 3. Latitudinal trends in major temperature-related variables. (a) Annual temperature variability (MAT_{SD}). (b) Preseason temperature variability ($Preseason T_{SD}$). (c) Preseason length. The color codes in (a)–(c) represent the apparent temperature sensitivity of leaf-out (S_T). (d) Chilling requirement (CD_{req} , left axis) and thermal forcing requirement (GDD_{req} , right axis). (e) Temporal changes in CD_{req} and GDD_{req} and the dash line indicates no change in CD_{req} during the period 1980–2016. Data were averaged per $0.5^\circ N^{-1}$, the shaded areas represent 95% confidence intervals, and “N.S.” indicates no significant changes.

ysis showed that Std_{LO} at higher latitudes was smaller than at lower latitudes (Fig. 4a), suggesting that photoperiod likely does not explain the higher levels of S_T at lower latitudes. However, we cannot exclude the effects of photoperiod, due to a lack of direct evidence. Although studies have reported that under continued future climate warming, leaf-out may become earlier and therefore less sensitive to temperature because of the shortening day length of these advanced days [17, 46–48], the latitudinal differences in photoperiod effects on spring phenology remain unclear and require further investigation.

We further tested the possible influence of potential water availability on species' leaf-out across latitudes, based on levels of total preseason precipitation (P_{sum} , Fig. 4b). We examined the relation between S_T and P_{sum} , and found decreasing S_T with increasing P_{sum} , at a rate of $-3.1 \pm 1.1 d \cdot ^\circ C^{-1} 10^3 mm^{-1}$ (Fig. 4c). We also estimated site-level partial correlations between latitude and R_p (Fig. S5), and interestingly, we found that P_{sum} correlated with leaf-out date (R_p), but only at lower latitudes ($< 45^\circ N$, Fig. 4d). This could indicate that P_{sum} co-determines temperature responses of spring phenology at lower latitudes and increasing levels of precipitation contribute to a weaker correlation between temperature and spring phenology. The same spatial pattern of the precipitation effect on spring phenology has also been reported in subtropical China [49]. Earlier leaf-out might increase water stress for spring

growth, but sufficient rainfall at low latitudes may offset this negative effect [50].

For regional and global modelling, it is common to use a uniform temperature relationship for determining spring phenology [16, 51], and neglect its spatial heterogeneity. The differences that we observed in temperature sensitivity and correlations between spring phenology and temperature at lower and higher latitudes implies that other environmental factors, i.e. preseason precipitation, should be applied in large scale phenology modeling but its important role is spatial specific. Furthermore, the amplified warming in the high latitudes could mean that although with less S_T as we reported, and complicated spatial differences in the CD_{req} and GDD_{req} , the larger increase in temperature magnitude could potentially smooth the spatial differences in terms of the advance of spring leaf-out. With predicted future warming and more frequent and intensive drought in the northern hemisphere [11], the estimation accuracy of spring leaf-out becomes more and more essential, because the advance of leaf-out can largely influence the available water during the following growing season [52, 53] and thus play its substantial role in determining ecosystem water and carbon budgets. Besides, it is undeniable that the effects of genetic and evolutionary (e.g. phylogeny [54, 55]), other environmental factors (e.g. temperature threshold [56], diurnal and night temperature [57–59]), as well as leaf senescence [60,

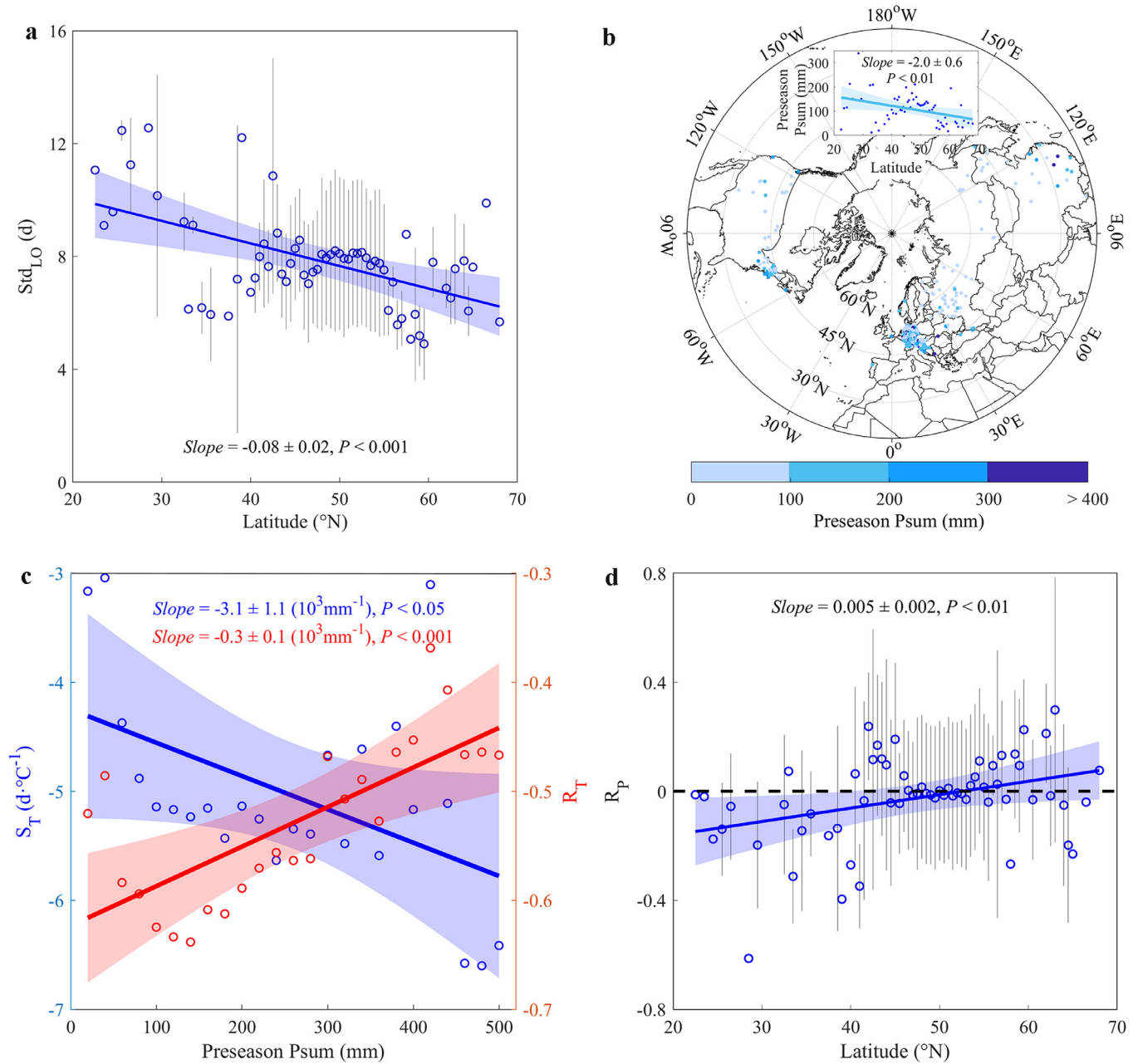


Fig. 4. Evidence for photoperiod and precipitation effects on apparent temperature sensitivity and their association with leaf-out dates. (a) Latitudinal changes in inter-annual variation of leaf-out dates (Std_{LO}). (b) Spatial pattern of cumulative preseason precipitation (Psum) and latitudinal variation in Psum (subpanel). (c) Apparent temperature sensitivity (S_T) and partial correlation between leaf-out date and preseason temperature (R_T) in relation to Psum. (d) Partial correlation between leaf-out dates and Psum (R_P). Data in (a), subpanel of (b), and (d) were averaged per $0.5^{\circ}N^{-1}$, and error bars are $1 \times SD$ of site data; the dashed line in (d) indicates the zero line. Data in (c) were averaged per 20 mm increase in Psum. Shaded areas represent 95% confidence intervals.

61] on spring phenology exist objectively, and further studies on the spatial patterns and underlying mechanisms are of great necessity to be further studied.

4. Conclusion

Using massive in situ observation data, our results revealed lower sensitivity levels of spring leaf-out to temperature, but stronger associations with the temperature at higher latitudes in the northern hemisphere. We found that this spatially heterogeneous phenological response to climate change is a result of long-term adaption to annual temperature variations and spatial differences in environmental conditions. At higher latitudes with a colder climate, spring leaf-out variation

is primarily determined by temperature, whereas at lower latitudes, it is co-determined by temperature and other environmental cues, such as precipitation. It is likely that spatial heterogeneity of temperature sensitivity will lead to spatial variation in temporal trends of spring leaf-out, with implications for species distributions and ecosystem carbon and water balances. Our findings also provide evidence of the impacts of precipitation on the apparent temperature sensitivity of spring leaf-out at lower latitudes. Under future climatic conditions, it is therefore important to quantify the interacting effects between temperature and precipitation on shifting spring phenology, and reveal the underlying mechanisms by conducting experiments and investigations in different regions to further improve the performance of phenological module in regional and global modeling and the assessments of the impacts on

ecosystem carbon, water, and energy exchanges with the atmosphere. Besides, in terms of the meaningfully representative of sites and species, we recommend strengthening the construction of phenological observation networks and providing continuous data services for scientific research.

Declaration of Competing Interest

The authors declare that they have no conflicts of interest in this work.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.fmre.2021.11.035](https://doi.org/10.1016/j.fmre.2021.11.035).

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