

# Poleward shifts in the maximum of spring phenological responsiveness of *Ginkgo biloba* to temperature in China

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## Summary

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Received: 23 May 2023  
Accepted: 5 August 2023

*New Phytologist* (2023) **240**: 1421–1432  
doi: 10.1111/nph.19229

**Key words:** chilling accumulation, climate change, *Ginkgo*, spatial variation, species distribution, spring phenology.

- Global warming is advancing the timing of spring leaf-out in temperate and boreal plants, affecting biological interactions and global biogeochemical cycles. However, spatial variation in spring phenological responsiveness to climate change within species remains poorly understood.
- Here, we investigated variation in the responsiveness of spring phenology to temperature (RSP; days to leaf-out at a given temperature) in 2754 *Ginkgo biloba* twigs of trees distributed across subtropical and temperate regions in China from 24°N to 44°N.
- We found a nonlinear effect of mean annual temperature on spatial variation in RSP, with the highest response rate at c. 12°C and lower response rates at warmer or colder temperatures due to declines in winter chilling accumulation. We then predicted the spatial maxima in RSP under current and future climate scenarios, and found that trees are currently most responsive in central China, which corresponds to the species' main distribution area. Under a high-emission scenario, we predict a 4-degree latitude shift in the responsiveness maximum toward higher latitudes over the rest of the century.
- The identification of the nonlinear responsiveness of spring phenology to climate gradients and the spatial shifts in phenological responsiveness expected under climate change represent new mechanistic insights that can inform models of spring phenology and ecosystem functioning.

## Introduction

Plant phenology exerts controls on global carbon, water, and nutrient cycles, driving feedbacks to the climate system (Bonan, 2008; Peñuelas *et al.*, 2009; Richardson *et al.*, 2013; Piao *et al.*, 2019). Anthropogenic climate warming has led to an unprecedented advancement in spring phenology since the 1980s (Menzel *et al.*, 2020; Vitasse *et al.*, 2022), affecting species distributions (Chuine & Beaubien, 2001), trophic interactions (Renner & Zohner, 2018), and the functioning of ecosystems (Keenan *et al.*, 2014; Piao *et al.*, 2019). These temporal changes in spring phenology have received extensive scientific attention in recent decades (Fu *et al.*, 2015; Zohner *et al.*, 2020b), yet the spatial variation in the phenological responsiveness to climate change remains poorly understood (Gao *et al.*, 2020; Geng *et al.*, 2022; Zhang *et al.*, 2022).

Understanding of regional variation in spring phenological responses requires quantification of the relative importance of the different environmental mechanisms driving leaf-out. Winter

chilling, spring forcing, and photoperiod are regarded as the three main drivers of spring phenology (Piao *et al.*, 2019; Wolkovich *et al.*, 2022). While spring forcing triggers bud development directly, chilling affects leaf-out time indirectly by modulating the amount of forcing required to leaf-out (Wang *et al.*, 2020; Beil *et al.*, 2021). Photoperiod can additionally modulate the forcing requirements of trees, with longer days reducing the time to leaf-out (Way & Montgomery, 2015; Zohner & Renner, 2015; Fu *et al.*, 2019). Photoperiod limitation on spring leaf-out time is often more pronounced when buds receive insufficient chilling (Laube *et al.*, 2014; Zohner *et al.*, 2016). Despite a robust understanding of these overarching mechanisms that collectively determine leaf emergence in spring, it remains unclear whether, and how, the relative importance of each driver differs across broad spatial scales, which limits our capacity to predict regional variation in spring phenology. The lack of climate-manipulation experiments at large spatial scales (Peaucelle *et al.*, 2019; Wu *et al.*, 2022b) limits our knowledge of the responsiveness of spring phenology (RSP) to environmental gradients and of the

drivers of such variation. Full-factorial experiments to identify spatial variation in the phenological responsiveness under varying climate conditions will be integral to improving our understanding of the responses of plants to climate change and to facilitating ecosystem conservation (Rosemartin *et al.*, 2014; Ettinger *et al.*, 2022; Walde *et al.*, 2022; Wolkovich *et al.*, 2022).

Previous large-scale studies on geographic variation in spring phenology have been based on observational approaches using ground or satellite-derived phenology data (Vitasse *et al.*, 2018; Gao *et al.*, 2020; Zeng *et al.*, 2020; Geng *et al.*, 2022). These approaches highlight the considerable spatial variation in phenological shifts across latitudinal and altitudinal gradients. However, conflicting patterns have emerged from these investigations (Parmesan, 2007; Lapenis *et al.*, 2014; Wang *et al.*, 2015; Geng *et al.*, 2022), with spring phenological responsiveness in the temperate and boreal regions of the Northern Hemisphere (from 30°N to 90°N) decreasing with latitude in 66% of the region and increasing in the remaining 34% (Gao *et al.*, 2020). The background climate, including mean annual temperature (MAT), precipitation (MAP), and climate seasonality, has therefore been suggested as reliable predictor of the RSP to climate change across the Northern Hemisphere (Parmesan, 2007; Lapenis *et al.*, 2014). However, similar to latitudinal gradients, contrasting results have also been reported for how the RSP varies along temperature gradients, with some studies detecting decreases (Cook *et al.*, 2012), increases (Wu *et al.*, 2022a), or nonlinear changes in the phenological responsiveness (Shen *et al.*, 2014) along temperature gradients. This lack of consensus in the effects of regional climate on the RSP limits our ability to forecast future ecological responses to climate change.

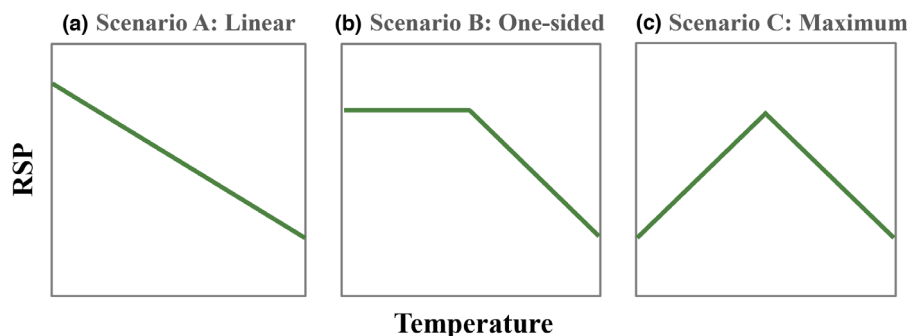
Large-scale observational approaches have provided valuable insights into phenological responsiveness to climate change, but they fall short in determining the causality or mechanisms underlying these trends (Cleland *et al.*, 2007; Peaucelle *et al.*, 2019). Therefore, manipulative experiments are necessary to identify the unifying mechanisms that can provide confidence in spatial predictions and overcome the spatial idiosyncrasies in previous studies. However, such experiments have been limited to narrow

geographic ranges (Wu *et al.*, 2022b), and so we lack the data to disentangle the drivers of spring phenological changes across broad latitudinal gradients. To address this gap, we conducted a full-factorial climate-manipulation experiment on *Ginkgo biloba* L., a deciduous dioecious tree species, across a wide environmental gradient from subtropical to temperate regions (ranging from 24° to 44° latitude). We tested three main scenarios for how temperature RSP shifts along temperature gradients (Fig. 1): If chilling and/or photoperiod limitations increase linearly with temperature (Weinberger, 1950; Cannell & Smith, 1983; Zohner *et al.*, 2016), RSP will linearly decrease along temperature gradients (Linear response scenario; Fig. 1a). If there is an upper threshold for chilling accumulation, RSP will decline once temperatures become too warm to induce chilling responses (One-sided response scenario; Fig. 1b). Lastly, if chilling limitation increases toward warm and cold environments due to the existence of both lower and upper-temperature thresholds for chilling accumulation (Peaucelle *et al.*, 2019), RSP will decrease in both directions (response-maximum scenario; Fig. 1c).

## Materials and Methods

### Study species

*Ginkgo biloba* L. (hereafter referred to as *Ginkgo*) is a deciduous, dioecious, gymnosperm tree species (Major, 1967; Lin *et al.*, 2022). *Ginkgo* fossils date back to the Middle Jurassic *c.* 170 million years ago (Major, 1967). *Ginkgo* is one of the most widely distributed trees in China and is commonly planted in other regions of the world (Zhao *et al.*, 2019), making it a well-suited species for investigating environmental gradients in spring phenological responsiveness (RSP; Rasheid *et al.*, 2018; Wu *et al.*, 2022a). We derived information on the distribution of *Ginkgo* from PictureThis, an efficient plant identification tool capable of identifying various plant species, including flowers, leaves, and trees (<http://www.picturethisai.com/>). The species database within PictureThis contains a collection of human-recorded observations, providing a valuable resource for



**Fig. 1** Conceptual diagram of the responsiveness of spring phenology (RSP) to temperature along environmental gradients. We proposed and tested three main scenarios for how RSP may shift along spatial temperature gradients. (a) Chilling accumulation may be linearly related to temperature, predicting that RSP linearly decreases along temperature gradients (Scenario A, Linear response). (b) If the accumulation of chilling has an upper threshold, RSP should initially be stable and start to decrease when temperatures become too warm to induce chilling accumulation (Scenario B, One-sided response). (c) If the accumulation of chilling has lower and upper-temperature thresholds, then buds accumulate less chilling toward very warm and cold environments, and RSP will decrease in both directions (Scenario C, Response maximum).

acquiring data on both natural and cultivated occurrences of *Ginkgo* in China.

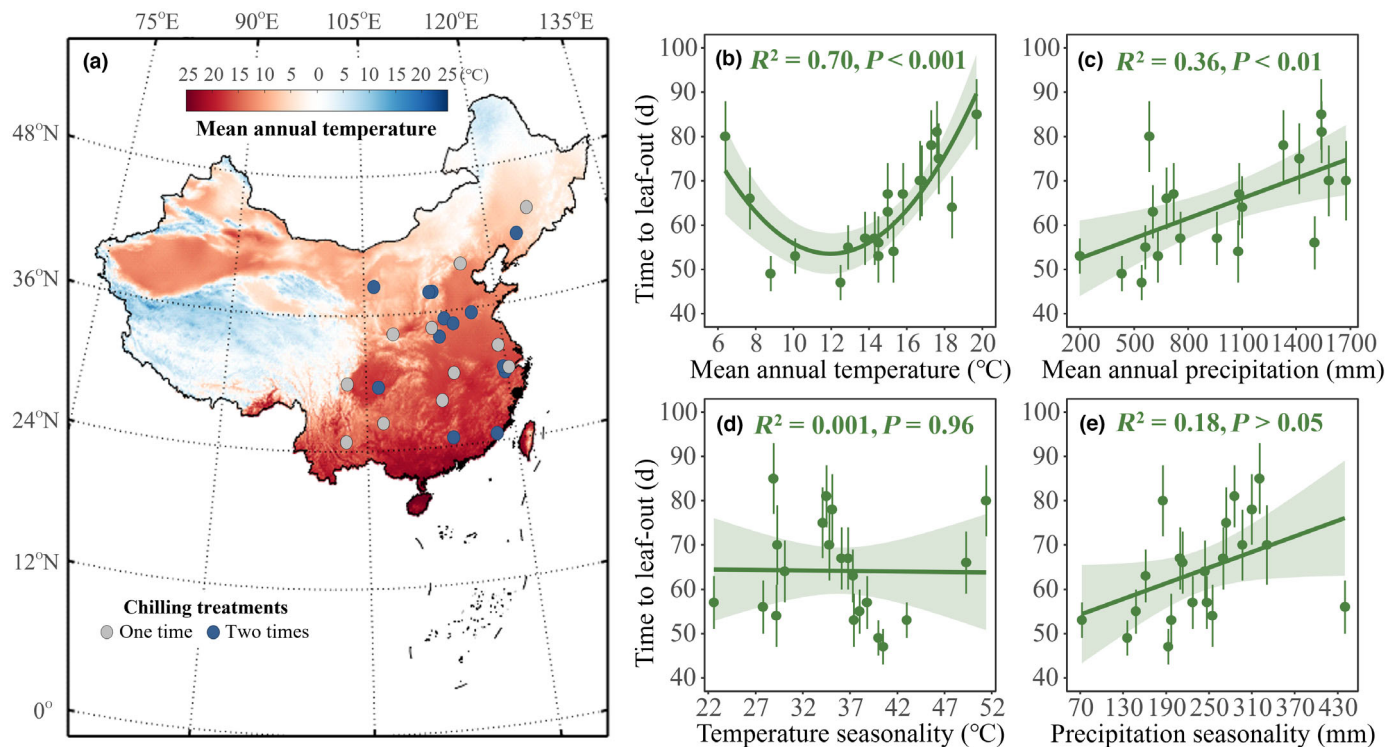
### Twig collection

The China Campus Phenology Observation Network (CCPON) was developed in 2020 and includes a total of 25 universities in China (updated in 2021), covering temperate and subtropical regions ranging from 24°N to 44°N and from 102°E to 125°E (Fig. 2a). We experimentally investigated the spatial variation in RSP by conducting a twig-cutting experiment using trees from all CCPON locations. For each location, we selected five adult males and five adult females with similar diameters at breast height (see more details in Supporting Information Table S1). Eight healthy twigs, each *c.* 40 cm in length, were sampled from the southern side of the canopy of each individual tree on 19 December 2021. We also collected twigs on 1 March 2022 at 11 of the 25 locations to represent a ‘high-chilling’ treatment in which trees had been exposed to outdoor winter conditions the entire winter (Fig. 2a).

In total, we collected 2754 twigs, which were disinfected using a commercial hypochlorite solution before placing them in 395 ml plastic bottles filled with 265 ml of cool tap water inside climate chambers. Every 1–2 wk, we recut the twigs by *c.* 2 cm at the base and changed the water in the bottles to avoid the occlusion of vessels.

### Experimental design

We conducted a full-factorial experiment, with two chilling, four temperature, and two photoperiod treatments in four climate chambers. The temperature of the control chamber ( $T_A$ ) followed historical (1979–2018) daily fluctuations of ambient spring (March) temperature at Beijing at 3-h intervals (Fig. S1). Temperatures in the other three chambers were 2°C, 5°C, and 10°C warmer than  $T_A$ . Each chamber was split into two parts using shade cloth, allowing us to apply two photoperiod treatments: daylengths of 10 and 14 h (Wu *et al.*, 2022a). Two chilling treatments were applied by collecting twigs early (19 December 19; Low chilling) and late (1 March 2022; High chilling) in winter to cause different exposure of twigs to outdoor winter conditions (Zohner *et al.*, 2016; Wang *et al.*, 2022). This setup had 16 treatment combinations (2 chilling  $\times$  4 temperature  $\times$  2 photoperiod treatments). The climate chambers were equipped with LED lights (Philips Greenpower LED Toplighting, Philips Lighting, Eindhoven, Netherlands), with an illuminance of *c.* 8944 lux (PPFD = 161  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). HOBO MX2202 temperature sensors (Onset Computer Corp., Bourne, MA, USA) were used to record the air temperature of each treatment every 30 min (Fig. S2). The average concentration of CO<sub>2</sub> and the relative air humidity in each chamber throughout the experiment was *c.* 440 ppm and *c.* 40%, respectively. The climatic conditions in the four chambers remained stable during the experiment, and



**Fig. 2** Effects of background climate on the responsiveness of spring phenology (RSP). The RSP is represented as the time to leaf-out after collection, and thus decreases with increasing time to leaf-out. (a) Mean annual temperature (MAT) in China and the distribution of sites included in the China Campus Phenology Observation Network. (b–e) Effects of MAT (b), mean annual precipitation (c), temperature seasonality (d), and precipitation seasonality (e) on leaf-out times across all environmental treatments. The points and error bars indicate the averages and SEs of leaf-out times across all environmental treatments, respectively. The trend line was fitted using linear or nonlinear regression models, with model effectiveness assessed using  $R^2$  and  $P$  value. The shaded area refers to the 95% confidence range of the fitted line.

the temperature did not differ significantly between the two photoperiod treatments.

### Phenological observations

We monitored the development of buds for each twig every 3 d. The date of leaf-out was defined as the date when the first bud scale had opened and the leaf was partially visible (Vitasse, 2013; Wu *et al.*, 2022b). We used the time to leaf-out, defined as the number of days from the start of treatment to the leaf-out date, to represent RSP, that is, the shorter the time to leaf-out, the higher the RSP. We calculated the leaf-out percentage of the twigs by dividing the number of twigs that achieved leaf-out by the total number of twigs collected at each site. In total, 85% (2346) of the collected twigs leafed out.

### Climate data

Climate data of China were derived from the China Meteorological Forcing Dataset (He *et al.*, 2020), which was developed by the Data Assimilation and Modeling Center for Tibetan Multi-spheres, Institute of Tibetan Plateau Research, Chinese Academy of Sciences (<http://data.tpdc.ac.cn/en/data/8028b944-daaa-4511-8769-965612652c49/>). Temperature and monthly precipitation at 3-h intervals and a spatial resolution of 0.1° from 1979 to 2018 were used to represent regional climate conditions, that is MAT, MAP, and the seasonalities of temperature and precipitation. Temperature seasonality was calculated as the difference between the highest and lowest daily temperature in a year, and precipitation seasonality was calculated as the difference between the highest and lowest monthly precipitation in a year. The daily temperatures for 2021 and 2022 at the collection sites were obtained from the NOAA National Center for Environmental Information (<https://ngdc.noaa.gov/>).

Predictions of future climate came from the Coupled Model Inter-comparison Project (CMIP6, <https://esgf-node.llnl.gov/projects/cmip6/>). We used three general circulation models (GCMs, including CAS-ESM2-0, CESM2-WACCM, and MRI-ESM2-0) under two emission scenarios (SSP1-2.6 and SSP5-8.5) to represent low-emission (low radiative forcing level with a peak at 2.6 W m<sup>-2</sup>) and high-emission (strong radiative forcing level with a peak at 8.5 W m<sup>-2</sup>) pathways, respectively. The multi-model ensemble means of the three CMIP6 models were used to obtain monthly near-surface air temperature and monthly precipitation for each year from 2081 to 2100.

### Data analysis

Accumulated chilling days were calculated as the number of days when the daily temperature was between 0°C and 7°C from 1 September 2020 to the start date of the experiment (Peaucelle *et al.*, 2019; Wang *et al.*, 2020). We also used another common temperature range between 0°C and 5°C to calculate the accumulation of chilling. The extent of chilling limitation was calculated based on the leaf-out difference (in days) between the twigs cultivated under low (early collection) and high chilling (late

collection), and the extent of photoperiod limitation was calculated using the leaf-out difference between the twigs cultivated under short- and long-day conditions. The heat requirement (growing degree days, GDD) of each twig to achieve leaf-out was calculated using a sigmoidal function:

$$\text{GDD} = \sum_{\text{Start}}^{\text{Leaf-out}} \begin{cases} 0 & \text{if } T_{\text{day}} < T_{\text{base}} \\ \frac{28.4}{1 + e^{-0.185(T_{\text{day}} - 18.4)}} & \text{if } T_{\text{day}} \geq T_{\text{base}} \end{cases}$$

where  $T_{\text{day}}$  is the mean daily temperature from 1 November to the leaf-out date (including both field and indoor conditions), and  $T_{\text{base}}$  is the base temperature of 0°C following ref (Wang *et al.*, 2022).

The spatial variation in RSP and the limitations in winter chilling and photoperiod along gradients of MAT, MAP, and the seasonalities of temperature and precipitation were estimated using linear or nonlinear regression analysis. The model equation for linear regression is of the form:  $Y = \beta_0 + \beta_1 X + \epsilon$ . The model equation for nonlinear regression includes a quadratic term ( $\beta_2 X^2$ ) to account for nonlinear patterns in the data:  $Y = \beta_0 + \beta_1 X + \beta_2 X^2 + \epsilon$ .  $Y$  is the dependent variable,  $X$  is the independent variable,  $\beta_0$ ,  $\beta_1$ , and  $\beta_2$  are the regression coefficients, and  $\epsilon$  represents the error term. The differences in RSP among and within the temperature, photoperiod, and chilling treatments were tested using paired  $t$ -tests.

### Spatial RSP model and future projections

We developed four RSP models based on the effect of regional climate on RSP, with climate factors as explanatory variables and RSP as response variable (Model 1: MAP as predictor; Model 2: MAT as predictor; Model 3: MAP and MAT as predictors; Model 4: MAT, MAP and temperature seasonality as predictors). The relative RSP ( $\text{RSP}_{\text{rel}}$ ) for each pixel was calculated as:

$$\text{RSP}_{\text{rel}} = \frac{\text{RSP}_{\text{min}}}{\text{RSP}_{\text{pred}}}$$

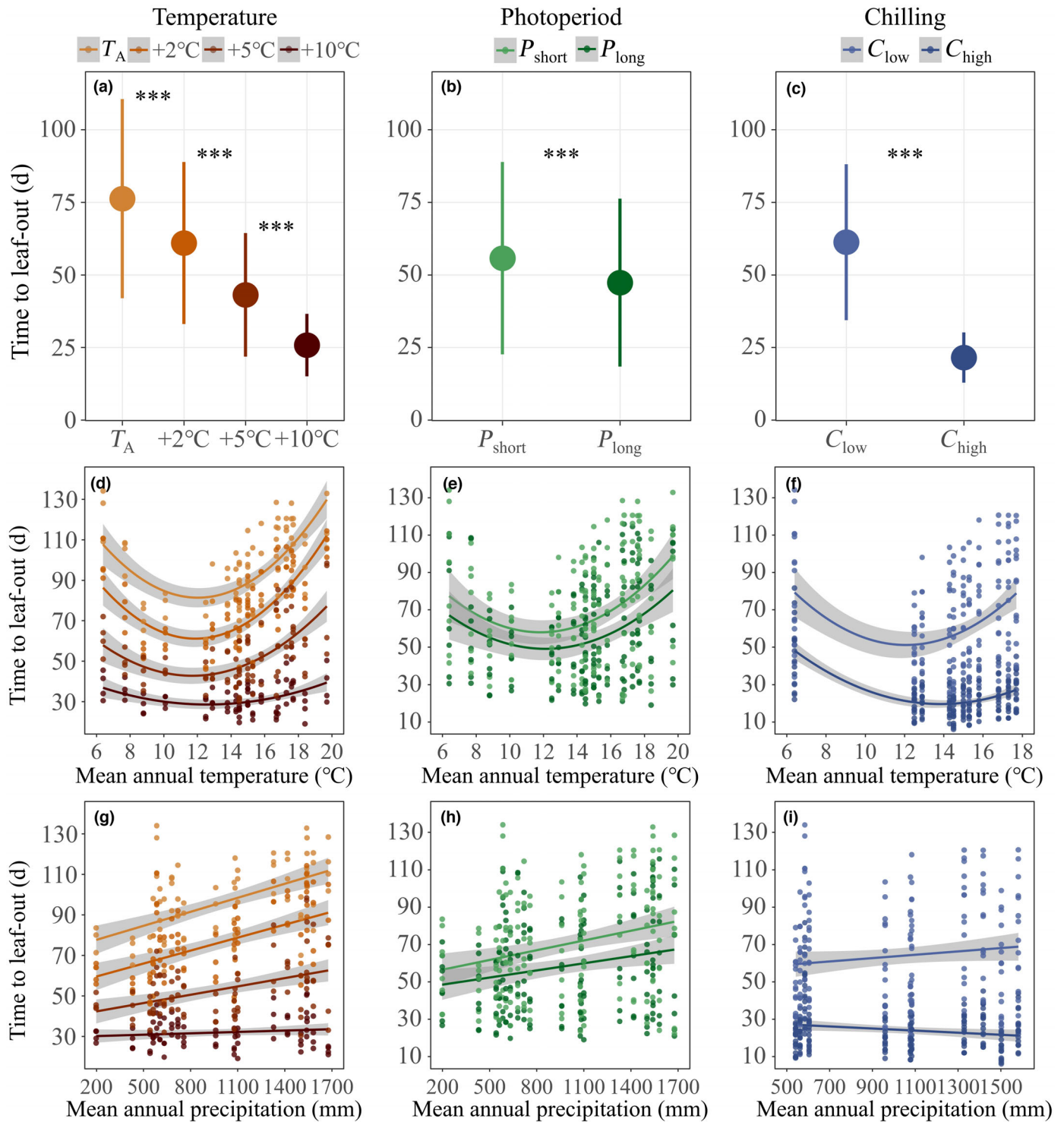
where  $\text{RSP}_{\text{pred}}$  is the predicted RSP and  $\text{RSP}_{\text{min}}$  is the minimum RSP across all sites.  $\text{RSP}_{\text{rel}}$  ranges from 0 to 1, with values close to 0 indicating low phenological responsiveness and values close to one indicating high responsiveness.

To project present and future  $\text{RSP}_{\text{rel}}$  across China, we used the multi-year average for 1979–2018 and the future climate expected for 2081–2100. All statistical analyses were conducted using R 4.2.2 and MATLAB R2021b.

## Results

### Spring phenological differences among treatments

Spring warming led to consistent advances in leaf-out timing (Fig. 3a), with leaf-out dates of twigs under the +2°C, +5°C, and +10°C temperature treatments occurring, on average



**Fig. 3** Effects of environmental treatments and background climate on the responsiveness of spring phenology (RSP). (a–c) Effects of the temperature (a), photoperiod (b), and chilling (c) treatments on the time to leaf-out. The points and error bars refer to the average and SD in each treatment. \*\*\*, Significant differences between treatments at  $P < 0.001$ . (d–i) Effects of mean annual temperature (MAT) and mean annual precipitation (MAP) on the RSP under different temperature, photoperiod, and chilling treatments, respectively. The RSP is represented as the time to leaf-out after collection, and thus decreases with increasing time to leaf-out. The trend line was fitted using either linear or nonlinear regression models, and the shaded area refers to the 95% confidence range of the fitted line.  $T_A$  refers to the control temperature treatment at the ambient air temperature; +2°C, +5°C, and +10°C refer to the 2°C, 5°C, and 10°C warming treatments;  $P_{long}$  and  $P_{short}$  refer to 14 and 10-h photoperiod treatments;  $C_{low}$  and  $C_{high}$  refer to the low and high-chilling treatments, respectively.

(mean  $\pm$  2 SE),  $15 \pm 1.6$ ,  $33 \pm 2.9$  and  $50 \pm 5.1$  d earlier than in the ambient temperature treatment. A long photoperiod (14-h) advanced leaf-out times by an average of  $8 \pm 1.0$  d compared with short photoperiod (10-h; Fig. 3b). Across all temperature treatments, short-day conditions delayed leaf-out, and this photoperiod limitation was most pronounced for the ambient temperature treatment (Fig. S3a). The date of collection (a proxy for chilling accumulation) also significantly affected leaf-out dates, with insufficient chilling delaying leaf-out by an average of  $39 \pm 3.0$  d (Fig. 3c). This chilling limitation was found for all temperature treatments, but the limitation was significantly lower for the warmer treatments (Fig. S3b): reduced chilling led to delays in leaf-out of  $61 \pm 4.1$ ,  $48 \pm 2.0$ ,  $31 \pm 3.4$ , and  $18 \pm 1.6$  d for the ambient,  $+2^\circ\text{C}$ ,  $+5^\circ\text{C}$ , and  $+10^\circ\text{C}$  temperature treatments, respectively. Photoperiod limitation on leaf-out time was more pronounced under the low chilling treatment, with long days advancing leaf-out by  $12 \pm 1.0$  d at low chilling and by only  $2 \pm 1.0$  d at high chilling (Fig. S3c).

### Spatial variation in the responsiveness of spring phenology

We identified considerable spatial variation in the RSP among collection sites, revealing a strong nonlinear dependency on site-specific MAT, with a maximum response at  $c. 12^\circ\text{C}$  and lower response rates at warmer or colder temperatures ( $P < 0.01$ , Fig. 2b). In addition, RSP decreased linearly along precipitation gradients ( $P < 0.01$ , Fig. 2c). Seasonality in temperature and precipitation did not significantly affect RSP ( $P > 0.05$ , Fig. 2d,e). We also analyzed the environmental gradients of RSP for each temperature, photoperiod, and chilling treatment to test whether these phenological differences among sites were consistent or depended on the treatment. The results showed consistent spatial patterns across all treatments (Figs 3d–i, S4). Only the magnitude of these spatial patterns varied among the treatments, with more pronounced spatial variation for the treatments with low temperature, short photoperiod, and low chilling (Fig. 3d–i). Site-level winter temperatures (the year before the twigs were collected) showed a similar relationship with leaf-out dates than MAT (Fig. S5). We also found a nonlinear relationship between site-specific MAT and the percentage of twigs that achieved leaf-out, with the leaf-out percentage decreasing toward very warm and cold sites (Fig. S6a). MAP did not significantly affect leaf-out percentage (Fig. S6b).

### Factors governing spatial variation in RSP

We used a common chilling model to analyze the effects of chilling accumulation before the twigs were collected on leaf-out time. These analyses indicated that higher chilling reduced the heat requirement for leaf-out, thus leading to earlier leaf-out dates (Figs S7a, S8a). Furthermore, we investigated the environmental gradients of chilling accumulation and chilling and photoperiod limitations on leaf-out time. We found a nonlinear relationship between chilling accumulation and MAT, with chilling first increasing and then decreasing with MAT (Fig. 4a). MAP was negatively correlated with chilling accumulation (Fig. 4b). These results remained similar when chilling was

defined as temperatures between  $0^\circ\text{C}$  and  $5^\circ\text{C}$  (Figs S7b, S8b, S9), and when using GDD to leaf-out instead of leaf-out dates as response variable (Fig. S7c,d). The effects of the chilling and photoperiod treatments on leaf-out also showed similar response patterns, first decreasing and then increasing along the MAT gradient, and increasing along the precipitation gradient (Fig. 4c–f).

### Mapping spatial variation in RSP

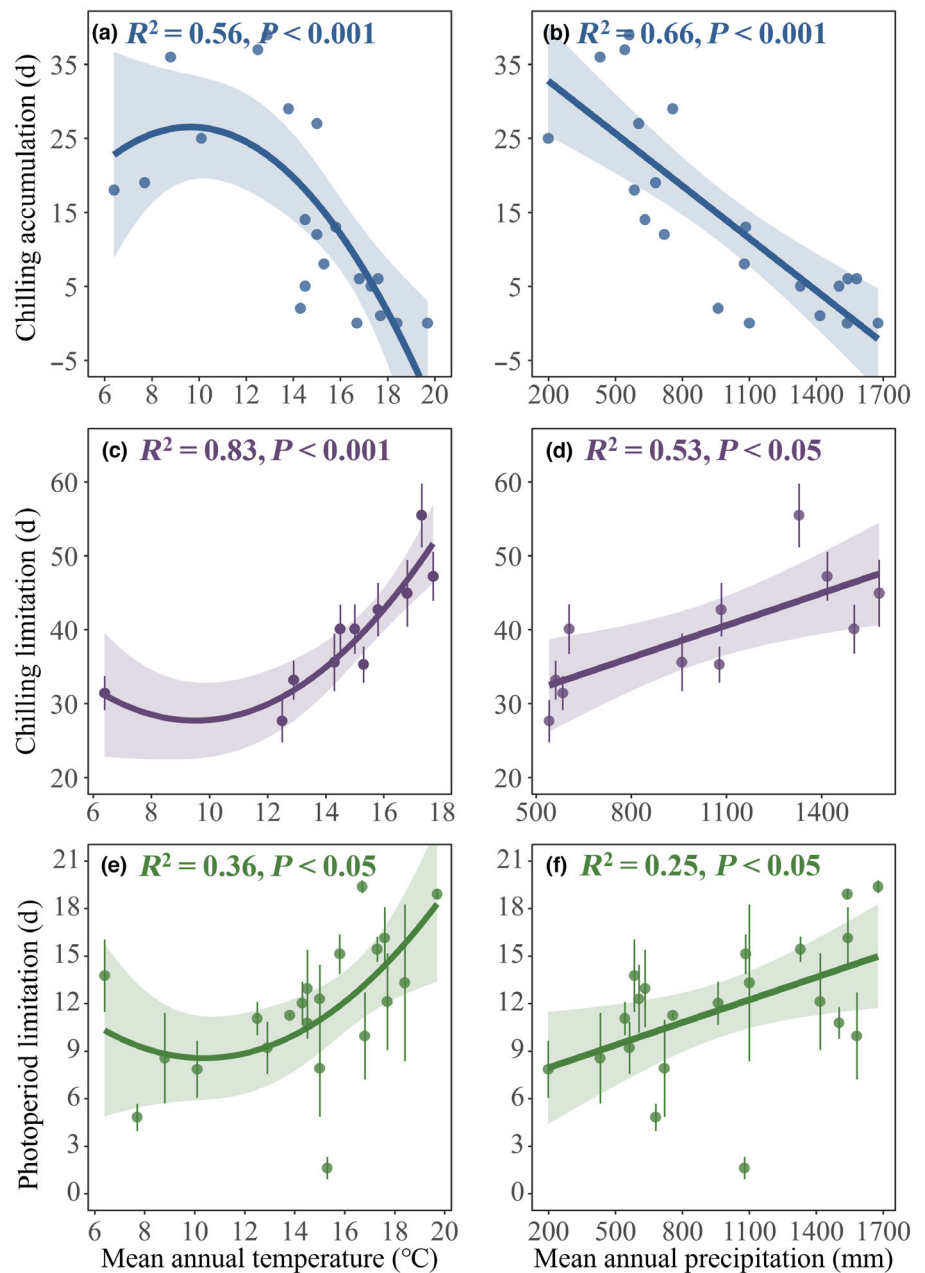
The full model (M4) had the best predictive performance ( $R^2_{\text{adj}} = 0.74$ , AIC = 132.64), and the M1 model, including only MAP, performed the worst ( $R^2_{\text{adj}} = 0.31$ , AIC = 150.18, Table S2). Based on the full model, we calculated the relative responsiveness of spring phenology (RSP<sub>rel</sub>) for each pixel by dividing the minimum RSP observed across all sites (RSP<sub>min</sub>) by RSP. We found that trees currently are most responsive in central China, consistent with the main distribution area of *Ginkgo* (Fig. 5a,b). Results were similar for the other models that included MAT as a predictor, that is models 2 and 3 (Fig. S10). Furthermore, we projected future shifts in RSP for the period from 2081 to 2100 using low- and high-emission scenarios from the Coupled Model Inter-comparison Project (CMIP6). These projections predict that RSP will exhibit an elevation-dependent increase, indicating that higher elevations will experience more pronounced phenological changes. Additionally, RSP is expected to decrease at low latitudes and increase at high latitudes (Fig. 5c–f). Accordingly, the responsiveness maximum is expected to shift toward higher latitudes in the future (Figs 5c,d, S11), by 1- and 4-degrees latitude under the low- and high-emission scenarios, respectively (Fig. S12).

### Discussion

Our large-scale experiment has provided valuable insights into the spatial variation of phenological responsiveness in temperate trees. The nonlinear relationship observed between phenological responsiveness and site-level MAT indicates that climate plays a crucial role in shaping the spatial dynamics of phenological sensitivity. This finding suggests that climate change will likely have an impact on the biogeographic distribution of spring phenological responsiveness. To further investigate this prediction, we used the experimental findings to develop models of phenological responsiveness. Our modeling results, considering a high-emission scenario, indicate that the maximum phenological responsiveness, currently observed in Central China, is projected to shift northward by  $c. 4$ -degree latitude over the course of the remaining century. These projections highlight the potential changes in the distribution of phenological responsiveness due to climate change, emphasizing the need for continued monitoring and adaptation strategies in the face of ongoing environmental shifts.

### Effects of the temperature, photoperiod, and chilling treatments on RSP

Our experimental results underscore the dominant effect of spring temperature on spring phenology (Rossi & Isabel, 2017;



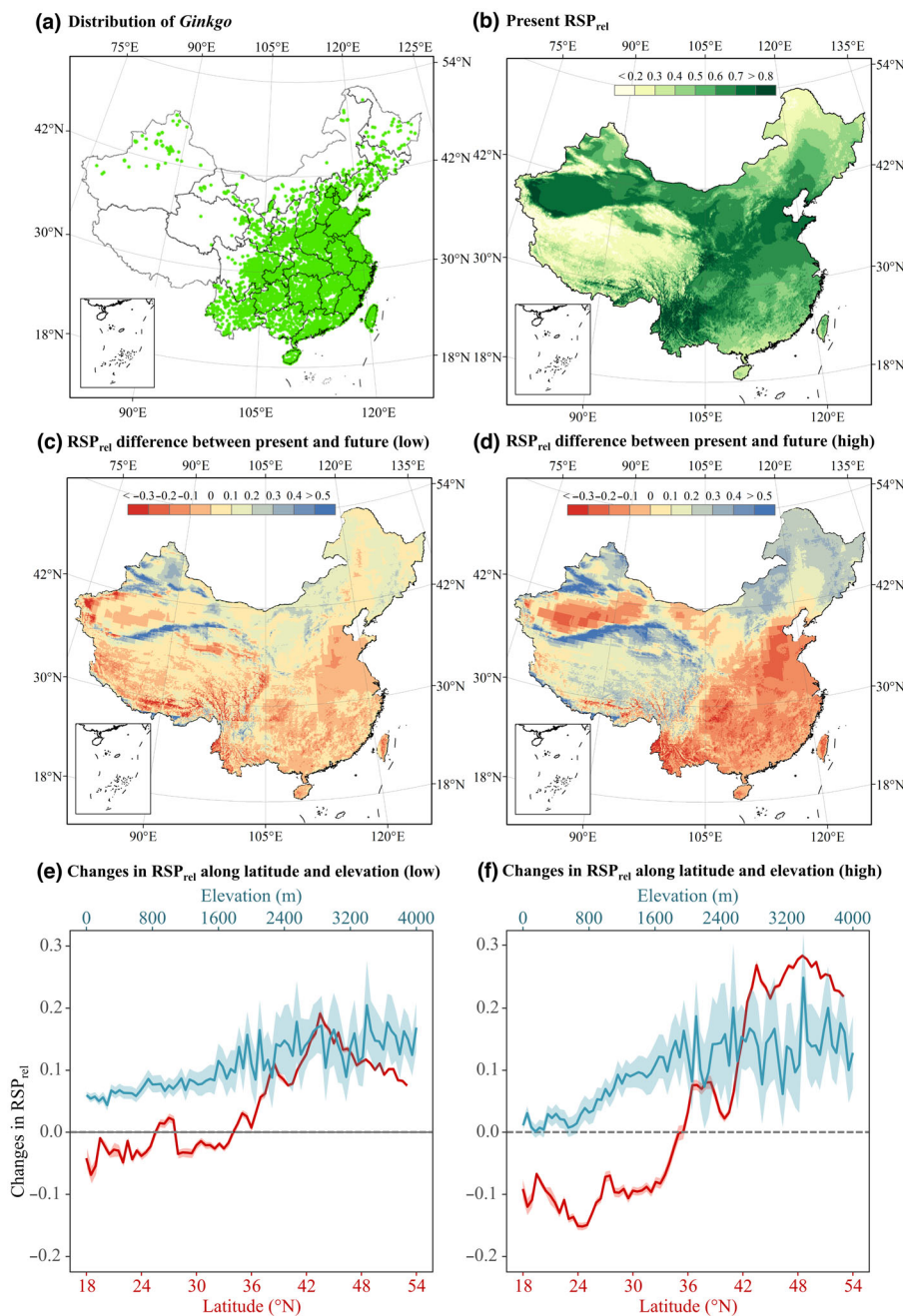
**Fig. 4** Roles of chilling and photoperiod limitation in driving environmental gradients in the responsiveness of spring phenology. (a, b) Effects of mean annual temperature (MAT) and mean annual precipitation (MAP) on winter chilling accumulation. (c–f) Effects of MAT and MAP on chilling and photoperiod limitations on spring phenology. The extent of chilling limitation was calculated based on the leaf-out difference (in days) between the twigs cultivated under low and high chilling, while the extent of photoperiod limitation was calculated using the leaf-out difference between the twigs cultivated under  $P_{short}$  and  $P_{long}$ . The points and error bars indicate the averages and SEs, respectively. The trend line was fitted using either linear or nonlinear regression models, with model effectiveness assessed using  $R^2$  and  $P$  values. The shaded area refers to the 95% confidence range of the fitted line.

Flynn & Wolkovich, 2018; Piao *et al.*, 2019; Vitasse *et al.*, 2022), with winter chilling and photoperiod modulating leaf-out. Reduced chilling accumulation during endodormancy increases the amount of heat required to induce leaf-out the next spring (Fu *et al.*, 2015; Walde *et al.*, 2022). Similarly, short photoperiods lead to higher heat requirements. We also identified an interaction between chilling and photoperiod requirements, with a stronger photoperiod limitation on spring leaf-out under low chilling. These mechanisms likely evolved as a safety strategy to avoid precocious leaf-out and frost damage to leaves under early warm spells (Liu *et al.*, 2018). Climate change is leading to warmer winters, and the resulting reduction in winter chilling and the shorter photoperiods when temperatures start to increase will likely lead to more pronounced constraints of chilling and

photoperiod in the future (Zohner *et al.*, 2016). Chilling and photoperiod requirements are thus expected to counteract increases in the risk of frost damage induced by climate warming (Chuine *et al.*, 2010; Basler & Körner, 2012; Zohner *et al.*, 2020a), and our results suggest that these constraints will be particularly pronounced at species' distribution limits (Fig. 5b).

#### Spatial variation of RSP

Our experiment revealed a tight link between climate and the spatial variation in RSP. The nonlinear relationship between RSP and MAT supports the response-maximum scenario (Scenario C in Fig. 1). Phenological responsiveness was found to be highest at



**Fig. 5** Projections of the present and future distributions of the relative responsiveness of spring phenology ( $RSP_{rel}$ ). (a) Geospatial distribution of *Ginkgo* in China. The green dots indicate the natural and cultivated occurrences of *Ginkgo* in China each dot represents a  $0.1 \times 0.1^\circ$  grid that contains at least three records. (b) Present  $RSP_{rel}$  across China, calculated using the full model (M4) based on the multi-year average mean annual temperature (MAT), mean annual precipitation (MAP), and temperature seasonality for the period 1979–2018. (c, d)  $RSP_{rel}$  shifts from the present to the future across China. The future  $RSP_{rel}$  across China for the period from 2081 to 2100 was based on climate projections by the general circulation models (GCMs) of the Coupled Model Inter-comparison Project (CMIP6) under two greenhouse gas emission scenarios, SSP2-4.5 (c, low emission) and SSP5-8.5 (d, high emission). (e, f) Changes in future  $RSP_{rel}$  compared with the present under the low (e) and high (f) emission scenarios. Means  $\pm$  95% confidence intervals are shown for each  $0.5^\circ$  latitude and each 50 m elevation interval.

sites with a MAT of  $\approx 12^\circ\text{C}$  and decreased toward warmer or colder sites (Fig. 2b). Our analyses further allowed us to test the idea that these patterns are due to an optimum temperature range for chilling accumulation, such that buds accumulate less chilling in very warm and cold environments. It is likely that this may ultimately be the result of adaptive strategies to avoid frost damage and maximize growth (Zohner *et al.*, 2020a).

The nonlinear relationship between RSP and MAT suggests that chilling accumulation has an optimum temperature range, with chilling requirements not being met once temperatures become too low or too high (Fu *et al.*, 2015; Peaucelle *et al.*, 2019). We found strong evidence to suggest that chilling indeed had a strong positive effect on RSP (Fig. S8) and that high

levels of chilling reduced the heat requirement for leaf-out (Fig. S7a,b). We also found a strong, nonlinear correlation between chilling and MAT (Fig. 4a), while chilling accumulation linearly decreased with MAP (Fig. 4b), matching the idea that winter chilling drove the observed spatial relationships between RSP and climate.

If chilling accumulation decreases toward cold and warm locations, then the limitations of chilling and photoperiod on spring phenology should nonlinearly depend on MAT. This is because the sensitivity to variation in both winter chilling and photoperiod should be highest in plants that have experienced the least amount of chilling before the collection. Based on the photoperiod and chilling treatments, we quantified the extent of chilling

and photoperiod limitation as the difference in the time to leaf-out between treatments. Both chilling and photoperiod limitation on spring leaf-out matched the relationships between the RSP and MAT or precipitation (Fig. 4c–f). Chilling and photoperiod limitation were nonlinearly correlated with MAT, and positively linearly correlated with MAP, consistent with the environmental gradients in phenological responsiveness. Previous studies have indicated that photoperiod limitation on spring leaf-out increases with MAT, because decreases in chilling accumulation toward warmer regions will lead to higher photoperiod sensitivity (Zhang *et al.*, 2007; Zohner *et al.*, 2016; Wu *et al.*, 2022b). Our study now provides evidence that photoperiod limitation may also increase toward cold regions, where temperatures are regularly below the effective chilling temperature range. Our experiment thus suggests nonlinear responses of chilling and photoperiod along temperature gradients, with very low and high winter temperatures increasing both photoperiod and chilling limitation.

Phenological plasticity and environment-induced local adaptation have been recognized as important factors contributing to the variation in forcing requirements for leaf-out among trees in different climatic conditions (Vitasse *et al.*, 2010; Firmat *et al.*, 2017). These factors might therefore contribute to the observed spatial variation in RSP among tree populations. However, it is important to note that natural populations of *Ginkgo* are rare and limited to specific areas, while the majority of *Ginkgo* trees in China are cultivated and genetically similar (Zhao *et al.*, 2019). Therefore, genetic adaptation is unlikely to be the primary driver of the observed effects, especially considering the relatively short time frame (hundreds of years) since the cultivation of *Ginkgo* trees in China.

However, over several decades, trees may exhibit phenological plasticity in response to their specific growing conditions, which can influence the spatial patterns of phenological responsiveness. In colder regions with greater temperature variability, trees may have responded to these unstable temperature conditions by reducing their RSP (Lechowicz, 1984; Wang *et al.*, 2014). Moreover, there is a trade-off between maximizing the length of the growth season and avoiding frost damage (Zohner *et al.*, 2020a). In warm areas, the higher risk of late spring frosts (Zohner *et al.*, 2020a) may contribute to a decrease in RSP as a strategy to mitigate potential frost damage. To achieve this, trees adapted to warmer climates may exhibit greater sensitivity to photoperiod limitation, resulting in a lower RSP (Zohner *et al.*, 2016; Wu *et al.*, 2022b).

### The relative responsiveness of spring phenology within species

Previous research has shown spatial variation in RSP within species. While some studies have indicated that individuals are phenologically most responsive at the northern limits of their distribution ranges (Morin *et al.*, 2009), others have suggested that populations are most responsive at lower latitudes, possibly allowing them to compete against southern plants that might expand northward under climate warming (Clark *et al.*, 2014).

Our experimental analysis on the climatic controls of RSP indicated that phenological responsiveness followed a nonlinear pattern along MAT and a linear response to MAP. Our RSP model considering these mechanisms suggested that trees are currently most responsive in central China, coinciding with the main distribution area of *Ginkgo* (Fig. 5a,b). The ability of trees to achieve leaf-out also decreased toward the upper and lower limits of their distribution range (Fig. S6), likely due to insufficient chilling.

We also found that the responsiveness maximum of spring phenology is expected to shift toward higher latitudes and elevations in the future under both low- and high-emission scenarios (Fig. 5c,d). Spatial shifts in the phenological responsiveness may thus co-occur with northward expansions of the range limits of species under climate warming (Walther *et al.*, 2002; Hamann & Wang, 2006), which could buffer species against increased risks of frost damage (Chuine & Beaubien, 2001). Under the high-emission scenario, Northeast China is projected to be the phenologically most sensitive area by the end of the century, and such changes should be taken into account when developing ways to maintain and stabilize ecological functions of the forests in these regions (Wu *et al.*, 2019; Luo *et al.*, 2020).

An essential aspect to consider is the level of local adaptation in driving the observed spatial patterns in RSP. Given the high genetic similarity among cultivated *Ginkgo* trees (see also 'Spatial variation of RSP' in the Discussion section), it is unlikely that adaptation alone can account for the results. However, it is important to note that if the phenological responses were adaptive, the changes would occur at a much slower rate than what is modeled in this study. Consequently, rapid changes over the next century would not be expected. The future responses predicted in this study are based on the assumption that all intra-species responses are nonadaptive and solely influenced by environmental factors. In reality, the presence of adaptation would likely slow down the predicted changes.

### Conclusion

Our large-scale climate-manipulation experiments have shed light on the crucial role of regional climate in determining the phenological responsiveness of temperate trees. These findings are based on a widespread Asian species, and future experimental investigations will be essential for examining these mechanisms in other species and biogeographic regions. We have presented evidence demonstrating that the relationship between temperature and chilling accumulation follows a nonlinear pattern, which drives spatial variation in phenological responsiveness. This discovery contributes new insights into our understanding of phenological changes under climate change. By incorporating these nonlinear phenological responses, we can enhance the accuracy of vegetation models, potentially leading to more precise predictions of growing season lengths and carbon uptake in a changing climate. Our model suggests that the phenologically most sensitive area aligns with the main distribution of *Ginkgo* trees, and we predict northward and upward expansions of this responsiveness

maximum for the future. However, it is important to note that our models of biogeographic shifts in phenological responsiveness do not consider population-level adaptation to local climate conditions, which could potentially slow down future changes. Nonetheless, these phenological shifts may play a key role in driving and facilitating northward range expansions of tree species under climate change.

## Acknowledgements

The work was supported by the National Science Fund for Distinguished Young Scholars (42025101), the International Cooperation and Exchange of the National Natural Science Foundation of China-FAPESP Program (Grant no. 42261144 755), the joint fund for regional innovation and development of NSFC (U21A2039) and the 111 Project (B18006). ZW was funded by the China Scholarship Council (no. 202206040112). CMZ was funded by the Ambizione grant PZ00P3\_193646. TWC was supported by DOB Ecology and the Bernina Foundation. Y-PZ was supported by the National Natural Science Foundation of China (no. 31870190). JP research was supported by TED2021-132627B-I00 and PID2022-140808NB-I00 grants funded by the Spanish MCIN, AEI/10.13039/European Union NextGenerationEU/PRTR, the Fundación Ramón Areces project CIVP20A6621 and the Catalan government grant SGR221-1333. We thank the China Campus Phenology Observation Network (CCPON, <http://campus.nsii.org.cn/>) and student teams from Zhejiang University, Guizhou University, Henan University of Urban Construction, Henan University, Henan University of Science and Technology, Henan Normal University, Hunan Food and Drug Vocational College, Huazhong Agricultural University, Jilin University, Ningxia University, Qufu Normal University, Shanxi University, Shaoguan University, Shenyang Agricultural University, Sichuan Agricultural University, Taiyuan Normal University, Wenzhou University, Northwest A&F University, Yangzhou University, Yunnan University, Zhejiang A&F University, Zhejiang Chinese Medical University, Chongqing University, Huaqiao University, Beijing Normal University. We thank Yi Xiao, Shouzhi Chen, Yahui Guo, Mingwei Li, Jing Zhang, Xinxi Li, Yaru Zhang, Yangjing Nie, Chenfeng Lin, Zhuang Miao, and Pengfei Zhou for help with conducting the experiment.








## Competing interests

None declared.

## Author contributions

YHF and ZW conceived the study. YHF, ZW and CMZ developed the methodology and analyses. ZW conducted the experiment in corporation with SW and YG. ZW analyzed the data. JZ offered assistance with data collection. ZW, CMZ and YHF led the writing of the manuscript with input from TWC, IJ, JP and Y-PZ. All authors discussed the results and reviewed the manuscript.

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## Data availability

The experimental datasets that support the findings of the current study are available at [https://github.com/Phenodoge/Ginkgo\\_experiment](https://github.com/Phenodoge/Ginkgo_experiment).

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## Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

**Fig. S1** Hourly temperature set for the four climate chambers.

**Fig. S2** Daily air temperature recorded in each temperature treatment during the experiment.

**Fig. S3** Interactive effects of temperature, photoperiod, and chilling on the time to leaf-out.

**Fig. S4** Effects of temperature and precipitation seasonality on the responsiveness of spring phenology under different treatments.

**Fig. S5** Effects of mean annual temperature and winter temperature on the responsiveness of spring phenology.

**Fig. S6** Effects of mean annual temperature and precipitation on leaf-out percent.

**Fig. S7** Effects of chilling accumulation on the heat requirement to achieve leaf-out and the spatial relationships between heat requirement and climate.

**Fig. S8** Effects of chilling accumulation on the responsiveness of spring phenology.

**Fig. S9** Effects of mean annual temperature and precipitation on winter chilling accumulation.

**Fig. S10** Projections of the relative responsiveness of spring phenology.

**Fig. S11** Projections of the relative responsiveness of spring phenology for 2081–2100 across China.

**Fig. S12** Relative responsiveness of spring phenology along latitude and elevation.

**Table S1** Details of the collection sites and individual trees.

**Table S2** Details of the models for projecting the relative responsiveness of spring phenology.

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