

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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- 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

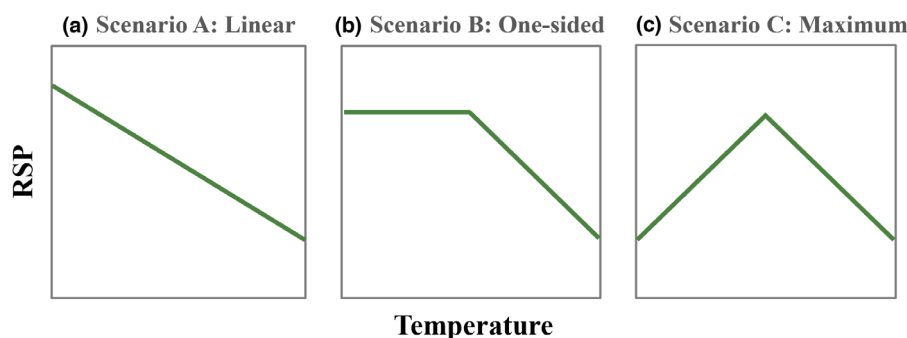


Fig. 1 Conceptual diagram of the responsiveness of spring phenology (RSP) to temperature along environmental gradients. We proposed and tested three main scenarios for how RSP may shift along spatial temperature gradients. (a) Chilling accumulation may be linearly related to temperature, predicting that 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 × 4 temperature × 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 CO₂ 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

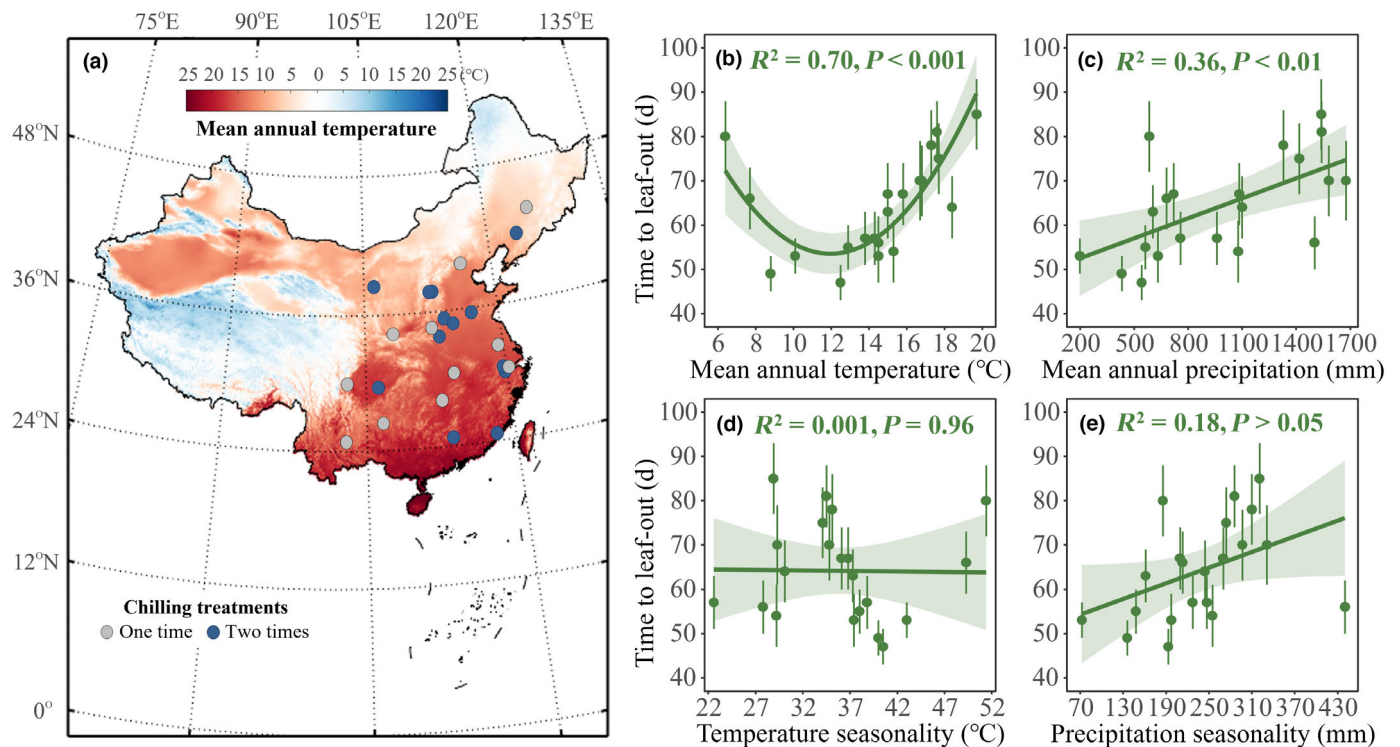


Fig. 2 Effects of background climate on the responsiveness of spring phenology (RSP). The RSP is represented as the time to leaf-out after collection, and thus decreases with increasing time to leaf-out. (a) Mean annual temperature (MAT) in China and the distribution of sites included in the China Campus 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.

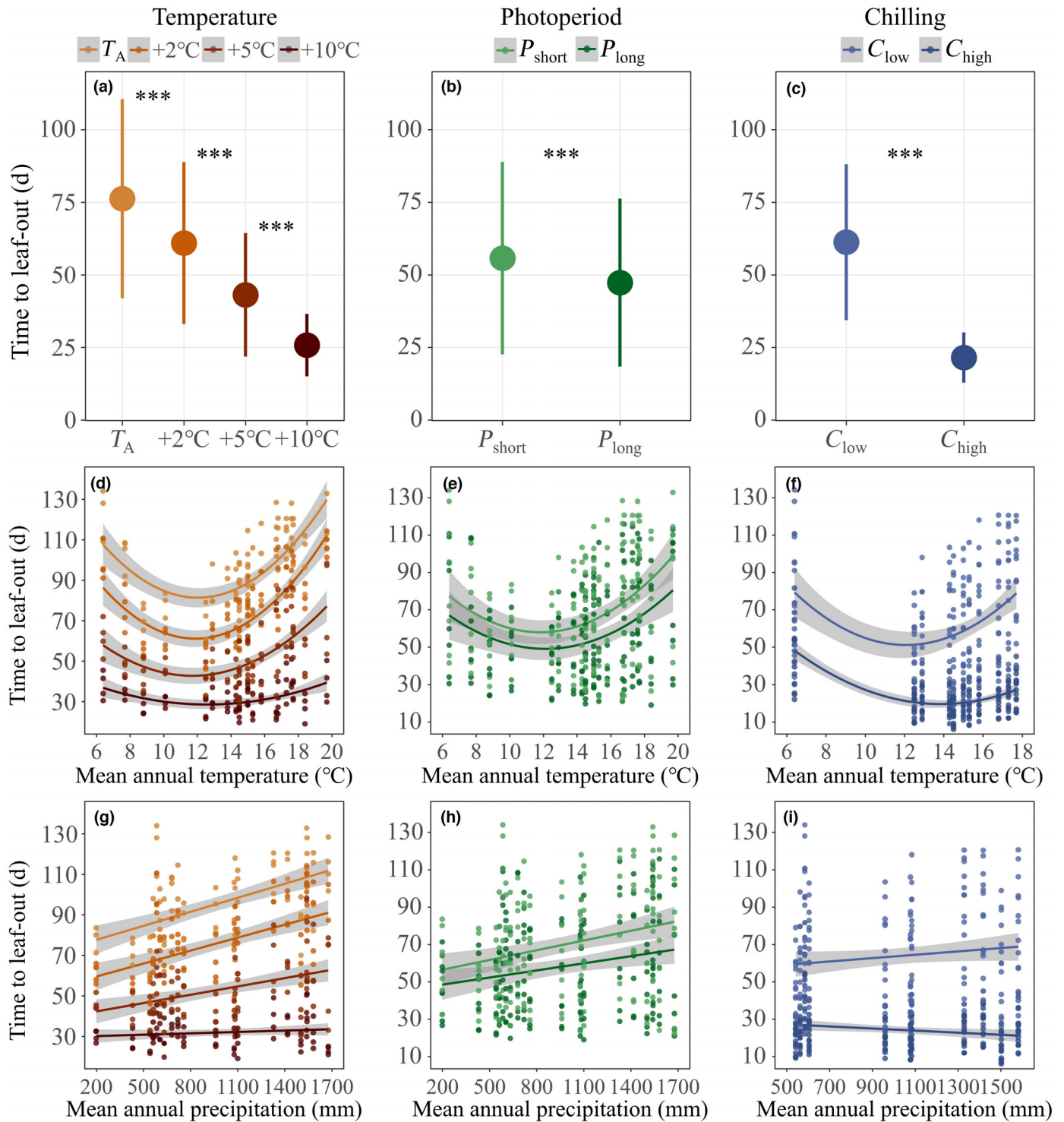


Fig. 3 Effects of environmental treatments and background climate on the responsiveness of spring phenology (RSP). (a–c) Effects of the temperature (a), photoperiod (b), and chilling (c) treatments on the time to leaf-out. The points and error bars refer to the average and SD in each treatment. ***, 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 ± 1.6 , 33 ± 2.9 and 50 ± 5.1 d earlier than in the ambient temperature treatment. A long photoperiod (14-h) advanced leaf-out times by an average of 8 ± 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 ± 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 ± 4.1 , 48 ± 2.0 , 31 ± 3.4 , and 18 ± 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 ± 1.0 d at low chilling and by only 2 ± 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°C and 5°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 ($R^2_{\text{adj}} = 0.74$, $\text{AIC} = 132.64$), and the M1 model, including only MAP, performed the worst ($R^2_{\text{adj}} = 0.31$, $\text{AIC} = 150.18$, Table S2). Based on the full model, we calculated the relative responsiveness of spring phenology (RSP_{rel}) for each pixel by dividing the minimum RSP observed across all sites (RSP_{min}) 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;

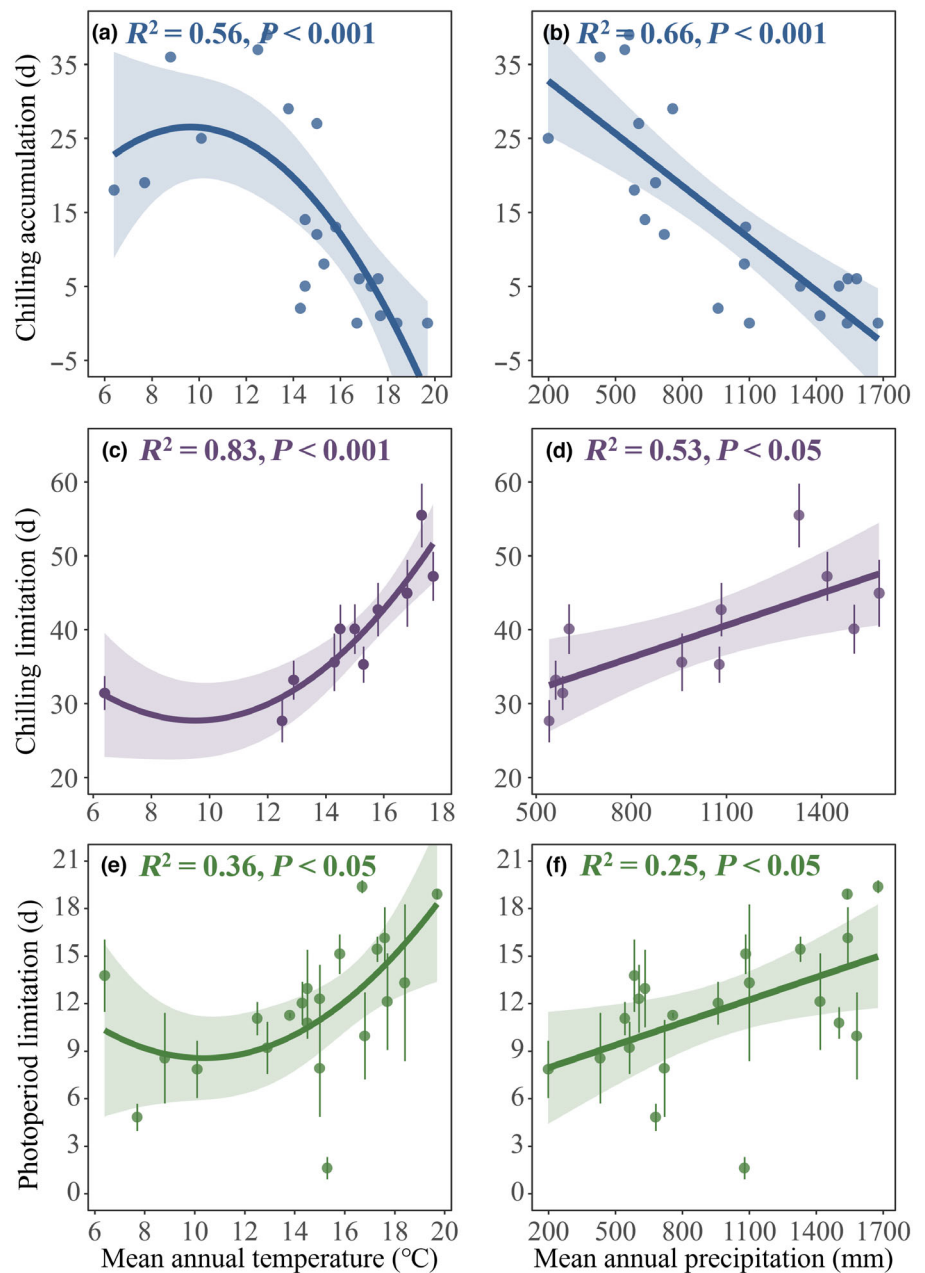


Fig. 4 Roles of chilling and photoperiod limitation in driving environmental gradients in the responsiveness of spring phenology. (a, b) Effects of mean annual temperature (MAT) and mean annual precipitation (MAP) on winter chilling accumulation. (c–f) Effects of MAT and MAP on chilling and photoperiod 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

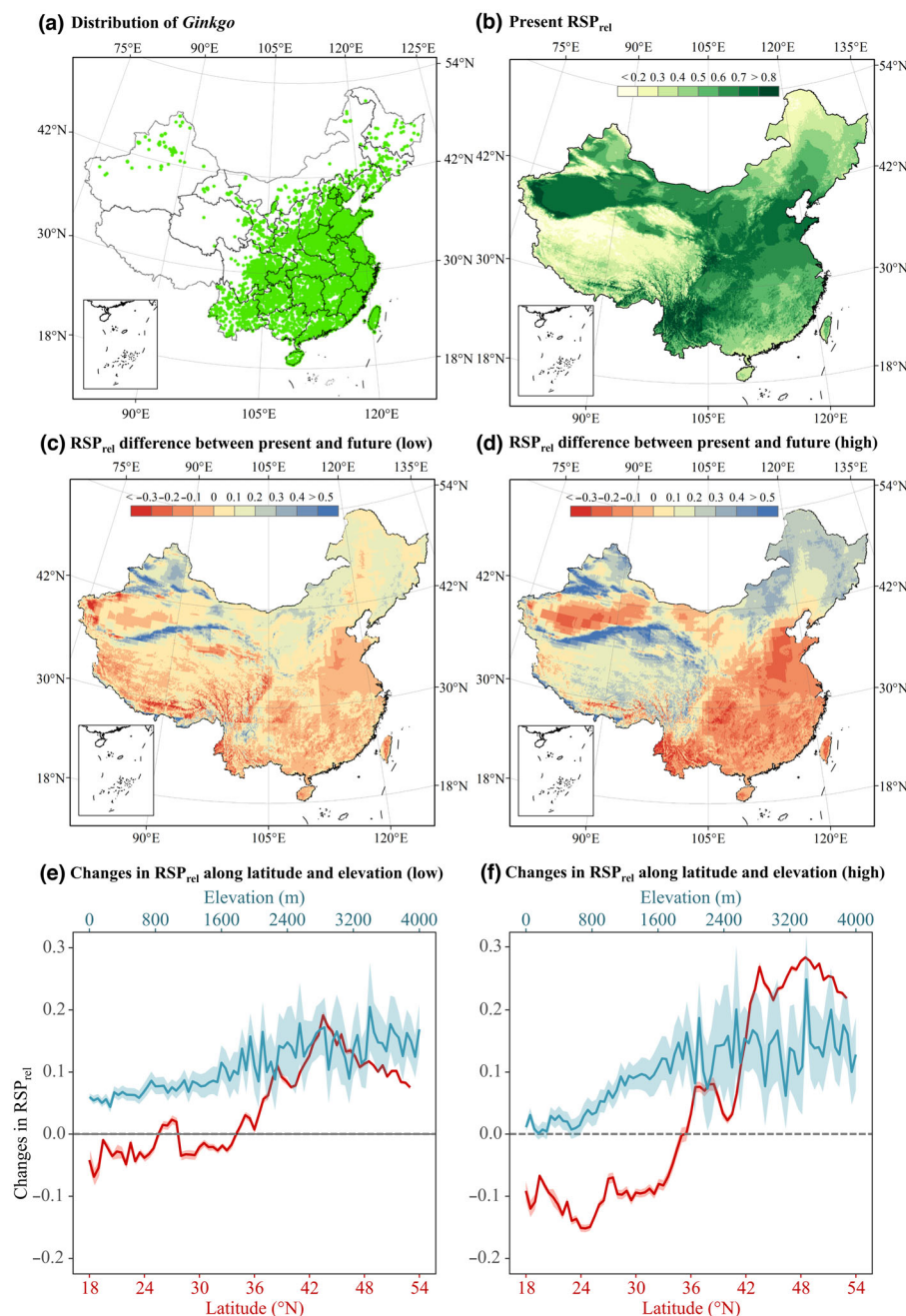


Fig. 5 Projections of the present and future distributions of the relative responsiveness of spring phenology (RSP_{rel}). (a) Geospatial distribution of *Ginkgo* in China. The green dots indicate the natural and cultivated occurrences of *Ginkgo* in China each dot represents a $0.1 \times 0.1^\circ$ 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° latitude and each 50 m elevation interval.

sites with a MAT of $c. 12^\circ\text{C}$ 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

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.

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


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.

References

- Basler D, Körner C. 2012. Photoperiod sensitivity of bud burst in 14 temperate forest tree species. *Agricultural and Forest Meteorology* 165: 73–81.
- Beil I, Kreyling J, Meyer C, Lemcke N, Malyshev AV. 2021. Late to bed, late to rise – warmer autumn temperatures delay spring phenology by delaying dormancy. *Global Change Biology* 27: 5806–5817.
- Bonan GB. 2008. Forests and climate change: forcings, feedbacks, and the climate benefits of forests. *Science* 320: 1444–1449.
- Cannell MGR, Smith RI. 1983. Thermal time, chill days and prediction of budburst in *Picea sitchensis*. *Journal of Applied Ecology* 20: 951–963.
- Chuine I, Beaubien EG. 2001. Phenology is a major determinant of tree species range. *Ecology Letters* 4: 500–510.
- Chuine I, Morin X, Bugmann H. 2010. Warming, photoperiods, and tree phenology. *Science* 329: 277–278.
- Clark JS, Salk C, Melillo J, Mohan J. 2014. Tree phenology responses to winter chilling, spring warming, at north and south range limits. *Functional Ecology* 28: 1344–1355.
- Cleland EE, Chuine I, Menzel A, Mooney HA, Schwartz MD. 2007. Shifting plant phenology in response to global change. *Trends in Ecology & Evolution* 22: 357–365.
- Cook BI, Wolkovich EM, Davies TJ, Ault TR, Betancourt JL, Allen JM, Bolmgren K, Cleland EE, Crimmins TM, Kraft NJB *et al.* 2012. Sensitivity of spring phenology to warming across temporal and spatial climate gradients in two independent databases. *Ecosystems* 15: 1283–1294.
- Ettinger AK, Chamberlain CJ, Wolkovich EM. 2022. The increasing relevance of phenology to conservation. *Nature Climate Change* 12: 305–307.
- Firmat C, Delzon S, Louvet JM, Parmentier J, Kremer A. 2017. Evolutionary dynamics of the leaf phenological cycle in an oak metapopulation along an elevation gradient. *Journal of Evolutionary Biology* 30: 2116–2131.
- Flynn DFB, Wolkovich EM. 2018. Temperature and photoperiod drive spring phenology across all species in a temperate forest community. *New Phytologist* 219: 1353–1362.
- Fu YH, Zhang X, Piao S, Hao F, Geng X, Vitasse Y, Zohner C, Peñuelas J, Janssens IA. 2019. Daylength helps temperate deciduous trees to leaf-out at the optimal time. *Global Change Biology* 25: 2410–2418.
- Fu YH, Zhao H, Piao S, Peaucelle M, Peng S, Zhou G, Ciais P, Huang M, Menzel A, Peñuelas J *et al.* 2015. Declining global warming effects on the phenology of spring leaf unfolding. *Nature* 526: 104–107.
- Gao M, Wang X, Meng F, Liu Q, Li X, Zhang Y, Piao S. 2020. Three-dimensional change in temperature sensitivity of northern vegetation phenology. *Global Change Biology* 26: 5189–5201.
- Geng X, Zhang Y, Fu YH, Hao F, Janssens IA, Peñuelas J, Piao S, Tang J, Wu Z, Zhang J *et al.* 2022. Contrasting phenology responses to climate warming across the northern extra-tropics. *Fundamental Research* 2: 708–715.

- Hamann A, Wang T. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. *Ecology* 87: 2773–2786.
- He J, Yang K, Tang W, Lu H, Qin J, Chen Y, Li X. 2020. The first high-resolution meteorological forcing dataset for land process studies over China. *Scientific Data* 7: 25.
- Keenan TF, Gray J, Friedl MA, Toomey M, Bohrer G, Hollinger DY, Munger JW, O'Keefe J, Schmid HP, Wing IS *et al.* 2014. Net carbon uptake has increased through warming-induced changes in temperate forest phenology. *Nature Climate Change* 4: 598–604.
- Lapenis A, Henry H, Vuille M, Mower J. 2014. Climatic factors controlling plant sensitivity to warming. *Climatic Change* 122: 723–734.
- Laube J, Sparks TH, Estrella N, Höfler J, Ankerst DP, Menzel A. 2014. Chilling outweighs photoperiod in preventing precocious spring development. *Global Change Biology* 20: 170–182.
- Lechowicz MJ. 1984. Why do temperate deciduous trees leaf out at different times? Adaptation and ecology of forest communities. *The American Naturalist* 124: 821–842.
- Lin H-Y, Li W-H, Lin C-F, Wu H-R, Zhao Y-P. 2022. International biological flora: *Ginkgo biloba*. *Journal of Ecology* 110: 951–982.
- Liu Q, Piao S, Janssens IA, Fu Y, Peng S, Lian X, Ciais P, Myneni RB, Peñuelas J, Wang T. 2018. Extension of the growing season increases vegetation exposure to frost. *Nature Communications* 9: 426.
- Luo W, Kim HS, Zhao X, Ryu D, Jung I, Cho H, Harris N, Ghosh S, Zhang C, Liang J. 2020. New forest biomass carbon stock estimates in Northeast Asia based on multisource data. *Global Change Biology* 26: 7045–7066.
- Major RT. 1967. The *Ginkgo*, the most ancient living tree. *Science* 157: 1270–1273.
- Menzel A, Yuan Y, Matiu M, Sparks T, Scheffinger H, Gehrig R, Estrella N. 2020. Climate change fingerprints in recent European plant phenology. *Global Change Biology* 26: 2599–2612.
- Morin X, Lechowicz MJ, Augspurger C, O'Keefe J, Viner D, Chuine I. 2009. Leaf phenology in 22 North American tree species during the 21st century. *Global Change Biology* 15: 961–975.
- Parmesan C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13: 1860–1872.
- Peaucelle M, Janssens IA, Stocker BD, Descals Ferrando A, Fu YH, Molowny-Horas R, Ciais P, Peñuelas J. 2019. Spatial variance of spring phenology in temperate deciduous forests is constrained by background climatic conditions. *Nature Communications* 10: 5388.
- Peñuelas J, Rutishauser T, Filella I. 2009. Phenology feedbacks on climate change. *Science* 324: 887–888.
- Piao S, Liu Q, Chen A, Janssens IA, Fu Y, Dai J, Liu L, Lian X, Shen M, Zhu X. 2019. Plant phenology and global climate change: current progresses and challenges. *Global Change Biology* 25: 1922–1940.
- Rasheid N, Sofi PA, Masoodi TH. 2018. Phenodynamics of *Ginkgo biloba* L. – a living fossil under threat under temperate conditions of Kashmir Himalayas, India. *Chemical Science Review and Letters* 7: 469–473.
- Renner SS, Zohner CM. 2018. Climate change and phenological mismatch in trophic interactions among plants, insects, and vertebrates. *Annual Review of Ecology, Evolution, and Systematics* 49: 165–182.
- Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169: 156–173.
- Rosemartin AH, Crimmins TM, Enquist CAF, Gerst KL, Kellermann JL, Posthumus EE, Denny EG, Guertin P, Marsh L, Weltzin JF. 2014. Organizing phenological data resources to inform natural resource conservation. *Biological Conservation* 173: 90–97.
- Rossi S, Isabel N. 2017. Bud break responds more strongly to daytime than night-time temperature under asymmetric experimental warming. *Global Change Biology* 23: 446–454.
- Shen M, Tang Y, Chen J, Yang X, Wang C, Cui X, Yang Y, Han L, Li L, Du J *et al.* 2014. Earlier-season vegetation has greater temperature sensitivity of spring phenology in Northern Hemisphere. *PLoS ONE* 9: e88178.
- Vitasse Y. 2013. Ontogenetic changes rather than difference in temperature cause understory trees to leaf out earlier. *New Phytologist* 198: 149–155.
- Vitasse Y, Baumgarten F, Zohner CM, Rutishauser T, Pietragalla B, Gehrig R, Dai J, Wang H, Aono Y, Sparks TH. 2022. The great acceleration of plant phenological shifts. *Nature Climate Change* 12: 300–302.
- Vitasse Y, Bresson CC, Kremer A, Michalet R, Delzon S. 2010. Quantifying phenological plasticity to temperature in two temperate tree species. *Functional Ecology* 24: 1211–1218.
- Vitasse Y, Signarbieux C, Fu YH. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences, USA* 115: 1004–1008.
- Walde MG, Wu Z, Fox T, Baumgarten F, Fu YH, Wang S, Vitasse Y. 2022. Higher spring phenological sensitivity to forcing temperatures of Asian compared to European tree species under low and high pre-chilling conditions. *Frontiers in Forests and Global Change* 5: 1063127.
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F. 2002. Ecological responses to recent climate change. *Nature* 416: 389–395.
- Wang C, Cao R, Chen J, Rao Y, Tang Y. 2015. Temperature sensitivity of spring vegetation phenology correlates to within-spring warming speed over the Northern Hemisphere. *Ecological Indicators* 50: 62–68.
- Wang T, Otlé C, Peng S, Janssens IA, Lin X, Poulter B, Yue C, Ciais P. 2014. The influence of local spring temperature variance on temperature sensitivity of spring phenology. *Global Change Biology* 20: 1473–1480.
- Wang H, Wu C, Ciais P, Peñuelas J, Dai J, Fu Y, Ge Q. 2020. Overestimation of the effect of climatic warming on spring phenology due to misrepresentation of chilling. *Nature Communications* 11: 4945.
- Wang S, Wu Z, Gong Y, Wang S, Zhang W, Zhang S, De Boeck HJ, Fu YH. 2022. Climate warming shifts the time interval between flowering and leaf unfolding depending on the warming period. *Science China Life Sciences* 65: 2316–2324.
- Way DA, Montgomery RA. 2015. Photoperiod constraints on tree phenology, performance and migration in a warming world. *Plant, Cell & Environment* 38: 1725–1736.
- Weinberger JH. 1950. Chilling requirements of peach varieties. *Proceedings of the American Society for Horticultural Science* 56: 122–128.
- Wolkovich EM, Chamberlain CJ, Buonaiuto DM, Ettinger AK, Morales-Castilla I. 2022. Integrating experiments to predict interactive cue effects on spring phenology with warming. *New Phytologist* 235: 1719–1728.
- Wu Z, Lin C-F, Wang S, Gong Y, Fu YH, Tang J, De Boeck HJ, Vitasse Y, Zhao Y-P. 2022a. The sensitivity of *Ginkgo* leaf unfolding to the temperature and photoperiod decreases with increasing elevation. *Agricultural and Forest Meteorology* 315: 108840.
- Wu Z, Wang S, Fu YH, Gong Y, Lin C-F, Zhao Y-P, Prevéy JS, Zohner C. 2022b. Spatial difference of interactive effect between temperature and daylength on *Ginkgo* budburst. *Frontiers in Plant Science* 13: 887226.
- Wu Z, Zhang Z, Wang J. 2019. Estimating the productive potential of five natural forest types in northeastern China. *Forest Ecosystems* 6: 42.
- Zeng L, Wardlaw BD, Xiang D, Hu S, Li D. 2020. A review of vegetation phenological metrics extraction using time-series, multispectral satellite data. *Remote Sensing of Environment* 237: 111511.
- Zhang J, Li X, Ren P, Chai C, Julio Camarero J, Leavitt SW, Rossi S, Liang E. 2022. Lengthening height-growth duration in Smith fir as onset becomes more synchronous across elevations under climate warming scenarios. *Agricultural and Forest Meteorology* 326: 109193.
- Zhang X, Tarpley D, Sullivan JT. 2007. Diverse responses of vegetation phenology to a warming climate. *Geophysical Research Letters* 34.
- Zhao Y-P, Fan G, Yin P-P, Sun S, Li N, Hong X, Hu G, Zhang H, Zhang F-M, Han J-D *et al.* 2019. Resequencing 545 *Ginkgo* genomes across the world reveals the evolutionary history of the living fossil. *Nature Communications* 10: 4201.
- Zohner CM, Benito BM, Svenning J-C, Renner SS. 2016. Day length unlikely to constrain climate-driven shifts in leaf-out times of northern woody plants. *Nature Climate Change* 6: 1120–1123.
- Zohner CM, Mo L, Renner SS, Svenning J-C, Vitasse Y, Benito BM, Ordóñez A, Baumgarten F, Bastin J-F, Sebold V *et al.* 2020a. Late-spring frost risk between 1959 and 2017 decreased in North America but increased in Europe and Asia. *Proceedings of the National Academy of Sciences, USA* 117: 12192–12200.

Zohner CM, Mo L, Sebald V, Renner SS. 2020b. Leaf-out in northern ecotypes of wide-ranging trees requires less spring warming, enhancing the risk of spring frost damage at cold range limits. *Global Ecology and Biogeography* 29: 1065–1072.

Zohner CM, Renner SS. 2015. Perception of photoperiod in individual buds of mature trees regulates leaf-out. *New Phytologist* 208: 1023–1030.

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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