Diminishing warming effects on plant phenology over time

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Summary

- Plant phenology, the timing of recurrent biological events, shows key and complex response to climate warming, with consequences for ecosystem functions and services. A key challenge for predicting plant phenology under future climates is to determine whether the phenological changes will persist with more intensive and long-term warming.
- Here, we conducted a meta-analysis of 103 experimental warming studies around the globe to investigate the responses of four phenophases – leaf-out, first flowering, last flowering, and leaf coloring.
- We showed that warming advanced leaf-out and flowering but delayed leaf coloring across herbaceous and woody plants. As the magnitude of warming increased, the response of most plant phenophases gradually leveled off for herbaceous plants, while phenology responded in proportion to warming in woody plants. We also found that the experimental effects of warming on plant phenology diminished over time across all phenophases. Specifically, the rate of changes in first flowering for herbaceous species, as well as leaf-out and leaf coloring for woody species, decreased as the experimental duration extended.
- Together, these results suggest that the real-world impact of global warming on plant phenology will diminish over time as temperatures continue to increase.

Introduction

Global temperatures are expected to rise by 3.3–5.7°C by the end of this century, with far-reaching consequences for terrestrial ecosystems around the world (IPCC, 2023). In particular, plant phenology – the timing of recurrent life history events – is expected to be a key element of changing ecosystem dynamics (Piao *et al*., 2019; May *et al*., 2020; Collins *et al*., 2021). Shifts in plant phenology under climate warming, such as earlier leaf-out and flowering, may affect several ecological attributes, including plant species fitness and distributions (Sherry *et al*., 2007; Alexander & Levine, 2019), plant–animal interactions (Post *et al*., 2009; Thackeray *et al*., 2016; Richert *et al*., 2021), and land–atmospheric exchanges of carbon, water, and energy (Peñuelas *et al*., 2009; Jespersen *et al*., 2018; Wang *et al*., 2020). It is therefore imperative that we continue to monitor and research plant phenology as the global environment changes.

Much of the current knowledge of plant phenology shifts comes from experimental warming studies, where plot-level manipulations typically enhance temperatures by 1–4°C often resulting in earlier spring leaf-out and flowering, as well as delayed leaf coloring in temperate, boreal, and Arctic ecosystems

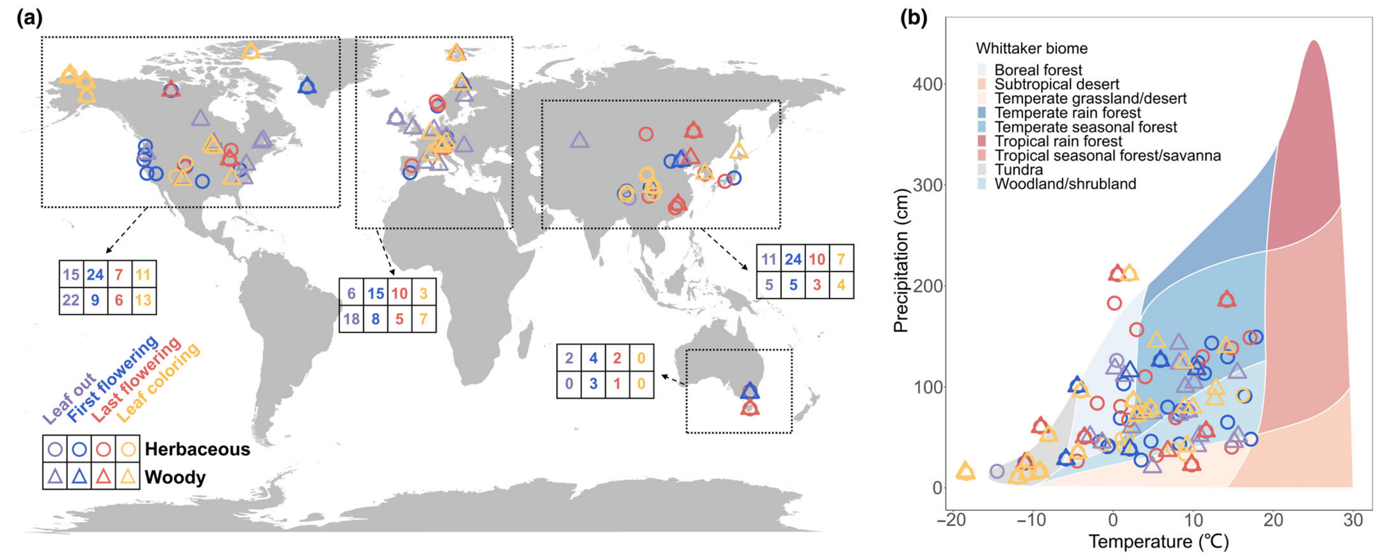

Fig. 1 Geographical distribution (a) and climatic conditions (b) of the warming experimental sites in the meta-analysis. Circles and triangles indicate the sites focusing on herbaceous and woody species, respectively. Symbols with different colors indicate different plant phenophases. The number of sites corresponding to specific phenophases is shown in the boxes.

(Arft *et al.*, 1999; Wolkovich *et al.*, 2012; Collins *et al.*, 2021). However, there is disagreement on whether the phenological responses will gradually level off as the magnitude of warming increases (Morin *et al.*, 2010; Richardson *et al.*, 2018). For example, previous experiments have reported that the advancement of leaf-out in temperate species plateaus as the magnitude of warming intensifies (Morin *et al.*, 2010; Fu *et al.*, 2015). It is likely that other factors may interact with temperature increase to cause such nonlinear response, such as photoperiod and chilling requirements for breaking endodormancy (Luedeling *et al.*, 2013; Piao *et al.*, 2019). It may also be due to warm temperatures being beyond maximum thresholds that a plant can capitalize upon (Elmendorf & Hollister, 2023). By contrast, the leaf-out stage in boreal forests advanced linearly with the magnitude of warming from 0°C to 9°C in a whole-ecosystem warming experiment (Richardson *et al.*, 2018). The uncertainty regarding whether plant phenological responses level off along warming gradients poses a significant challenge for predicting plant dynamics.

Another key issue affecting our understanding of future changes is whether the warming effects on plant phenology decrease over time. Photosynthesis and plant respiration can acclimate to warming over time (Reich *et al.*, 2016; Smith & Keenan, 2020), possibly because of changes in resource availability, phenotypic plasticity, and genetic adaptation (Luo *et al.*, 2001; Leuzinger *et al.*, 2011). However, whether plant phenology exhibits similar behavior is still unclear. Moreover, the temporal trends in phenological response to warming may vary between plant types, because herbaceous species possess larger proportions of belowground biomass stores and shorter generation times than woody species (Shaver & Laundre, 1997; Arft *et al.*, 1999; Smith & Donoghue, 2008; Chmura *et al.*, 2019).

A further complication to future predictions is the fact that the impact of climate warming depends highly on local climate and plant types (Liu *et al.*, 2021; Stuble *et al.*, 2021). For instance, plants may benefit more from warming in wetter regions because they are not additionally constrained by water availability (Gao *et al.*, 2020; H. Liu *et al.*, 2022). The response of phenology to warming may also vary between species because; for example, herbaceous plants have shallower root distributions and more flexible morphology than woody species (Shaver & Laundre, 1997; Šímová *et al.*, 2018). Thus, further investigation is required to understand how these factors mediate the warming effect on plant phenology across various magnitudes of warming and over prolonged periods.

For this meta-analysis, we compiled a dataset on four phenophases (leaf-out, first flowering, last flowering, and leaf coloring) recorded from 103 experimental warming studies (Fig. 1). We hypothesize that (1) the magnitude of phenological response to warming will level off as greater degrees of warming are reached because larger phenological shifts are more likely be constrained by water or nutrient availability (Shen *et al.*, 2015); (2) the magnitude of phenological responses will decline over time because of depletion of the plant belowground resources or plant acclimation (Fu *et al.*, 2014; Duputié *et al.*, 2015); and (3) prevailing regional climate factors may modulate the response of phenology to warming magnitude and experimental duration. For example, the decelerated rate of phenological response with increasing warming may be more pronounced in dry regions, as plants in these regions are more vulnerable to water stress caused by warming (Xu *et al.*, 2013).

Materials and Methods

Data compilation

Peer-reviewed literature published before January 2021 was searched using Google Scholar, Web of Science, and China National Knowledge Infrastructure. The search keywords included are as follows: (warming OR heat* OR increase* temperature OR elevate* temperature OR climate change) AND (bud* OR "bud burst" OR leaf-out OR "leaf unfold*" OR "growing season" OR phenolog* OR reproducti* OR flowering OR senescence OR anthesis OR "leaf color" OR "leaf colour") AND (experiment* OR treatment* OR control*). Studies were included in our meta-analysis if they met the following criteria: (1) The temperature difference between experimental treatments was achieved by warming rather than cooling; (2) control and warming plots had the same initial conditions including vegetation structure, microclimate, and soil type; and (3) experiments were focused on species in natural terrestrial ecosystems. Overall, we identified 103 published articles that met these criteria (Supporting Information Fig. S1).

We gathered data from each publication, focusing specifically on the average timing of phenophase occurrence (measured in days of the year) and the phenological differences (in days) observed between the warming and control treatments. Phenological data were either obtained directly from tables or extracted from figures by using GetData Graph Digitizer (v.2.24). The sample sizes and the species names associated with each study were also compiled. Additionally, we obtained relevant data on the phenological responses of alpine or arctic plants to warming directly from researchers. In total, we compiled 8023 phenology observations in warming experiments and paired control plots, mainly distributed in the northern hemisphere, and focused predominately in deciduous forests and on short-lived herbs (https://doi.org/10.6084/m9.figshare.25460665.v1). To identify the key predictors for the response of phenology to experimental warming, we gathered data on experimental variables, including warming magnitude, duration, and method, as well as ecological variables such as latitude and ecosystem types, based on Whittaker's biome classification (Whittaker, 1975; Fig. 1; Table S1).

Climatic variables, such as mean annual temperature (MAT), mean annual precipitation (MAP), potential evapotranspiration, and monthly climate values (2001–2014), were extracted from the Centre for Environmental Data Analysis according to the geographic coordinates of the reported study sites (version CRUTS 4.00, https://catalogue.ceda.ac.uk). The monthly and annual aridity index was calculated as the ratio of potential evapotranspiration to precipitation. We also calculated the temperature, precipitation, and aridity index during the preseason. We defined the preseason as the 3 months preceding the average month in which the phenophase occurs at each respective site in our study (Fu *et al.*, 2015). Following commonly used criterion (Knapp *et al.*, 2015; X. Liu *et al.*, 2022), we classified regions as warm or cold based on a threshold of 0°C of MAT, and as wet or dry based on a threshold of 500 mm of MAP.

Meta-analysis

We quantified the response of four phenophases of plant phenology (leaf-out, first flowering, last flowering, and leaf coloring) by computing the number of days of shift induced by warming, which is a commonly used metric in meta-analysis to assess phenological responses (Arft *et al.*, 1999; Liu *et al.*, 2021; Stuble *et al.*, 2021):

$$\text{Warming effect} = X_{\mathrm{w}} - X_{\mathrm{c}}$$

where X_{w} and X_{c} are the day of the year when the phenophase occurs in the warming and control treatments, respectively. Negative values of the effect size indicate an advancement of phenophases under warming, while positive values indicate a delay.

We conducted hierarchical meta-analyses using the '*rma.mv*' function in R package '*metafor*' 2.4-0 to control for nonindependence due to multiple observations per site and species (Viechtbauer, 2010; Nakagawa & Santos, 2012; Benítez-López *et al.*, 2017). All analyses were conducted for overall shifts of the four phenophases listed above, and separately for herbaceous and woody species. We included site identity, observation identity (ID), and species identity as random factors in the hierarchical models. The random effect structure for herbaceous and woody species was set as (1|Sites/ID) + (1|Species) using the syntax for the R function 'rma.mv' (Viechtbauer, 2010). We used a sample size-based weighting scheme instead of inverse variance weighting to avoid an undue influence on parameter estimates from a few studies that showed minimal variation among replicates. The weights were calculated following previous works (Adams *et al.*, 1997; Peng *et al.*, 2017; H. Liu *et al.*, 2022):

$$w = \frac{N_{\mathrm{c}} N_{\mathrm{w}}}{N_{\mathrm{c}} + N_{\mathrm{w}}}$$

where N_{c} and N_{w} are the sample sizes for control and warming treatments, respectively. The hierarchical random effect meta-analysis was used to assess the overall phenological responses of herbaceous and woody plants to warming across all studies. If the 95% confidence intervals of the overall responses did not overlap zero, the warming effects were considered significant at the $P < 0.05$ level.

Q-statistics were used to assess the heterogeneity of responses of phenology explained by each experimental and ecological variable in our dataset, using hierarchical mixed effect meta-analyses (Hedges & Olkin, 1985; Viechtbauer, 2010). The total heterogeneity was divided into the heterogeneity explained by the moderator (Q_{m}) and residual heterogeneity. When the P value for Q_{m} was <0.05, we considered the significant contributions of moderators to the total heterogeneity in effect sizes. Linear and nonlinear models were compared using the Akaike information criterion (AIC) to determine the most appropriate model structure to predict the relationships between phenological responses and warming magnitude/experimental duration.

Finally, we investigated whether the sensitivity of plant phenology to warming (expressed as days per °C) varied with the duration of the experiments. We calculated the slope coefficients of warming magnitude as a measure of phenological sensitivity using meta-regression models, where the experimental duration was treated as an interaction term. We examined the relationships between climatic variables, latitude, and phenological responses by incorporating the magnitude of warming and the duration of experiments as fixed terms in the mixed effects model. We also included MAT and MAP as interaction terms (e.g. MAT × experimental duration) in our models to test whether the relationships between phenological responses and warming magnitude, as well as experimental duration, are influenced by climatic factors. We used Rosenberg's fail-safe number and Trim-and-fill tests to assess the publication bias in our meta-analysis. All statistical analyses were carried out using the R programming environment (R Development Core Team, 2023).

Results

Responses of phenology to warming magnitude and experimental duration

Despite the fact that all phenophases exhibited large variations (Fig. S2; Table S2), experimental warming significantly advanced leaf-out by an average of −3.5 d (95% CI −5.0 to −2.0 d, $P < 0.001$), first flowering by −3.9 d (95% CI −4.8 to −3.0 d, $P < 0.001$), and last flowering by −3.0 d (95% CI −4.1 to −1.8 d, $P < 0.001$). By contrast, experimental warming delayed leaf coloring by 2.8 d (95% CI 1.1–4.4 d, $P = 0.001$) across the entire dataset (Fig. 2a). This overall trend of phenological changes was present even when considering the woody and herbaceous plants separately (Fig. 2b,c). However, the advancement of leaf-out was nonsignificant for evergreen woody plants (95% CI −4.6 to 0.4 d, $P = 0.103$), but strongly significant for deciduous woody plants (95% CI −6.3 to −2.8 d, $P < 0.001$), (Fig. S3). These results were not affected by publication bias (Table S3).

The advancement of leaf-out and first flowering for herbaceous plants level off with the magnitude of warming (Fig. 3a). The logarithmic models were better than linear models at predicting the responses of both leaf-out (AIC: 9468.9 vs 9469.5) and first flowering (AIC: 15491.1 vs 15494.0) of herbaceous species (Table S4). Conversely, the advancement of leaf-out, first/last flowering, and the delay of leaf coloring were linearly correlated with rising warming magnitude for woody species (Fig. 3b), and these models performed better than logarithmic models (Table S4). The patterns were similar for those experiments that applied multiple levels of warming (span >4°C) at the same site (Fig. S4).

The variations in phenological responses to warming could partly be explained by experimental duration (Table S4). Specifically, the advancement of herbaceous first flowering under warming became less pronounced over time (Fig. 3c). The advancement of woody leaf-out and the delay of leaf coloring also weakened over time (Fig. 3d). The shifts in plant phenology per degree warming (sensitivity) also weakened in long-term experiments (Fig. 4). Specifically, the sensitivity of flowering phenophases and leaf coloring to warming for herbaceous species diminished with increased experimental duration (Fig. 4a–c). Moreover, the sensitivity of leaf-out to warming for woody species diminished with the experimental duration (Fig. 4e).

Other factors influencing responses of phenology to experimental warming

Besides warming magnitude and experimental duration, several other variables affected the responses of phenology to warming (Tables S5–S7). For herbaceous species, the advancement of leaf-out and the delay of leaf coloring became stronger with increasing MAT (Fig. 5a), the advancement of leaf-out and first flowering became stronger with increasing MAP (Fig. 5c), and the delay of leaf coloring decreased with latitude (Fig. S5a). For woody species, the advancement of first flowering became stronger with increasing MAT (Fig. 5b), and the advancement of leaf-out and last flowering for woody species became stronger with increasing aridity index (Fig. S5b,c). In addition, the responses of leaf-out for herbaceous species in boreal forest and temperate grassland were greater than those located in tundra, and the responses of first flowering for woody species in temperate forest were greater than those in other ecosystem types (Fig. S6). There was also an experimental methodology pattern,

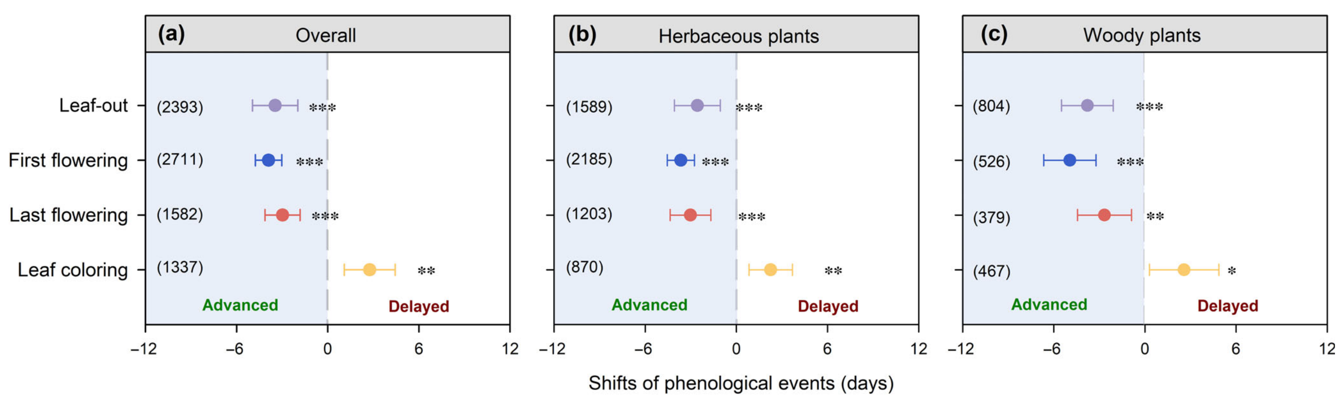

Fig. 2 Responses of plant phenology to experimental warming. (a) All terrestrial species. (b) Herbaceous species. (c) Woody species. The weighted average shifts for different phenophases are presented, with error bars indicating the 95% confidence intervals. The number in parentheses represents the sample sizes *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. The P-values and confidence intervals are generated from Wald-type tests in the hierarchical random-effect meta-analysis.

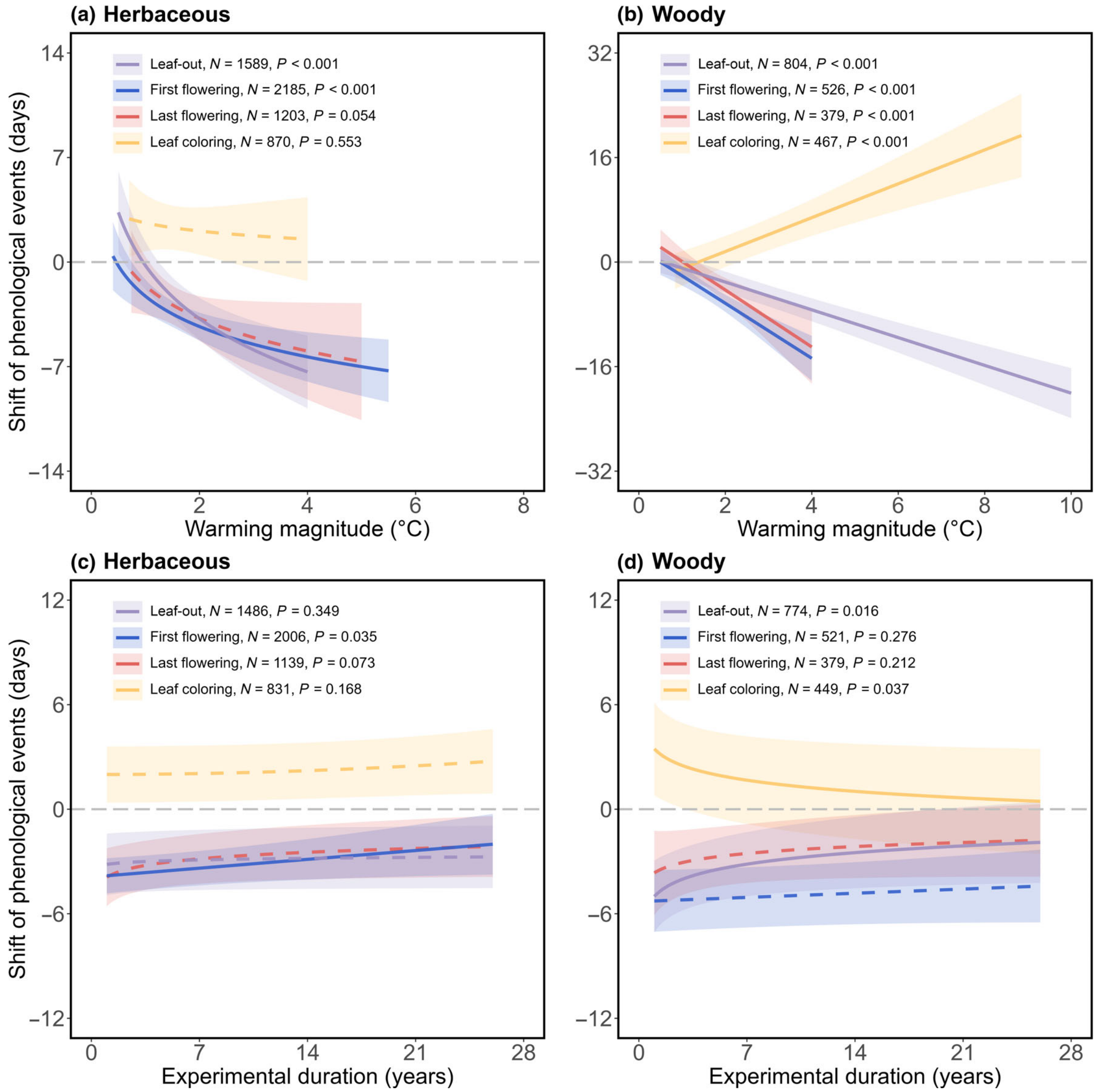

Fig. 3 Effects of warming magnitude and experimental duration on phenological responses. (a, b) Warming magnitude. (c, d) Experimental duration. Lines with 95% confidence intervals (shaded areas) are fitted from meta-regressions. Different colors represent leaf-out, first flowering, last flowering, and leaf coloring, respectively. Solid and dotted lines indicate whether the regressions are statistically significant (the *P*-values for Q_m-test < 0.05) or not ($P > 0.05$), respectively. *N* represents the number of observations.

with studies using infrared heaters exhibited greater phenological responses than those using open-top chambers and heater cables (Fig. S7).

The phenological response to the magnitude of warming varied between climatic regions (Fig. S8; Table S8). In particular, the advancement of leaf-out for herbaceous plants and first flowering for woody species became more pronounced with increased warming magnitude in warm regions, but there was no trend in cold regions (Fig. S8a,c). The delays in leaf coloring for woody species increased with warming magnitude in wet regions but not in dry regions (Fig. S8i). Furthermore, warming-induced delays of leaf coloring in woody plants decreased over time in warm and wet regions, but not in cold and dry regions (Fig. S9; Table S9).

Discussion

Most terrestrial ecosystems have experienced rapid climate warming over the past decades (IPCC, 2023), and plant phenological responses to warming have been a central focus of climate change research (Post *et al*., 2009; H. Liu *et al*., 2022). However, our research provides two particularly novel insights that distinguish it from previous phenological research in this area. First, we demonstrate that responses of plant phenology for herbaceous species, but not woody species, level off with the increasing simulated warming magnitude. Second, we show that responses of plant phenology to warming attenuate with experimental duration. Short-term responses to warming can likely be attributed to

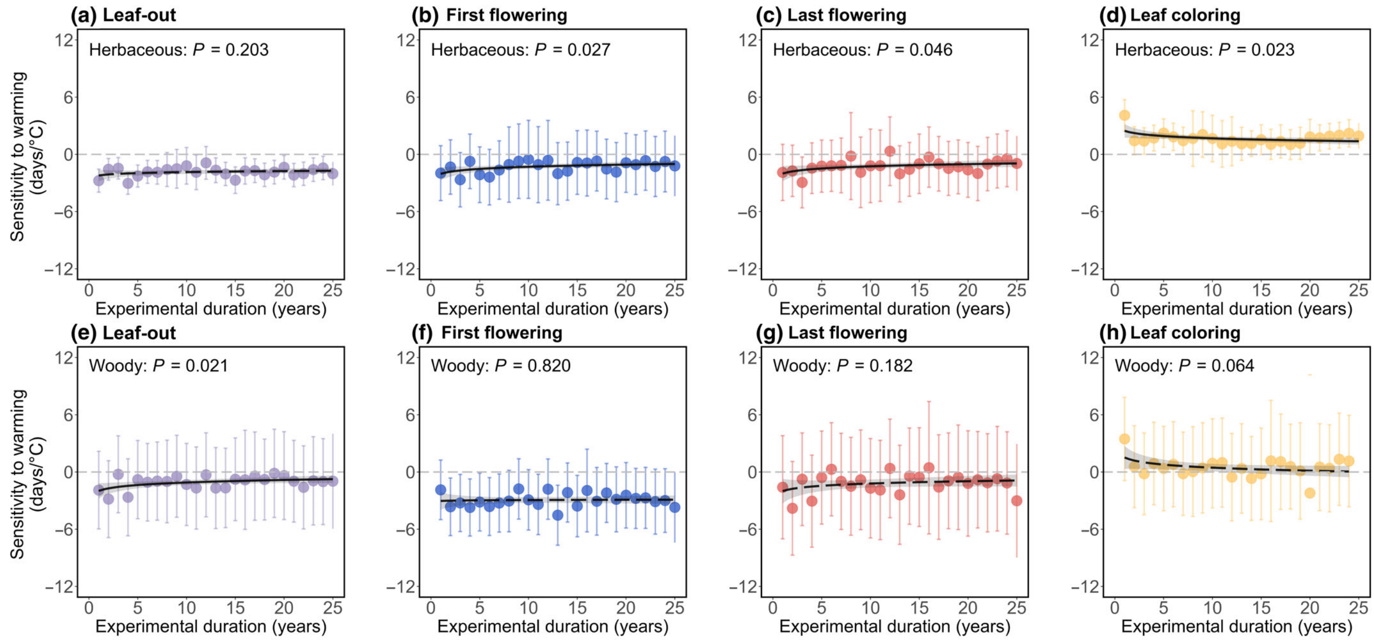

Fig. 4 Relationships between the sensitivity of plant phenophases to warming and experimental duration. (a–d) Herbaceous species. (e–h) Woody species. Values are the slope coefficients of warming magnitude from meta-regression models, where the duration of warming was treated as an interaction term. Values are fitted by logarithmic regressions with 95% confidence intervals (shaded areas). Solid and dashed lines indicate whether the regressions are statistically significant ($P < 0.05$) or not ($P > 0.05$), respectively. The *P*-values of the slope are generated from the logarithmic regression model using lm function.

plant plasticity (Ramirez-Parada *et al*., 2024). As we observed a gradual decrease in the variance of phenological changes with the extension of experiment duration, this implies that as time passes and plasticity becomes inadequate, plants may undergo evolutionary responses to better adapt to changing conditions (Wu *et al*., 2012; Mathiasen & Premoli, 2016).

Differential trends of plant phenology to increasing warming magnitude

Our first hypothesis was partially supported as the responses of leaf-out, first flowering, last flowering, and leaf coloring plateaued with rising warming magnitude for herbaceous species, but not for woody species (Table S4). The linear responses of woody species may have occurred because high-level warming can continuously stimulate mineralization rates and soil nutrient availability (Schaeffer *et al*., 2013). In addition, longer growing seasons caused by high-level warming may produce more photosynthate and lead to larger root nutrient reservoirs, which may support shifts in phenology (Fu *et al*., 2014).

Although herbaceous plants can also benefit from increased resources or nutrients released by warmer temperatures, their phenological responses may be more constrained by other factors than woody plants, such as water availability and photoperiod (Fu *et al*., 2015; Richardson *et al*., 2018). Our analysis results further support this idea by demonstrating that the responses of herbaceous plants to warming are constrained by precipitation, whereas those of woody plants are not (Fig. 5). The shallow root systems of herbaceous plants, in contrast to the deeper systems of woody plants, likely make them more susceptible to water stress caused by high-level warming, potentially leading to constraints on the ability to respond phenologically (Schenk & Jackson, 2002; Xu *et al*., 2013; Naumann *et al*., 2018). This diminished response implies a potential reduction in frost damage risk for herbaceous plants, especially if warming is accompanied by occasional cold temperature episodes in early spring (Inouye, 2008; Wipf *et al*., 2009; Inouye & Wielgolaski, 2013).

The differential responses of woody and herbaceous plants to high-level warming may lead to greater benefits for woody plants under warming conditions (Lin *et al*., 2010). Previous research indicates that in communities where both types coexist, woody plants tended to initiate growth earlier than herbaceous species, aiding in niche occupation and suppressing herbaceous growth through shading effects (Castro & Freitas, 2009). This tendency together with the patterns revealed by our study provides a potential explanation for the prevalent phenomenon of shrub encroachment currently observed (Saintilan & Rogers, 2015), and we encourage long-term monitoring that focuses on trait-based responses to continued warming.

Decreased phenological responses with long-term experimental warming

A crucial finding in our study is that responses of plant phenology for both woody and herbaceous species became less pronounced over time, supporting our second hypothesis. Our results were consistent with a previous study that demonstrated diminished responses of plant reproductive phenology to warming over several years (Barrett & Hollister, 2016). This long-term attenuating response can be explained by the fact that accelerated

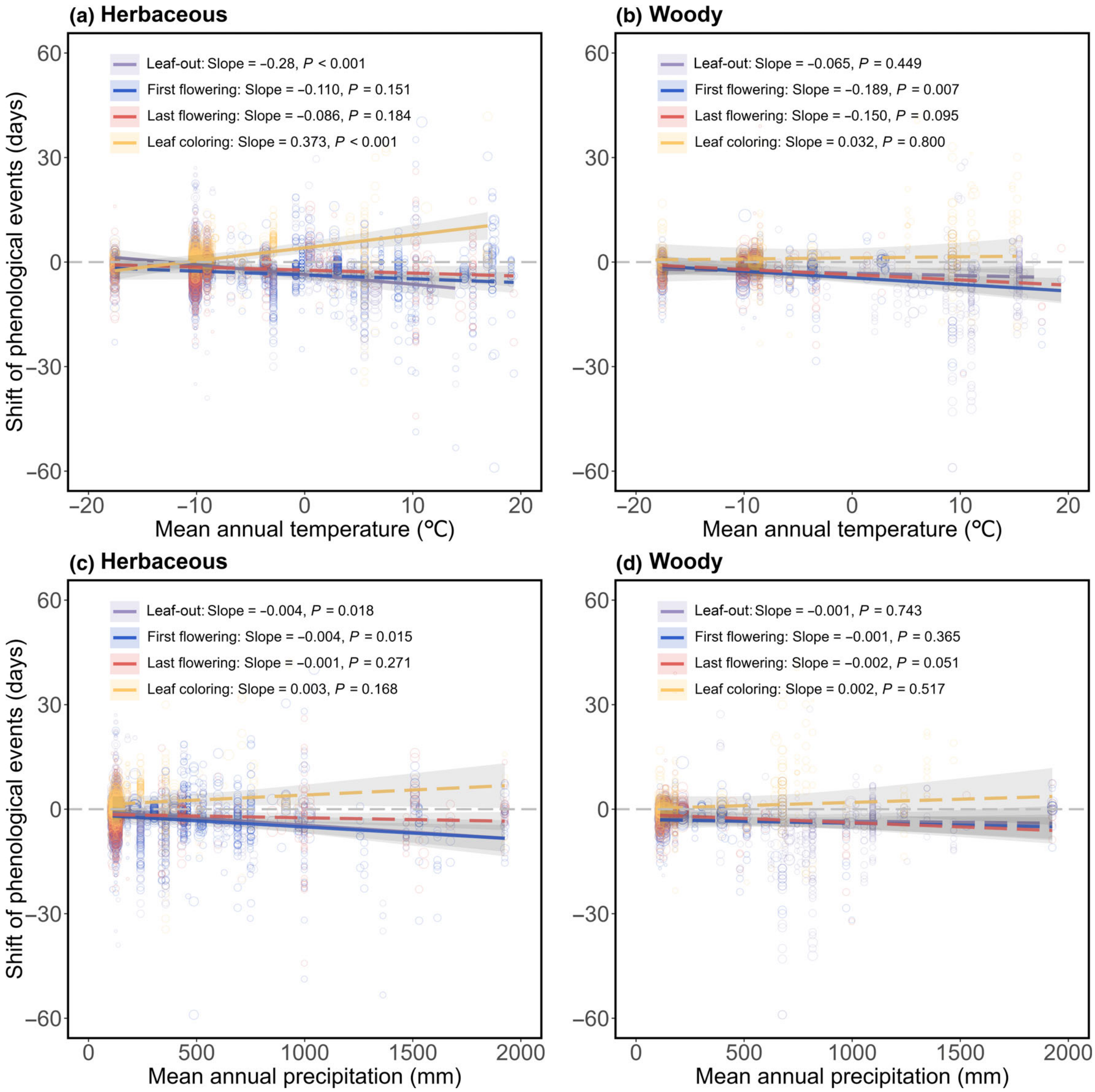

Fig. 5 Relationships between responses of plant phenology to warming and local temperature and precipitation. (a, b) Mean annual temperature. (c, d) Mean annual precipitation. The sizes of the circles are proportional to the weights of study cases. Dots are fitted by meta-regressions with 95% confidence intervals (shaded areas). Different colors represent leaf-out, first flowering, last flowering, and leaf coloring, respectively. Solid and dotted lines indicate whether the regressions are statistically significant ($P < 0.05$) or not ($P > 0.05$), respectively. The *P*-values and confidence intervals are generated from Wald-type tests in the hierarchical mixed-effect meta-analysis.

changes in plant phenology consume large amounts of nutrients and nonstructural carbohydrates in underground storage at the early warming stage (Wu *et al.*, 2012; Fu *et al.*, 2014; Naumann *et al.*, 2018). Furthermore, temperature may not be the most important contributing factor for plant phenology as the warming continues, and other constraints may become more important over longer timescales (Wookey *et al.*, 1995; Welker *et al.*, 1997; Barrett & Hollister, 2016). For instance, previous studies suggest that the dominant controls of plant phenology gradually shifted from temperature to soil nutrient availability in infertile ecosystems, or to light availability in forest systems (Ernakovich *et al.*, 2014; Forkel *et al.*, 2015). All of these mechanisms may potentially contribute to a decrease in plant phenological responses over time, and further experimentation is necessary to quantify their respective significance.

Based on theory and previous studies, it can be inferred that the observed short-term changes in phenology are predominantly driven by plant plasticity (Ramirez-Parada *et al.*, 2024). However, as the experimental duration increased, the variance of phenological changes gradually decreased (Fig. S10), suggesting a reduction in the level of plant plasticity (Salmela, 2014). The predictive theory suggests that if a species' plastic phenological responses become inadequate, plants may undergo evolutionary changes to better adapt to shifting conditions. Alternatively, a shift in reaction norms could lead to the replacement of less adaptive species by more suitable ones (Chevin *et al.*, 2010; Cleland *et al*., 2012; Zeng & Wolkovich, 2024). Herbaceous species, with their higher evolutionary rates and shorter generation times, are more likely to exhibit rapid evolutionary responses compared with woody plants (Smith & Donoghue, 2008). We did not detect particularly strong differences between the two groups of species, suggesting that the ability to adapt to new conditions is inherent for both types. In any case, this finding indicates that plants may be more phenologically adaptable to climate change than previously thought and that future long-term studies of climate warming should consider more abiotic constraints to plant fitness than just temperature.

Climatic factors that regulate plant phenology in response to climate warming

Supporting our third hypothesis, we found that the decelerated rates of phenological response with increasing warming magnitude were more pronounced in dry regions compared with wet regions. Warming increases evapotranspiration, and in more arid regions, the impact on plant water availability may inhibit the ability of plants to capitalize on warmer temperatures (Welker *et al*., 2004; Dorji *et al*., 2013; Xu *et al*., 2013). Furthermore, changes in plant phenology could be limited by their intrinsic life cycles (Forrest & Miller-Rushing, 2010; Piao *et al*., 2019). Short-lived plants that inhabit dry locations with brief seasonal windows have limited opportunities to expand phenophases under conditions of significant warming (Hereford *et al*., 2017). We also found that the species living in cold regions respond less to a high magnitude of warming than those in warm areas. This suggests that the higher magnitudes of warming may exceed the maximum thresholds that the species can capitalize in under cold regions (Elmendorf & Hollister, 2023).

Considering warming may increase evapotranspiration and lead to soil drought, it is plausible that water availability will constrain plant phenological responses over time, especially in dry regions (Welker *et al*., 2004; Dorji *et al*., 2013; Su *et al*., 2018). However, we seldom observed significant effects of MAP on temporal trends of the warming effect. This suggests that warming-induced soil drought may not play a major role in the attenuation of phenological responses over time. We suggest that it is necessary to incorporate temporal trends of other indicators, such as soil nutrients and plant nonstructural carbohydrates, to accurately assess the drivers influencing plant responses over time (Wang *et al*., 2014).

Concluding remarks

Understanding the trajectory of plant phenology is crucial for projecting ecosystem dynamics and functioning under future scenarios of climate warming. Our meta-analysis reveals a compelling correlation between the phenological responses of terrestrial plant species and the increasing warming magnitude or experimental duration. Notably, these associations vary across different plant types and are mediated by climatic factors. However, most plant phenology models do not consider changes in phenological responses due to the increasing magnitude of warming and the duration of experiments (Chuine & Régnière, 2017). Our results suggest that next-generation phenology models could be improved by explicitly incorporating the taxon- and phenophase-specific responses to rising temperatures over longer periods.

We recommend that future experimental investigations prioritize regions that are currently underrepresented in our dataset. It is worth noting that the majority of warming experiments have been concentrated in North America, Europe, and China, with only a limited number of experiments conducted in the Southern Hemisphere. In addition, our dataset lacks sufficient decadal warming experiments at low latitudes and does not include phenological data for tropical ecosystems. There is an urgent need for long-term experiments in low-latitude regions to deepen our understanding of terrestrial plants' phenological responses to warming. This will also enable us to improve global predictions of ecosystem functioning as our climate continues to change.

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Competing interests

None declared.

Author contributions

HL designed the research. CL compiled and analyzed the data. HL and CL wrote the first draft. KJvG, MAKG and J-SH dedicated a substantial amount of input to writing. MAKG, RDH, EP, EJC, JMW, ISJ, MM and ES provided insightful suggestions and raw data. NC, SMN and UM provided their raw data. YH, XM, JC, TY and HW contributed to the writing and discussion of the paper.

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Data availability

The data and code that support the findings of this study are openly available in the Figshare repository at https://doi.org/10.6084/m9.figshare.25460665.v1.

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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 Article selection process according to Preferred Reporting Items for Systematic Reviews guidelines.

Fig. S2 Frequency distribution of shifts of phenological events under warming.

Fig. S3 Phenological responses of deciduous and evergreen woody plants to experimental warming.

Fig. S4 Relationships between responses of plant phenology to warming and warming magnitude for experiments with multiple magnitudes of warming (span >4°C) at the same site.

Fig. S5 Significant relationships between responses of plant phenology across herbaceous and woody plants with latitude and climate factors.

Fig. S6 Responses of plant phenology to warming among different ecosystems.

Fig. S7 Comparisons of the responses of plant phenology among different warming methods.

Fig. S8 Significant interactive effects of warming magnitude and mean annual temperature and mean annual precipitation on responses of plant phenology.

Fig. S9 Significant interactive effects of experimental duration and mean annual temperature and mean annual precipitation on responses of plant phenology.

Fig. S10 Effect of experimental duration on variance in responses of phenophases to warming.

Table S1 Moderators for the warming responses of the different phenophases in this meta-analysis.

Table S2 Summary of specific phenophases concerning leaf-out, first flowering, last flowering, and leaf coloring in our dataset.

Table S3 Summary of results of publication bias analyses from Rosenthal's fail-safe number and Trim-and-fill tests for each phenophase.

Table S4 Model comparison results from several mixed effect models relating warming magnitude and experimental duration with the responses of plant phenology.

Table S5 Slope coefficients and *P* value of the climate factors in mixed effects models, with the warming magnitude and experimental duration being the fixed terms.

Table S6 Summary of partial correlation analysis between responses of phenology and mean annual temperature or mean annual precipitation.

Table S7 Summary of between-group *Q*-test statistics used to test the heterogeneity of responses of phenology explained by ecosystem type and warming method.

Table S8 *P* value of the estimated coefficient from mixed effect models relating warming magnitude and mean annual temperature or mean annual precipitation with the responses of plant phenology.

Table S9 *P* value of the estimated coefficient from mixed effect models relating experimental duration and mean annual temperature or mean annual precipitation with the responses of plant phenology.

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