

Wildflower phenological escape differs by continent and spring temperature

Received: 18 July 2022

Accepted: 11 November 2022

Published online: 22 November 2022

Benjamin R. Lee^{1,2,3,4}✉, Tara K. Miller⁴, Christoph Rosche^{5,6}, Yong Yang⁷, J. Mason Heberling^{1,2}, Sara E. Kuebbing^{2,8} & Richard B. Primack⁴

Temperate understory plant species are at risk from climate change and anthropogenic threats that include increased deer herbivory, habitat loss, pollinator declines and mismatch, and nutrient pollution. Recent work suggests that spring ephemeral wildflowers may be at additional risk due to phenological mismatch with deciduous canopy trees. The study of this dynamic, commonly referred to as “phenological escape”, and its sensitivity to spring temperature is limited to eastern North America. Here, we use herbarium specimens to show that phenological sensitivity to spring temperature is remarkably conserved for understory wildflowers across North America, Europe, and Asia, but that canopy trees in North America are significantly more sensitive to spring temperature compared to in Asia and Europe. We predict that advancing tree phenology will lead to decreasing spring light windows in North America while spring light windows will be maintained or even increase in Asia and Europe in response to projected climate warming.

Temperate deciduous forests are a dominant biome in the northern hemisphere, covering extensive regions in eastern Asia, continental Europe, and eastern North America¹. They are characterized by winter-deciduous plant species, and the phenology of leaf out and flowering on all three continents is sensitive to variation in average spring temperature^{2–5}. Furthermore, recent research has found disparities in phenological sensitivity among plants from different continents^{2,6}, suggesting that climate change may affect temperate forests differently depending on location.

Previous studies indicate differences in spring phenological sensitivity between woody and herbaceous plants in forests, with direct comparisons available for plants in Asia³ and North America^{5,7}. Evidence in Europe similarly suggests differences in sensitivities between woody and herbaceous plants^{8,9}. Herbaceous plants may be less sensitive to spring temperature than trees because the former often overwinter underground and, therefore, may not respond to the same phenological cues as the latter, which have extensive aboveground

structures^{10,11}, but this mechanism has only been studied in North American forests. This potential phenological mismatch is important because spring-active wildflowers in temperate deciduous forests, as well as some woody understory species^{12–15}, often rely on leafing out before the canopy closes in order to assimilate 40–100% of their annual carbon budget¹⁶. The success of this strategy to maximize the spring light window, referred to as “phenological escape”^{12,17}, is directly associated with patterns of growth^{10,12,17–19}, survival^{12,18–20}, flowering^{17,20}, and reproductive output^{10,17,21,22}. Recent studies suggest that the duration of spring light windows in eastern North America is likely to be significantly altered with warming climates^{7,13}, with herbaceous species generally expected to experience shorter spring light windows in the coming decades.

Experimental evidence for such mismatches, however, has generally been limited to comparisons of woody plants located in common garden experiments, which are limited in geographical and temporal extent and have not evaluated mismatch with understory

¹Section of Botany, Carnegie Museum of Natural History, Pittsburgh, PA, USA. ²Department of Biological Sciences, University of Pittsburgh, Pittsburgh, PA, USA. ³Holden Forests and Gardens, Kirtland, OH, USA. ⁴Biology Department, Boston University, Boston, MA, USA. ⁵Institute of Biology/Geobotany and Botanical Garden, Martin-Luther-University Halle-Wittenberg, Halle, Germany. ⁶German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Germany. ⁷Co-Innovation Center for Sustainable Forestry in Southern China, College of Biology and the Environment, Nanjing Forestry University, 159 Longpan Rd., Nanjing 210037, China. ⁸Yale Applied Science Synthesis Program, The Forest School at the School of the Environment, Yale University, 195 Prospect Street, New Haven, CT, USA. ✉e-mail: LeeB@CarnegieMNH.org

species. For example, Zohner and Renner^{6,23} have contributed valuable insights into interspecific variation in plant phenology using woody plants growing in European botanical gardens. It is unknown, however, if the variation in woody plant phenology found in common garden experiments are also observed at large scales, for forest trees growing in their natal environment, and across long time periods²⁴. It is similarly unknown whether understory herbaceous plant phenological sensitivity varies across large spatial and temporal scales.

Here we assess intercontinental, long-term data on the phenological sensitivity of canopy and understory forest plants and the potential for phenological mismatch across temperate forests in North America, Europe, and Asia. We evaluate the spring phenology of 5522 herbarium specimens collected between 1901 and 2020, representing 22 common tree and 18 common wildflower species found in temperate deciduous forests on three continents (six wildflower species per continent and six, six, and ten tree species in Europe, North America, and Asia, respectively; see full species list in Table S1 and distribution of observations in Fig. S1). Herbarium collections provide data from across large temporal (centuries) and spatial (intercontinental) scales difficult to match with other methods. Following previously validated methods^{25,26}, we model Leaf Out Date (LOD) of overstory canopy trees and First Flowering Date (FFD) of spring-blooming understory wildflowers (perennial herbaceous species that leaf out at approximately the same time as they flower in the early spring) in response to average spring (March–April) temperature of the collection year and location. This period is chosen because most (>99%) of the observed phenology occurred during or following this period (Fig. 1a; means and standard deviations are listed in Table S2) and because initial variable analysis identified this temperature variable as the best for predicting tree and wildflower spring phenology. Additionally, owing to the absence of daily weather records for the vast majority of years and sampling locations, especially Asia, we were unable to calculate and analyze finer-resolution daily temperature data for most geographic locations, which would be required for intercontinental comparisons (see Supplementary Information). We use estimated model parameter values to compare phenological sensitivities of trees and wildflowers among continents and to project how spring light window duration will change by the end of the current century based on projected climate trends. Our results suggest that there are differences in the sensitivity of trees (but not wildflowers), with North American trees considerably more sensitive to spring temperature than Asian or European trees. This difference has implications for phenological escape and the future conservation of the species-rich herbaceous layer in temperate deciduous forests as the climate continues to change.

Results and discussion

We used a hierarchical Bayesian modeling approach to evaluate the relationship between the spring phenology of tree and wildflower species and various climate drivers (see Methods). Following model selection, our final model structure included fixed effects of average spring (March–April) temperature and elevation, as well as species-level random effects. We show continental distributions of spring temperature values in Fig. 1b (means and standard deviations are listed in Table S2). We report estimates for spring temperature sensitivities from the final model structure in the main text. Parameter estimates for elevation sensitivities as well as the model performance of other potential drivers and combinations of drivers are reported in Tables S3 and S4. An extended discussion of model assumptions and limitations is included in the Supplementary Information.

Sensitivity differences by strata

Tree leaf out phenology (LOD) was substantially more sensitive to average spring temperature in North America (mean = -3.62 days $^{\circ}\text{C}^{-1}$; 95% credible interval (CI) = $[-3.76, -3.49]$) than in Europe (mean = -2.79 ; CI = $[-3.27, -2.30]$) and Asia (mean = -2.62 ; CI = $[-2.97, -2.26]$; Fig. 2). These values are consistent with previously reported phenological sensitivities in North America⁷ (-5.5 to -3.3 days $^{\circ}\text{C}^{-1}$) and Europe⁸ (-4.1 to -3.0 days $^{\circ}\text{C}^{-1}$), as the credible intervals from our results overlap with the reported credible intervals of prior studies. However, the Asian LOD sensitivity was less sensitive than previously reported²⁷ (-3.50 to -3.03 days $^{\circ}\text{C}^{-1}$), potentially owing to differences in species selection²⁸ or model structure. Previously reported sensitivities were determined in separate studies using either observational data^{7,8} or long-term observation-based weather station data²⁷. The general consistency between our findings suggests that phenology data from herbarium collections are good indicators of patterns in natural systems^{29–31}, a point supported by a recent study of phenological sensitivity derived from herbaria and from observed citizen science data³². These herbarium-based results provide evidence that phenological sensitivity differs across the temperate forest biome (but see ref. 33 for evidence of differences in response to warming and chilling accumulation). To our knowledge, our study is the first to contrast overstory and understory phenology across multiple continents and, therefore, to find differences in phenological sensitivity between trees and forest wildflowers across continents. We recommend future studies explore these differences using alternative approaches and methodologies that focus on the physiological basis for and mechanisms that underlie these patterns.

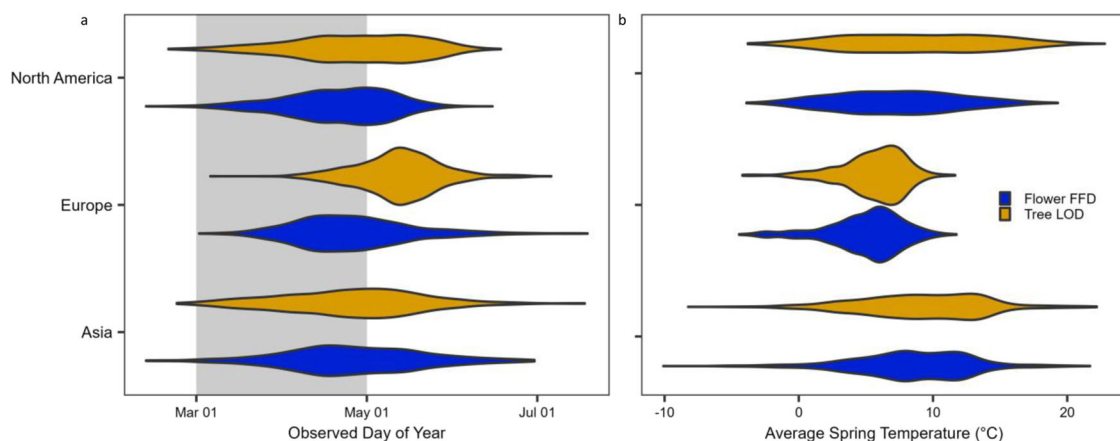


Fig. 1 | Distributions of observed phenology in the herbarium record by (a) observed date of phenology and (b) average spring (March–April) temperature ($^{\circ}\text{C}$). Distributions of observed understory wildflower First Flowering Date (FFD;

blue) and canopy tree Leaf-out Date (LOD; gold) in temperate forests in Asia, Europe, and North America. Grey shading behind the violin plots in panel a indicates the March–April period used to model and forecast phenology.

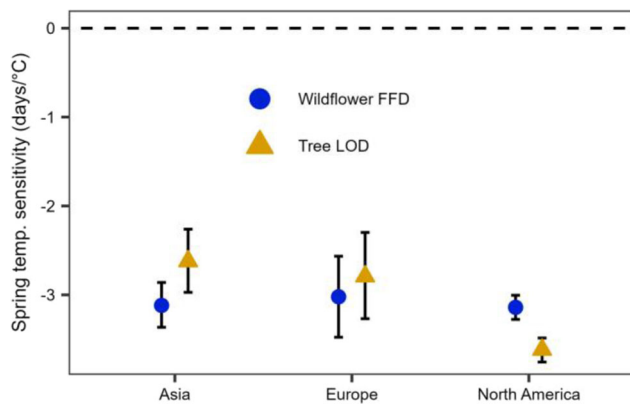


Fig. 2 | Posterior estimated means and 95% credible intervals for spring temperature sensitivity. Shapes represent parameter estimates for wildflower First Flower Date (FFD, blue circles; $n = 1418, 618$, and 1060 for Asia, Europe, and North America, respectively) and canopy tree Leaf Out Date (LOD, yellow triangles; $n = 899, 532$, and 995 , for Asia, Europe, and North America, respectively). Estimates are considered different from 0 if credible intervals do not overlap the dashed 0 line and are considered different from each other if credible intervals do not overlap.

In contrast to trees, wildflower sensitivity to spring temperature was similar across all three continents and exhibited no strong differences (i.e., overlap in 95% Bayesian credible intervals) among continents (means and 95% credible intervals in brackets: North America = -3.14 , $[-3.28, -3.00]$; Europe = -3.02 , $[-3.48, -2.56]$; Asia = -3.12 , $[-3.36, -2.86]$; Fig. 2). These values are also generally consistent with those reported elsewhere in the literature (i.e., 95% credible intervals overlap with those reported in other studies; -2.2 , $[-3.7, -0.76]$ days $^{\circ}\text{C}^{-1}$ in North America⁷ and -3.6 , $[-4.04, -3.18]$ days $^{\circ}\text{C}^{-1}$ in Europe⁹), although we are unaware of any studies that have estimated phenological sensitivity for Asian forest wildflowers in days $^{\circ}\text{C}^{-1}$. Ge et al.³ report herbaceous plant sensitivity of -5.71 days per decade in Asia (± 7.90 standard deviation; based primarily on long-term observational data), which appears to be roughly consistent with our model results, but the difference in units makes this more speculative than the other comparisons. Discrepancies in mean responses between this study and others may be due in part to different types of data (herbarium specimens versus field observations) and to choice in focal taxa, as temperature sensitivity has been shown to vary widely across taxa²⁸.

Particularly noticeable in our results was that r^2 coefficients of predicted versus observed phenology were much higher in North America (0.70 and 0.76 for wildflower and tree models, respectively) compared to Asian (0.40 and 0.44, respectively) and European models (0.41 and 0.25, respectively). This difference in model performance could be due to the higher interannual variability of spring temperatures in North America³³, leading to greater selective pressure for strong sensitivity to spring temperatures in North American plants. This difference could explain why North American species exhibit higher correlation of phenology with average spring temperatures (Table S4). Alternatively, European and Asian species may have stronger phenological responses to alternative spring forcing windows, winter chilling temperatures, or photoperiod, relative to the March–April temperature period used in this study (see Methods). We think the latter explanation is unlikely, given the strong correlations of phenology with spring temperature across all continents (see Supplementary Information – Justification for March–April Temperature Window).

Herbarium-based phenological models may be improved by accounting for spatial autocorrelation within the dataset. For example, Willems et al.⁹ found that including spatial autocorrelation significantly

improved predictability of European herbaceous flowering phenology, even when accounting for multiple drivers of spring phenology. We followed a similar approach as their study and found similar improvements in model performance with the addition of spatial autocorrelation (Tables S3–S4) that had substantial positive effects on r^2 values of Asian and European models. However, spatial distributions of specimens differed substantially among continents (see Figs. S2–S4), and these differences could lead to artifacts that make results unreliable to interpret (see Supplementary Information). Therefore, we focus here on results for models without spatial autocorrelation while acknowledging that spatial aggregation of herbarium specimens in Europe and Asia may be partially responsible for the relatively lower r^2 values. We encourage other researchers to explore this question further both with our data set and other datasets.

Climate change and spring light windows

The relative difference between wildflower and tree sensitivity varied substantially among continents, with wildflowers being approximately equally as sensitive to spring temperature as trees in Asia and Europe but substantially less sensitive (i.e., 95% BCI do not overlap) than trees in North America (Fig. 2). Importantly, these differences were driven by changes in tree phenological sensitivities among continents and resulted in different expectations for spring light window duration (i.e., the difference in time between estimated wildflower flowering date and canopy tree leaf out date) on different continents under current climate conditions (Fig. 3), based on modeled leaf out and flowering under a climate scenario derived from average climate conditions from 2009–2018 (Fig. S5).

Interestingly, the time between leaf out and flowering in North America is greater in the north than in the south (Fig. 3c), indicating a greater spring light window duration at higher latitudes. In addition, although there was regional variation in spring light window duration on each continent, there was broad overlap in duration among continents estimated under current environmental conditions (North America light window duration averages 11.7 ± 4.1 s.d. days; European duration averages 14.7 ± 3.0 s.d. days; and Asian duration averages 8.0 ± 4.6 s.d. days). This suggests that, under current climate conditions, wildflowers across all continents experience similar length of spring light windows, but the impact of warming on shrinking or expanding window size will differ among continents with uncertain impacts on wildflower populations.

Still, differences among continents resulted in different projections for how spring light window duration will respond to climate change over the coming century (Fig. 4), which will likely have implications for understory plant demography^{7,12,13,16}. We used climate change projections for 2081–2100 (assuming an extreme climate change scenario; Institut Pierre-Simon Laplace CM6A-LR climate model – shared socioeconomic pathway 585; see Methods for more details) to forecast wildflower flowering date and canopy tree leaf-out date for the end of the current century (Fig. S6) and then calculated the difference between forecasted wildflower flowering and tree leaf out phenology for the period of 2081–2100 (future spring light window duration; Fig. S7). To estimate the change in spring light window duration between now and the end of the century (Fig. 4), we subtracted the forecasted future light window duration from the modeled light window duration under current climate conditions.

Dramatic differences in the projected change in spring light window duration emerged, ranging from increasing spring light window durations for wildflowers in Asia, to minimal change in spring light window length in Europe, to decreasing spring light window length in North America. Importantly, these differences in phenological escape trajectories are primarily attributable to differences in phenological sensitivities between overstory and understory species and not to differences in projected spring temperature changes among

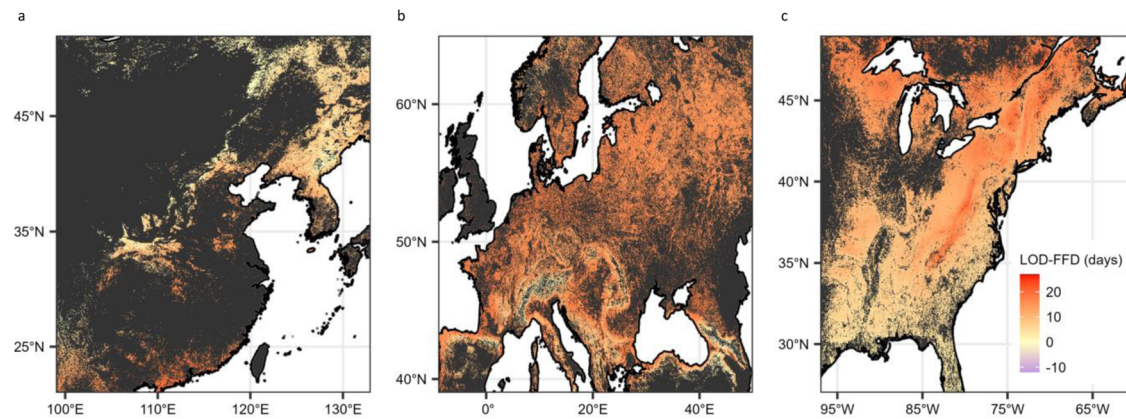


Fig. 3 | Current estimated phenological escape duration in northern temperate deciduous forests. Estimated mean difference between wildflower First Flower Date (FFD) and canopy tree Leaf Out Date (LOD) (in days) under current climate conditions (averaged from 2009–2018, see methods) in **a** Asia, **b** Europe, and **c** North America. Negative values indicate tree LOD is estimated to occur before

wildflower FFD. Estimations were cropped by the estimated area of broadleaf and mixed-broadleaf forest (see methods). Dark gray regions indicate areas where the consensus land classification is <1% deciduous or mixed deciduous forest cover. An uncropped version of this figure is available in Fig. S11.

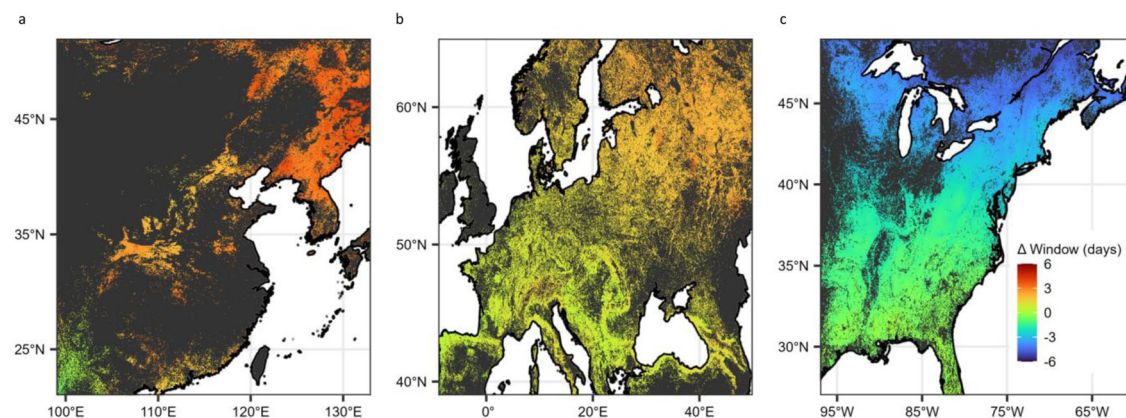


Fig. 4 | Projected changes in phenological escape between current climate conditions and those projected for the end of this century. Projected change in spring light window duration (Δ Window, days) in **a** Asia, **b** Europe, and **c** North America. Positive values indicate regions where light window duration is expected to increase with spring warming (particularly in northern Asia) and negative values

indicate where it is expected to decrease (particularly in northern North America). Dark gray regions indicate areas where the consensus land classification is <1% deciduous or mixed deciduous forest cover. An uncropped version of this figure is available in Fig. S12.

continents. Projected changes in March–April temperature broadly overlapped across continents (mean $\pm$ s.d. of projected change in spring temperature is $5.41 \pm 1.87^\circ\text{C}$, $6.36 \pm 2.36^\circ\text{C}$, and $5.04 \pm 2.92^\circ\text{C}$ in Asia, Europe, and North America, respectively; Fig. S8). Intracontinental differences, however, such as the more extreme projected changes in phenological escape in the northern regions of each continent, are due to gradients of projected spring temperature change across latitudes, with higher latitude regions expected to experience greater spring warming relative to lower latitudes^{34,35}.

The North American results are consistent with findings from a previous study that similarly predicted reduction in access to spring light at a single site in the U.S. Northeast⁷. Although no previous studies have specifically addressed phenological escape in Asia, our results are consistent with previous research that found higher sensitivity to spring temperature for Asian herbaceous plants compared to Asian woody trees and shrubs³. Similarly, we are not aware of European studies that have directly compared phenological sensitivity between wildflowers and trees nor that have quantified phenological escape, but our estimates of sensitivity are consistent with previously reported values^{8,9}. Together, this supports our conclusion that the duration of spring light windows will be differently affected by climate change on different continents.

Importantly, it is impossible to fully measure the ecological and demographic implications of these results using herbarium specimens. Linking changing access to light to changes in photosynthetic carbon assimilation, growth, and survival necessitates the use of experimental studies of living specimens such as those previously conducted in eastern North America^{7,12,13,16}. Previous studies that have done so have linked access to spring light before canopy closure with the growth^{10,12,17–19}, survival^{12,18–20}, flowering^{17,20}, and reproductive output^{10,17,21,22} of understory plant species. This large body of research suggests that reductions in access to spring light can have negative ramifications for the demographic success of understory species.

For example, projected reductions of several days in phenological escape may not intuitively seem like much, but the spring ephemeral wildflowers in this study have growing seasons that last only 3–5 weeks. A decrease in one day of phenological escape can therefore be as much as a 4% loss of total growing season length. In a study of phenological escape in sugar maple seedlings, Kwit et al.¹⁴ found that increasing access to spring light by three days could increase photosynthetic carbon assimilation by more than 50%, an amount that other studies suggest would substantially increase annual growth and probability of survival^{12,13}. For spring ephemeral herbaceous plants, Heberling et al.¹⁶ showed that a similar three-day loss in access to

spring light resulted in up to a 30% loss in spring carbon assimilation. It is important to note, however, that the exact impacts of change in phenological escape on plant performance in Asia and Europe remains to be directly measured.

Thus, although our results suggest strong differences in change in performance when assuming the minimal differences in photosynthetic rates among species on different continents, it is possible that systematic intercontinental differences could lead to different outcomes. For example, if spring wildflowers were to be shown to have much lower spring photosynthetic rates, differences in projected access to light could have much less impact on overall carbon assimilation and demographic performance. Still, others have found relatively strong relationships between spring light availability and understory plant performance on other continents²¹, suggesting that photosynthetic rates are similar enough to be comparable in this study. Therefore, we conclude that the relatively small changes in spring light availability projected here are likely to have substantial ecological consequences for the performance and demography of understory plant species.

The future for spring ephemerals

The herbaceous layer accounts for more than 80% of plant species in temperate forests worldwide³⁶ and provides a critical role in the functioning of these ecosystems³⁷. Understory wildflower species face many threats that include deer herbivory^{38–40}, habitat loss⁴¹, pollinator declines⁴² and mismatch^{43,44}, presence of nonnative, invasive plants^{45,46}, and nutrient pollution^{47,48}. Furthermore, there is substantial evidence that many of these species are limited in their dispersal ability^{41,49} and populations are likely unable to shift their distributions as rapidly as regional climates are predicted to warm. Our results show that mismatch between understory and overstory phenology, specifically in North America, is another concern for this already threatened group^{36,50}. Reductions in spring light windows will likely lead to reduced carbon gains each year for spring forest wildflowers^{7,16}, which may ultimately lead to population decline as plant fitness declines. Therefore, we highlight the need for future conservation efforts to consider the impact of loss of spring light in restoration planning, with simultaneous studies of overstory and understory responses together³⁷. Furthermore, this information may assist conservation practitioners in their decisions of where to focus management or conservation efforts based on projected changes to future forest ecosystems.

The patterns examined in this study point to distinctions in plant phenological responses among continents, but they cannot provide a mechanistic explanation for why these differences exist. Wildflowers and trees advance their phenology with warming spring temperatures, for example, but why are North American trees more responsive than co-occurring wildflower species to warming? Some speculate it is because perennial wildflowers overwinter underground whereas tree buds overwinter aboveground; trees may therefore be more affected by air temperature relative to wildflowers^{10,11}. Although global soil and near-surface temperature data are recently becoming available⁵¹, there are as yet no historical estimates of soil temperatures for use in herbarium studies. Thus, future empirical studies will be needed to directly test this theory. Similarly, what are the mechanisms that allow North American trees to be more sensitive to spring temperature than trees in Europe and Asia? Studies using dormant twigs, potted seedlings, and trees growing in botanical gardens are possible methods for investigating this. Common garden experiments with manipulated treatments may provide a more mechanistic understanding of our observations, including to rule out potentially confounding variables such as intercontinental differences in soil properties, precipitation, and photoperiod.

Other recent research highlights the growing need to assess the potential for nonlinear phenological responses to spring warming. As

reviewed by Wolkovich et al.⁵², future phenological responses to spring warming may be nonlinear owing to a number of reasons (including threshold responses to extreme environmental conditions and interactions among drivers besides spring forcing). Accounting for factors that might drive nonlinearities in plant phenological response to warming will necessitate controlled experiments^{52,53}, which was not possible with the observational herbarium dataset used in our study. We did not find evidence for nonlinear responses to spring temperature, but we acknowledge that experimental studies that can experimentally manipulate and test for the impacts of spring forcing, winter chilling, and photoperiodic effects on plant phenology could further illuminate how nonlinearity affects phenological escape. Also, nonlinear responses may become more evident in the future if extreme weather conditions occur more frequently.

Our study represents an early attempt to address phenological questions using herbarium specimens at the intercontinental level. Digitization of herbarium specimens and other historical data and citizen science programs like iNaturalist and iSpot are making data increasingly available and enabling new research⁵⁴. Additional research that utilizes international herbaria and collaborations to synthesize these data at a global scale will aid in addressing pressing ecological and climate change questions.

In sum, our results indicate that spring ephemeral wildflowers are similarly sensitive to spring warming across temperate forests in Asia, Europe, and North America, but that deciduous canopy trees in North America are more sensitive to spring warming compared to trees on the other two continents. Furthermore, differences in tree leaf-out sensitivity mean that North American wildflowers are projected to experience decreasing access to spring light under climate change conditions, whereas those in Asia and Europe are unlikely to experience substantial gains or losses in spring light availability. These intercontinental differences suggest that climate change may adversely affect spring ephemerals in North America more than on the other two continents, and thus that North American wildflowers may be especially threatened by warming springs.

Methods

Phenological data

Herbarium specimens from North America (see Miller et al.⁵), East Asia, and Europe were evaluated for common species of deciduous overstory tree species and understory deciduous wildflowers, prioritizing congeneric species living on more than one continent when possible, and with genus and family in mind when not possible. Specimens were scored for either Leaf Out Date²⁵ (LOD, tree species) or First Flowering Date^{26,31} (FFD, wildflower species), consistent with previous studies comparing phenology across forest strata^{7,55}. This approach assumes that herbaceous species' flowering time is tightly correlated with the timing of leaf out for these species⁷. This approach is currently widely accepted to be the best we have to assess shifts in phenology using herbarium specimens³¹, but see also Buonaiuto et al.⁵⁶. In particular, we selected wildflower species that flowered and leafed out at approximately the same time in early spring.

Specifically, we searched digitized repositories of herbarium collections on each of the three target continents. Digitized Asian herbarium specimens were provided by the Chinese Virtual Herbarium (<https://www.cvh.ac.cn/>) and Chinese Field Herbarium (<http://english.ib.cas.cn/>). European specimens were located and collated using the Global Biodiversity Information Facility (gbif; <https://www.gbif.org/>). In North America, digitized specimens were collated from seven online repositories, further detailed in Miller et al.⁵. We conducted searches for each species independently, prioritizing spring ephemeral wildflowers and deciduous tree species with the highest number of available observations across most of the relevant

geographic range. We then filtered our initial searches by phenophase (scored by hand), making sure we only included observations that were flowering (for the wildflowers) or newly leafed out (trees). Next, we identified specimens that were missing information but for which digitized images of the specimen sheet were available. For these individuals, we entered missing phenological and georeferencing data when available (see below). Individuals with missing information and that either were not fully digitized or that did not include the necessary information on the digitized herbarium sheet were excluded from further study.

Specimens were georeferenced by researchers fluent in the languages in which the specimen data were collected in. Georeferencing was completed using the most precise geographic scale recorded at time of collection (i.e., prioritized by exact coordinates, town/locality, county). Specimens that did not identify location to at least county (in North America) or locality-level (in Asia and Europe) were excluded from this analysis, which is common practice in herbarium studies given the lack of precise geolocation data for some older specimens. Only specimens collected within each species' native range were used. Specimens collected prior to 1901 were excluded because climate estimates were not available prior to this year⁵⁷. In total, after accounting for specimens that were excluded from our original search, we collected data for a total of 40 species (22 tree species and 18 herbaceous species; Table S1) consisting of 5,522 individual specimens. The complete dataset of herbarium specimens used in this analysis is freely available⁵⁸.

Climate data

Climate data were extracted from the Climate Research Unit gridded Temperature Series (CRU TS) data set⁵⁷ v4.05 using the georeferenced location for each specimen. Spring temperature was calculated as the average of the March and April average monthly temperatures for the year and the location associated with each specimen. This metric is consistent with other studies which found this period to be important in cueing temperate plant phenology^{5,7,13,55} and preliminary analysis indicated that this was the best spring temperature metric for modeling plant phenological responses in our dataset (see *Justification for March–April Temperature Window*). Daily weather records were not available for many years and many locations.

Justification for March–April Temperature Window

Prior to conducting our analysis, we explored the correlation strengths between different spring temperature windows and observed phenology day of year (DOY). We made the decision to use a fixed average March–April temperature window for several reasons. First, we were limited in how we evaluated spring forcing effects by the type of data/climate estimates we were able to access. Due to the nature of the historical herbarium specimens we used in this study, we were limited to using historical average temperature estimates aggregated at the monthly level. We were, therefore, unable to use more nuanced modeling approaches such as moving windows or accumulation metrics like growing degree days (e.g., ref. 59).

Next, we evaluated correlation coefficients between different spring temperature windows (one-, two-, or three-month averages) from between February and May to determine which window led to the highest correlative strength with observed phenology. We determined that the March–April window had consistently high correlative strength for wildflower and tree phenology across all continents (Fig. S9), indicating that it was a robust predictor of spring phenology. This makes intuitive sense, as the vast majority (83%) of observations in our study occurred during or after DOY 96 (–March 15th) and nearly all observations (99%) occurring on or after DOY 60 (–March 1st; Fig. 1a).

Lastly, using a fixed March–April temperature window allows us to directly compare our results to other phenological escape studies using the same window^{5,7,13}.

Models and analysis

We modeled the day of the observed phenological event (OPE) for individual i of species j using a normal likelihood distribution:

$$OPE_{i,j} \sim N(\mu_{i,j}, \sigma^2) \quad (1)$$

The mean, μ , was modeled with an intercept term (β_0), slope terms representing phenological sensitivity to average spring temperature (β_1) and elevation (β_2), and species random effects (α_j):

$$\mu_{i,j} = \beta_0 + \beta_1 \times \text{SpringT}_i + \beta_2 \times \text{Elevation}_i + \alpha_j \quad (2)$$

We used slightly informative priors to estimate parameters: $\beta_0, \beta_1, \beta_2, \alpha_j \sim N(0, 1E-3)$; $1/\sigma^2 \sim \text{Uniform}(0, 100)$. Other potential drivers of leaf-out and flowering phenology were explored in preliminary analysis (i.e., winter temperatures, annual precipitation, and spring precipitation), but these drivers did not generally improve model performance (Table S3) and were thus excluded from the model structure.

Models were run separately for each stratum (i.e., tree vs. herbaceous) x continent combination using the *R2jags* package⁶⁰ (v0.7-1) in R v4.1.0. Parameter values (means, variances, and covariances) were estimated from posterior distributions and are considered significantly different if the 95% Bayesian credible intervals (BCIs) of their posterior distributions do not overlap. Model code and data used to fit each model are publicly available⁵⁸.

Description of spatial autocorrelation models

Spring leaf-out and flowering phenology have been extensively linked to many drivers, including spring and winter temperatures, inter-annual variability in temperature, photoperiod, the timing of snow-melt, precipitation, and elevation^{2,5,7,9,12,61,62}. Importantly, many of these drivers covary along geographical gradients and particularly latitudinal gradients. Recent work published by Willems et al.⁹ found that spatial autocorrelation among observations improved predictability of understory plant phenology in Europe, even when a host of other drivers were already accounted for. Their results thus suggest that there may be effects that are not commonly accounted for in phenology models associated with spatial proximity of the observations and that including spatial autocorrelation in such models could be important.

In this study, we first evaluated the fit of our phenological models using different combinations of potential drivers that included average spring temperature, average winter temperature, annual precipitation, spring precipitation, and elevation. We then assessed how incorporating spatial autocorrelation into the model structure affected model fit and posterior distributions of model parameters. To do so, we incorporated Integrated Nested Laplace Approximations (INLA) that include a spatial autocorrelation term into the model structure via the *inlabru* package⁶³ in R.

INLA modeling uses Stochastic Partial Differential Equations (SPDEs) as opposed to MCMC approximation methods⁶⁴ but has been demonstrated to maintain high fidelity to MCMC posterior estimates^{65,66} and has the added advantage of allowing for the much faster estimation of spatial autocorrelative effects^{64,66}. To account for the potential effects of including spatial autocorrelation on our results, we ran the original model structure using *inlabru* instead of *rjags* without and then with the spatial autocorrelation term added to it. Model fit and performance for *inlabru* models with and without spatial autocorrelation are located in Table S3. Comparison of parameter posterior estimates are located in Table S4. Matérn correlation functions were constructed in *inlabru* with a maximum edge length of 0.5 decimal degrees and a cutoff value of 0.25 decimal degrees. Resulting meshes can be found in Fig. S10.

A summary of results from this version of the analysis that includes spatial autocorrelation effects, as well as a detailed justification for having excluded them in the final analysis presented here, is included in the Supplementary Information.

Climate Change Modeling

To forecast changes in the duration of spring light windows, we compared FFD and LOD from two different climate simulations. The first simulation represented current environmental conditions and was estimated by taking the average of spring (March–April) temperatures from a recent ten-year period (2009–2018). Climate and elevation data were downscaled from the CRU TS4.03⁵⁷ dataset using WorldClim 2.1⁶⁷ for bias correction at a resolution of 2.5 min. The average monthly temperature for each month and each year was calculated as the mean of monthly minimum and maximum temperatures.

The second simulation represents projected environmental conditions under climate change at the end of this century (2081–2100). Climate data used in this simulation were downscaled (using WorldClim 2.1⁶⁷) from the Institut Pierre-Simon Laplace (IPSL) CM6A-LR climate model^{34,68}, which is part of the ongoing Climate Model Intercomparison Project³⁵ (CMIP6). We specifically used forecasts based on the Shared Socioeconomic Pathway (SSP) 585, which is analogous to the Representative Concentration Pathway (RCP) 8.5 from CMIP5 and earlier. This SSP is the most extreme, “business as usual”, pathway used by the Intergovernmental Panel on Climate Change (IPCC). Therefore, projections made using this pathway represent the extreme threshold of climate change effects by the end of the century.

Model output is presented for regions where land-use is classified as > 1% temperate deciduous forest type according to a consensus of four global land-use models¹ (uncropped versions of figures can be found in the Supplementary Information as Figs. S11–12). Herbarium specimens were included in the above analyses regardless of the land-use classification of the respective georeferenced locations. We did not find consistent effects of land-use on phenological sensitivity, so we did not include this variable as a fixed effect in the final model. Still, we only present output for land areas currently covered by deciduous forests as those are so far the only systems where phenological escape has been shown to be important^{5,7,10,12,13,16}.

Approximations of FFD and LOD (for wildflowers and trees, respectively), were calculated using posterior mean estimates of the slopes, intercepts, and species-level random effects of our models (Tables S4–S7). Spring light window length was then calculated as the difference (in days) between FLD and LOD in each simulation X continent combination. Data processing and handling were completed primarily using the *ncdf4*⁶⁹, *stars*⁷⁰, and *sp*⁷¹ packages in R v4.1.0.

Inclusion and ethics statement. The work presented here is the culmination of international collaboration and facilitation. Herbarium specimens were collated across three continents by researchers in those locations who spoke the language(s) in which information was recorded. All researchers who led these efforts are coauthors of this manuscript, and their employees and lab members who assisted in this effort are listed in the Acknowledgements section. Local and regional studies have been cited throughout this document, further acknowledging the contributions of global scholars to our work and to science as a whole.

Reporting summary

Further information on research design is available in the Nature Portfolio Reporting Summary linked to this article.

Data availability

The individual specimen phenology and environmental conditions data generated in this study have been deposited in the Zenodo

database at <https://doi.org/10.5281/zenodo.7080193>. The processed spatial autocorrelation data are available in the same location. Past, current, and future climate estimates were acquired from the WorldClim 2.1 [<https://www.worldclim.org/data/index.html>] and CRU TS4.03 [<https://crudata.uea.ac.uk/cru/data/hrg/>] datasets.

Code availability

Examples of code used in this analysis are freely available at <https://doi.org/10.5281/zenodo.7080193>.

References

1. Tuanmu, M. N. & Jetz, W. A global 1-km consensus land-cover product for biodiversity and ecosystem modelling. *Glob. Ecol. Biogeogr.* **23**, 1031–1045 (2014).
2. Piao, S. et al. Plant phenology and global climate change: current progresses and challenges. *Glob. Change Biol.* **25**, 1922–1940 (2019).
3. Ge, Q., Wang, H., Rutishauser, T. & Dai, J. Phenological response to climate change in China: A meta-analysis. *Glob. Change Biol.* **21**, 265–274 (2015).
4. Menzel, A. et al. European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12**, 1969–1976 (2006).
5. Miller, T. K., Heberling, J. M., Kuebbing, S. E. & Primack, R. B. Warming temperatures are linked to phenological mismatch among native and non-native trees, shrubs, and wildflowers across the Eastern Deciduous Forest of North America. *J. Ecol.* <https://doi.org/10.1111/1365-2745.14021> (2022).
6. Zohner, C. M. & Renner, S. S. Common garden comparison of the leaf-out phenology of woody species from different native climates, combined with herbarium records, forecasts long-term change. *Ecol. Lett.* **17**, 1016–1025 (2014).
7. Heberling, J. M., McDonough MacKenzie, C., Fridley, J. D., Kalisz, S. & Primack, R. B. Phenological mismatch with trees reduces wildflower carbon budgets. *Ecol. Lett.* **22**, 616–623 (2019).
8. Wang, H. et al. Impacts of global warming on phenology of spring leaf unfolding remain stable in the long run. *Int. J. Biometeorol.* **61**, 287–292 (2017).
9. Willems, F. M., Scheepens, J. F. & Bosdorf, O. Forest wildflowers bloom earlier as Europe warms: lessons from herbaria and spatial modelling. *N. Phytologist* **235**, 52–65 (2022).
10. Routhier, M. C. & Lapointe, L. Impact of tree leaf phenology on growth rates and reproduction in the spring flowering species *Trillium erectum* (Liliaceae). *Am. J. Bot.* **89**, 500–505 (2002).
11. Neufeld, H. S. & Young, D. R. Ecophysiology of the Herbaceous Layer in Temperate Deciduous Forests. In *The Herbaceous Layer in Forests of Eastern North America* (ed. Gilliam, F. S.) 35–95 (Oxford University Press, 2014). <https://doi.org/10.1093/acprof:osobl/9780199837656.003.0003>.
12. Lee, B. R. & Ibáñez, I. Spring phenological escape is critical for the survival of temperate tree seedlings. *Funct. Ecol.* 1365–2435.13821 <https://doi.org/10.1111/1365-2435.13821> (2021).
13. Lee, B. R. & Ibáñez, I. Improved phenological escape can help temperate tree seedlings maintain demographic performance under climate change conditions. *Glob. Chang. Biol.* 3883–3897 <https://doi.org/10.1111/gcb.15678> (2021).
14. Kwit, M. C., Rigg, L. S. & Goldblum, D. Sugar maple seedling carbon assimilation at the northern limit of its range: the importance of seasonal light. *Can. J. Res.* **40**, 385–393 (2010).
15. Augspurger, C. K. & Bartlett, E. A. Differences in leaf phenology between juvenile and adult trees in a temperate deciduous forest. *Tree Physiol.* **23**, 517–525 (2003).
16. Heberling, J. M., Cassidy, S. T., Fridley, J. D. & Kalisz, S. Carbon gain phenologies of spring-flowering perennials in a deciduous forest

- indicate a novel niche for a widespread invader. *N. Phytologist* **221**, 778–788 (2019).
17. Jacques, M. H. et al. Responses of two understory herbs, *Maianthemum canadense* and *Eurybia macrophylla*, to experimental forest warming: Early emergence is the key to enhanced reproductive output. *Am. J. Bot.* **102**, 1610–1624 (2015).
 18. Augspurger, C. K. Early spring leaf out enhances growth and survival of saplings in a temperate deciduous forest. *Oecologia* **156**, 281–286 (2008).
 19. Seiwa, K. Advantages of early germination for growth and survival of seedlings of *Acer mono* under different overstorey phenologies in deciduous broad-leaved forests. *J. Ecol.* **86**, 219–228 (1998).
 20. Augspurger, C. K. & Salk, C. F. Constraints of cold and shade on the phenology of spring ephemeral herb species. *J. Ecol.* **105**, 246–254 (2017).
 21. Ida, T. Y. & Kudo, G. Timing of canopy closure influences carbon translocation and seed production of an understory herb, *Trillium apetalon* (Trilliaceae). *Ann. Bot.* **101**, 435–446 (2008).
 22. Lapointe, L. Fruit development in *trillium*: dependence on stem carbohydrate reserves. *Plant. Physiol.* **117**, 183–188 (1998).
 23. Zohner, C. M. & Renner, S. S. Innately shorter vegetation periods in North American species explain native-non-native phenological asymmetries. *Nat. Ecol. Evol.* **1**, 1655–1660 (2017).
 24. Cleland, E. E. et al. Phenological tracking enables positive species responses to climate change. *Ecology* **93**, 1765–1771 (2012).
 25. Everill, P. H., Primack, R. B., Ellwood, E. R. & Melaas, E. K. Determining past leaf-out times of New England's deciduous forests from herbarium specimens. *Am. J. Bot.* **101**, 1293–1300 (2014).
 26. Primack, D., Imbres, C., Primack, R. B. & Miller-Rushing, A. J. & Del Tredici, P. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *Am. J. Bot.* **91**, 1260–1264 (2004).
 27. Ibáñez, I. et al. Forecasting phenology under global warming. *Philos. Trans. R. Soc. B: Biol. Sci.* **365**, 3247–3260 (2010).
 28. Vitasse, Y. et al. Leaf phenology sensitivity to temperature in European trees: Do within-species populations exhibit similar responses? *Agric. Meteorol.* **149**, 735–744 (2009).
 29. Miller, T. K., Gallinat, A. S., Smith, L. C. & Primack, R. B. Comparing fruiting phenology across two historical datasets: Thoreau's observations and herbarium specimens. *Ann. Bot.* **128**, 159–170 (2021).
 30. Heberling, J. M. Herbaria as big data sources of plant traits. *Int. J. Plant. Sci.* **183**, 87–118 (2022).
 31. Davis, C. C., Willis, C. G., Connolly, B., Kelly, C. & Ellison, A. M. Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *Am. J. Bot.* **102**, 1599–1609 (2015).
 32. Ramirez-Parada, T. H., Park, I. W. & Mazer, S. J. Herbarium specimens provide reliable estimates of phenological responses to climate at unparalleled taxonomic and spatiotemporal scales. *Ecography* **2022**, <https://doi.org/10.1111/ecog.06173> (2022).
 33. Zohner, C. M., Benito, B. M., Fridley, J. D., Svenning, J. C. & Renner, S. S. Spring predictability explains different leaf-out strategies in the woody floras of North America, Europe and East Asia. *Ecol. Lett.* **20**, 452–460 (2017).
 34. Boucher, O. et al. Presentation and evaluation of the IPSL-CM6A-LR climate model. *J. Adv. Modeling Earth Syst.* **12**, 1–52 (2020).
 35. Eyring, V. et al. Overview of the coupled model intercomparison project phase 6 (CMIP6) experimental design and organization. *Geoscientific Model. Dev.* **9**, 1937–1958 (2016).
 36. Gilliam, F. S. The ecological significance of the herbaceous layer in temperate forest ecosystems. *BioScience* **57**, 845–858 (2007).
 37. Landuyt, D. et al. The functional role of temperate forest understory vegetation in a changing world. *Glob. Change Biol.* **25**, 3625–3641 (2019).
 38. Frerker, K., Sabo, A. & Waller, D. Long-term regional shifts in plant community composition are largely explained by local deer impact experiments. *PLoS ONE* **9**, 1–17 (2014).
 39. Knight, T. M., Dunn, J. L., Smith, L. A., Davis, J. & Kalisz, S. Deer facilitate invasive plant success in a Pennsylvania forest understory. *Nat. Areas J.* **29**, 110–116 (2009).
 40. Knight, T. M. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. *Ecol. Appl.* **14**, 915–928 (2004).
 41. Dullinger, S. et al. Modelling the effect of habitat fragmentation on climate-driven migration of European forest understory plants. *Diversity Distrib.* **21**, 1375–1387 (2015).
 42. Dicks, L. V. et al. A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nat. Ecol. Evol.* **5**, 1453–1461 (2021).
 43. Kudo, G. & Ida, T. Y. Early onset of spring increases the phenological mismatch between plants and pollinators. *Ecology* **94**, 2311–2320 (2013).
 44. Hegland, S. J., Nielsen, A., Lázaro, A., Bjerknes, A. L. & Totland, Ø. How does climate warming affect plant-pollinator interactions? *Ecol. Lett.* **12**, 184–195 (2009).
 45. McKinney, A. M. & Goodell, K. Shading by invasive shrub reduces seed production and pollinator services in a native herb. *Biol. Invasions* **12**, 2751–2763 (2010).
 46. Gorchov, D. L. et al. Differential and interacting impacts of invasive plants and white-tailed deer in eastern U.S. forests. *Biol. Invasions* **23**, 2711–2727 (2021).
 47. Bobbink, R. et al. Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. *Ecol. Appl.* **20**, 30–59 (2010).
 48. Small, C. J. & McCarthy, B. C. Relationship of understory diversity to soil nitrogen, topographic variation, and stand age in an eastern oak forest, USA. *Ecol. Manag.* **217**, 229–243 (2005).
 49. Miller, C. N., Papeş, M., Schilling, E. E. & Kwit, C. Reproductive traits explain occupancy of predicted distributions in a genus of eastern North American understory herbs. *Divers. Distrib.* 13297 <https://doi.org/10.1111/ddi.13297> (2021).
 50. Whigham, D. F. Ecology of woodland herbs in temperate deciduous forests. *Annu. Rev. Ecol., Evolution, Syst.* **35**, 583–621 (2004).
 51. Lembrechts, J. J. et al. SoilTemp: a global database of near-surface temperature. *Glob. Change Biol.* **26**, 6616–6629 (2020).
 52. Wolkovich, E. M., Chamberlain, C. J., Buonaiuto, D. M., Ettinger, A. K. & Morales-Castilla, I. Integrating experiments to predict interactive cue effects on spring phenology with warming. *N. Phytologist* **235**, 1719–1728 (2022).
 53. Chuine, I. & Régnière, J. Process-based models of phenology for plants and animals. *Annu. Rev. Ecol. Evol. Syst.* **48**, 159–182 (2017).
 54. Heberling, J. M., Miller, J. T., Noesgaard, D., Weingart, S. B. & Schigel, D. Data integration enables global biodiversity synthesis. *Proc. Natl Acad. Sci. USA* **118**, 1–7 (2021).
 55. Miller-Rushing, A. J. & Primack, R. B. Global warming and flowering times in Thoreau's Concord: A community perspective. *Ecology* **89**, 332–341 (2008).
 56. Buonaiuto, D. M. & Wolkovich, E. M. Differences between flower and leaf phenological responses to environmental variation drive shifts in spring phenological sequences of temperate woody plants. *J. Ecol.* **109**, 2922–2933 (2021).
 57. Harris, I., Osborn, T. J., Jones, P. & Lister, D. Version 4 of the CRU TS monthly high-resolution gridded multivariate climate dataset. *Sci. Data* **7**, 1–18 (2020).
 58. Lee, B. R. Data and model code for article 'Wildflower phenological escape differs by continent and spring temperature'. <https://doi.org/10.5281/ZENODO.7080193> (2022).

59. Roberts, A. M. I., Tansey, C., Smithers, R. J. & Phillimore, A. B. Predicting a change in the order of spring phenology in temperate forests. *Glob. Change Biol.* **21**, 2603–2611 (2015).
60. Su, Y.-S. & Yajima, M. Package 'R2jags'. (2015).
61. Ettinger, A. K. et al. Winter temperatures predominate in spring phenological responses to warming. *Nat. Clim. Change* **10**, 1137–1142 (2020).
62. Winkler, D. E., Butz, R. J., Germino, M. J., Reinhardt, K. & Kueppers, L. M. Snowmelt timing regulates community composition, phenology, and physiological performance of alpine plants. *Front. Plant. Sci.* **9**, 1–13 (2018).
63. Bachl, F. E., Lindgren, F., Borchers, D. L. & Illian, J. B. inlabru: an R package for Bayesian spatial modelling from ecological survey data. *Methods Ecol. Evol.* **10**, 760–766 (2019).
64. Krainski, E. T. et al. *Advanced spatial modeling with stochastic partial differential equations using R and INLA*. (Chapman & Hall/CRC Press, 2019).
65. De Smedt, T., Simons, K., Van Nieuwenhuysse, A. & Molenberghs, G. Comparing MCMC and INLA for disease mapping with Bayesian hierarchical models. *Arch. Public. Health* **73**, 02 (2015).
66. Rue, H., Martino, S. & Chopin, N. Approximate Bayesian inference for latent Gaussian models by using integrated nested Laplace approximations. *J. R. Stat. Soc. Ser. B: Stat. Methodol.* **71**, 319–392 (2009).
67. Fick, S. E. & Hijmans, R. J. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.* **37**, 4302–4315 (2017).
68. Boucher, O. et al. IPSL IPSL-CM6A-LR-INCA model output prepared for CMIP6 AerChemMIP. Downloaded 20210914. <https://doi.org/10.22033/ESGF/CMIP6.13581> (2020).
69. Pierce, D. ncdf4: Interface to Unidata netCDF (Version 4 or Earlier) Format Data Files. (2019).
70. Pebesma, E. stars: Spatiotemporal Arrays, Raster and Vector Data Cubes. (2021).
71. Bivand, R. S., Pebesma, E. & Gomez-Rubio, V. *Applied spatial data analysis with R*. (Springer, 2013).

Acknowledgements

We thank A. Helmling, L. de Castro Machado de Souza, P.Y. Lai, C. Terry, and M. Rothendler (North American specimens); I. Vogler, M. Schramm, V. Bastian, K. Adler, and B. Müller (European specimens); and Z. Yang, C. Tan, L. Wang, and X. Huo (East Asian specimens) for their efforts in databasing and georeferencing the herbarium specimens analyzed for this project. We also thank C. Römermann, E. Welk, and B. Liu for their suggestions on the European and Asian species list. We are grateful to the Chinese Virtual Herbarium and Chinese Field Herbarium for providing the East Asian specimen data and digitized photos and to the *Metasequoia* funding of Nanjing Forestry University [YY], which helped fund the Asian data extraction. We thank F. Lindgren and F. Willems for providing guidance on INLA methodology for the models with spatial autocorrelation. BRL, TKM, JMH, SEK, and RBP were funded by National Science Foundation Grants Nos. DEB 1936971, 1936877, and 1936960.

We acknowledge the World Climate Research Program, which, through its Working Group on Coupled Modeling, coordinated and promoted CMIP6. We thank the climate modeling groups for producing and making available their model output, the Earth System Grid Federation (ESGF) for archiving the data and providing access, and the multiple funding agencies who support CMIP6 and ESGF. We thank Abe Miller-Rushing and Amanda S. Gallinat for providing valuable feedback on this manuscript.

Author contributions

J.M.H., S.E.K., and R.B.P. initially conceived this project. T.K.M., C.R., and Y.Y. collected, scored, and georeferenced the herbarium collections used in this analysis. BRL conducted the statistical analysis and wrote the article. All authors contributed equally to reviewing and editing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41467-022-34936-9>.

Correspondence and requests for materials should be addressed to Benjamin R. Lee.

Peer review information *Nature Communications* thanks the anonymous reviewer(s) for their contribution to the peer review of this work. Peer reviewer reports are available.

Reprints and permissions information is available at <http://www.nature.com/reprints>

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons license, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons license, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons license and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this license, visit <http://creativecommons.org/licenses/by/4.0/>.

© The Author(s) 2022

Wildflower phenological escape differs by continent and spring temperature

Authors: Benjamin R. Lee, Tara K. Miller, Christoph Rosche, Yong Yang, J. Mason Heberling, Sara E. Kuebbing, and Richard B. Primack

Supplementary Methods

Model design and spatial autocorrelation

Summary of INLA spatial autocorrelation analysis

There were no significant differences (and high similarity in mean values) among the estimated intercepts or phenological sensitivities to spring temperature and elevation when comparing the posterior estimates from the analogous JAGS and INLA-SPDE models (Table S4). This suggests that the high fidelity between the two approaches found by other studies apply to our phenological models as well.

In contrast, incorporating spatial autocorrelation into the model structure changed model fit and performance as well as posterior estimates of parameter values, sometimes in statistically significant ways (Tables S3-S4). The model versions that included spatial autocorrelation had elevated predicted vs. observed r^2 values and significantly lower DIC values compared to those that did not for all combinations of plant group and continent (Table S3). Specifically, models that included spring temperature and elevation as fixed effects, species as a random effect, and the spatial autocorrelation term were the best-performing or among the best-performing model structures for five of the six plant group-continent combinations (the only exception being tree LOD in Asia, which was better predicted by either including winter temperature or annual precipitation instead of elevation).

Including spatial autocorrelation had a particularly strong effect on model fit and performance in Asia and Europe (Table S3), where predicted vs. observed r^2 values increased by 69-86% and 50-65%, respectively. North American models, which had the best-performing

models prior to the addition of spatial autocorrelation terms, only experienced increases in predicted vs. observed r^2 values of 3-6%. In contrast to these large differences in how model performance was affected, the only parameter values that significantly changed with the addition of spatial autocorrelation terms were in the North American models (Table S4). North American phenological sensitivity to spring temperature was significantly less negative with the addition of spatial autocorrelation terms for both wildflower FFD and canopy tree LOD models. Importantly, the difference in phenological sensitivity between trees and wildflowers that was statistically significant in the original model structure disappeared – there was no significant difference in sensitivity to spring temperature when spatial autocorrelation was included in the model. This was the only continent where the relationship in spring temperature sensitivity between wildflowers and canopy trees changed in response to adding spatial autocorrelation into the model. Model intercepts and sensitivities to elevation did not significantly change for any plant group-continent combination when spatial autocorrelation was added to the model structure (Table S4).

Justification for exclusion of spatial autocorrelation

The addition of the spatial autocorrelation term had qualitatively different effects depending on the continent. This is most noticeable for the Asian models, where the posterior-predicted mean effects of the spatial autocorrelation term ranged from -37.2 to 50.1 days for trees and -38.8 to 36.0 days for wildflowers (Fig. S2), meaning that the spatial relationship between data points altered predicted phenology by more than a month in either direction even after spring temperature and elevation had been accounted for in the model structure. This range was narrower in both Europe (Fig. S3; -10.8 to 6.0 days for trees and -24.6 to 33.1 days for

wildflowers) and eastern North America (Fig. S4, -18.8 to 19.3 days for trees and -10.3 to 9.5 days for wildflowers), suggesting that spatial relationships (which could include relationships with climate or geographic drivers that covary with the spatial relationships) are more influential on the predictive accuracy of spring phenology models in Asia compared to on the other two continents.

Potentially even more apparent when comparing Figures S2-S4 is the difference in the smooth clines in North America and the patchy, hot-spot patterns in Europe and Asia. The patterns in North America appear to follow latitudinal trends, potentially reflecting photoperiodic effects that have been previously found to strongly affect spring phenology of deciduous tree species¹. Europe is somewhat like North America in that there are relatively smooth gradients that appear to be somewhat linked to geographic features (for example, strong spatial autocorrelative effects appear for wildflower species along major mountain ranges). However, different ranges have different effects on phenology with delayed flowering in the Pyrenees and earlier flowering in the Alps. On one hand, this makes some sense because our models already account for elevational effects, but on the other hand, it seems to contradict other potential drivers associated with mountains such as the timing of snowmelt. It is also interesting to note that our results qualitatively differ from a recent European study also using herbarium collections to model spring phenology shifts², which found early-shifts associated with both mountain ranges when elevation, year, spring and winter temperature, and spring precipitation had all been accounted for as phenological drivers.

Sharply contrasting the North American and European results, however, spatial autocorrelation in East Asia appears extremely heterogeneous, with regions of extremely delayed phenology immediately next to regions with strong early shifts (Fig. S2). We could think of no

reasonable explanations to explain the observed patterns of spatial autocorrelative effects (for example, some adjacent areas differed by a total of about 2 months in predicted effects) and therefore posit that they are the result of nuances in where and how the herbarium specimens were collected. In support of this hypothesis, Asian spatial autocorrelation had overall much wider standard deviation (Fig. S2b, d) compared to both Europe and North America, suggesting a greater degree of uncertainty in the spatial relationships inherent to the collections. This appears to be, in part, due to the concentration of collections in certain areas (i.e., the areas with much lower standard deviations). That is, areas with strong spatial autocorrelational mean effects are typically also the areas with the lowest standard deviation, suggesting that collections are concentrated in these areas. This could therefore also suggest that some regions were simply collected earlier on average than others as a function of logistical constraints (e.g., it is easier to collect specimens closer to urban areas as opposed to rural areas) rather than through accurate reflection of ecological processes.

Due to the inconsistencies in how spatial autocorrelation affected predicted phenology across the three continents, we decided not to include this term in the models presented in the main body of the manuscript. Still, we want to highlight the importance in how these effects can influence model performance both in terms of predicted effects (e.g., spring temperature sensitivity changed for North American plant species depending on if spatial autocorrelation was included in the model or not) and in terms of predictive power (European and Asian models experienced substantial increases in predicted vs. observed r^2 values when spatial autocorrelation was added to the models). We would also like to note that because the nuances and discrepancies that arose with the Asian phenology models are likely related to concentrated observations and

- 94 uneven sampling distributions, further collections and digitization efforts should resolve these
- 95 biases in the near future.

Supplementary Tables

Table S1: Number of individual specimens of each species used in this study. Total number of specimens across all continents N = 5,522.

Region	Lifeform	Species	#Specimens
Eastern Asia	Trees n = 899	<i>Acer pictum subsp. Mono</i> (Maxim.)	37
		<i>Acer truncatum</i> (Bunge)	94
		<i>Betula platyphylla</i> (Sukaczew)	113
		<i>Fraxinus chinensis</i> (Roxb.)	99
		<i>Juglans mandshurica</i> (Maxim.)	53
		<i>Populus davidiana</i> (Dode)	125
		<i>Quercus aliena</i> (Blume)	44
		<i>Quercus mongolica</i> (Fisch.)	66
		<i>Quercus variabilis</i> (Blume)	186
		<i>Ulmus pumila</i> (L.)	82
	Wildflowers n = 1,418	<i>Androsace umbellata</i> (Lour.)	486
		<i>Astragalus scaberrimus</i> (Bunge)	203
		<i>Gueldenstaedtia verna</i> (Georgi)	185
		<i>Leibnitzia anandria</i> (L.)	206
		<i>Pulsatilla chinensis</i> (Bunge)	177
		<i>Viola prionantha</i> (Bunge)	161
Europe	Trees n = 532	<i>Acer platanoides</i> (L.)	96
		<i>Acer pseudoplatanus</i> (L.)	69
		<i>Carpinus betulus</i> (L.)	62
		<i>Fagus sylvatica</i> (L.)	184
		<i>Quercus petraea</i> (Matt.)	54
		<i>Quercus robur</i> (L.)	67
	Wildflowers n = 618	<i>Allium ursinum</i> (L.)	79
		<i>Anemone nemorosa</i> (L.)	130
		<i>Anemone ranunculoides</i> (L.)	52
		<i>Corydalis cava</i> (L.)	124
		<i>Corydalis solida</i> (L.)	50
		<i>Hepatica nobilis</i> (L.)	183
Eastern North America	Trees n = 995	<i>Acer rubrum</i> (L.)	308
		<i>Acer saccharum</i> (Marshall)	138
		<i>Carya glabra</i> (Miller)	111
		<i>Fagus grandifolia</i> (Ehrh.)	161
		<i>Quercus alba</i> (L.)	158
		<i>Quercus rubra</i> (L.)	119
	Wildflowers n = 1,060	<i>Anemone quinquefolia</i> (L.)	188
		<i>Dicentra canadensis</i> (L.)	143
		<i>Dicentra cucullaria</i> (L.)	169
		<i>Erythronium americanum</i> (Ker-Gawl.)	191
		<i>Hepatica americana</i> (DC.)	148
		<i>Sanguinaria canadensis</i> (L.)	221

Table S2: Means and standard deviations of day of year of observed phenology and estimated spring temperature of each observation, grouped by continent and lifeform (trees or wildflowers).

Continent	Group	Observed Day of Year		March-April Temperature (°C)	
		Mean	S.d.	Mean	S.d.
Asia	Trees	115.72	24.83	9.12	4.57
	Wildflowers	116.77	24.44	8.48	4.32
Europe	Trees	132.24	15.12	5.54	2.44
	Wildflowers	115.92	20.75	5.01	2.80
N. America	Trees	116.87	22.57	8.84	5.42
	Wildflowers	110.55	19.00	7.19	4.52

Table S3: Model comparison statistics for the different model versions evaluated as part of this study. Values in bold italics indicate the model(s) with the best deviance information criterion (DIC) value, assessed as being at least two less than all other models for the combination of continent and plant lifeform (wildflower or tree).

Region	Model	Wildflower FFD		Canopy Tree LOD	
		r ²	DIC	r ²	DIC
Asia	Spring T	0.388	12407.66	0.437	7832.79
	SpringT + S.A.	<i>0.740</i>	<i>11881.22</i>	0.738	7556.18
	Spring T + Elevation	0.398	12385.98	0.437	7833.75
	Spring T + S.A. + Elevation	<i>0.739</i>	<i>11881.01</i>	0.738	7557.06
	Spring T + S.A. + Winter T	0.739	11885.25	<i>0.740</i>	<i>7551.11</i>
	Spring T + S.A. + Annual Prec.	0.739	11886.79	<i>0.739</i>	<i>7551.04</i>
	Spring T + S.A. + Spring Prec.	<i>0.741</i>	<i>11882.06</i>	0.737	7557.83
Europe	Spring T	0.356	5246.99	0.236	4270.80
	SpringT + S.A.	0.678	5012.63	0.387	4248.59
	Spring T + Elevation	0.407	5198.44	0.252	4261.37
	Spring T + S.A. + Elevation	<i>0.672</i>	<i>5005.54</i>	<i>0.380</i>	<i>4237.75</i>
	Spring T + S.A. + Winter T	0.678	5013.31	0.370	4248.04
	Spring T + S.A. + Annual Prec.	0.679	5013.94	0.388	4248.09
	Spring T + S.A. + Spring Prec.	0.678	5014.48	0.382	4249.59
North America	Spring T	0.705	7968.63	0.754	7646.52
	SpringT + S.A.	0.725	7939.67	0.814	7498.66
	Spring T + Elevation	0.705	7969.54	0.761	7621.36
	Spring T + S.A. + Elevation	<i>0.726</i>	<i>7927.93</i>	<i>0.809</i>	<i>7483.74</i>
	Spring T + S.A. + Winter T	0.733	7943.83	0.814	7500.58
	Spring T + S.A. + Annual Prec.	0.731	7941.40	0.814	7500.18
	Spring T + S.A. + Spring Prec.	0.725	7939.06	0.814	7499.84

Table S4: Posterior estimated mean and 95% Bayesian credible intervals of model slopes and intercepts for models that include average spring temperature and elevation as fixed effects. Posterior estimates are presented for models both with and without spatial autocorrelation terms.

		Sp. Temp. + Elev. (JAGS)			Sp. Temp. + Elev. (INLA)			Sp. Temp., Elev., + S.A.			
		2.5% CI	Mean	97.5% CI	2.5% CI	Mean	97.5% CI	2.5% CI	Mean	97.5% CI	
Asia	FFD	β_1 (SpT)	-3.364	-3.118	-2.861	-3.382	-3.131	-2.879	-3.417	-3.053	-2.686
		Intercept	96.78	120.46	144.11	111.33	134.90	158.46	112.31	136.09	159.85
		β_2 (Elev)	2.335	3.794	5.242	2.239	3.733	5.227	0.406	2.940	5.482
	LOD	β_1 (SpT)	-2.971	-2.621	-2.261	-3.000	-2.647	-2.293	-2.834	-2.354	-1.865
		Intercept	110.57	129.37	148.13	119.28	138.30	157.31	116.45	135.98	155.49
		β_2 (Elev)	-2.544	-0.840	0.882	-2.668	-0.894	0.878	-2.530	0.335	3.263
Europe	FFD	β_1 (SpT)	-3.476	-3.021	-2.565	-3.510	-3.044	-2.578	-3.833	-3.245	-2.656
		Intercept	85.64	108.91	132.54	99.49	123.11	146.70	103.35	127.29	151.21
		β_2 (Elev)	10.722	14.768	18.678	10.694	14.682	18.666	6.940	12.538	18.103
	LOD	β_1 (SpT)	-3.268	-2.792	-2.298	-3.310	-2.815	-2.321	-3.440	-2.853	-2.259
		Intercept	101.39	125.22	149.10	116.32	139.94	163.55	115.51	139.31	163.08
		β_2 (Elev)	3.094	7.098	11.162	2.997	7.093	11.187	4.293	9.649	15.297
North America	FFD	β_1 (SpT)	-3.276	-3.141	-3.004	-3.279	-3.141	-3.002	-2.793	-2.403	-2.009
		Intercept	91.11	113.95	136.98	104.66	128.16	151.63	91.06	119.70	147.39
		β_2 (Elev)	-1.394	1.779	4.951	-1.467	1.715	4.894	2.854	7.189	11.565
	LOD	β_1 (SpT)	-3.756	-3.617	-3.485	-3.752	-3.619	-3.485	-2.865	-2.422	-1.977
		Intercept	104.03	127.07	149.88	117.90	141.40	164.89	105.11	131.68	157.58
		β_2 (Elev)	6.863	10.835	15.037	6.733	10.765	14.793	8.502	14.257	20.009

Table S5: Posterior estimated species-level random effects (means and 95% Bayesian credible intervals) for East Asian tree and wildflower species. Estimates are provided for the parameters derived from the JAGS model described in the main methods section.

Tree Species	Posterior estimates for JAGS model		
	2.5 BCI	Mean	97.5 BCI
<i>Acer pictum</i> ssp. <i>mono</i>	-4.02	16.032	34.763
<i>Acer truncatum</i>	-7.489	11.93	31.63
<i>Betula platyphylla</i>	-3.439	16.033	34.84
<i>Fraxinus chinensis</i>	-0.761	18.535	37.14
<i>Juglans mandshurica</i>	3.872	23.562	42.211
<i>Populus davidiana</i>	-20.846	-1.648	17.295
<i>Quercus aliena</i>	-1.879	17.659	37.179
<i>Quercus mongolica</i>	4.582	24.411	43.4
<i>Quercus variabilis</i>	-8.225	11.018	30.302
<i>Ulmus pumila</i>	-33.017	-12.825	6.226
Wildflower Species			
<i>Androsace umbellata</i>	-2.874	20.763	44.233
<i>Astragalus scaberrimus</i>	1.773	25.941	49.428
<i>Gueldenstaedtia verna</i>	-2.861	21.045	43.999
<i>Leibnitzia anandria</i>	-0.886	22.688	46.489
<i>Pulsatilla chinensis</i>	-6.085	17.687	41.292
<i>Viola prionantha</i>	-11.351	12.456	35.209

Table S6: Posterior estimated species-level random effects (means and 95% Bayesian credible intervals) for European tree and wildflower species. Estimates are provided for the parameters derived from the JAGS model described in the main methods section.

	Posterior estimates for JAGS model		
Tree Species	2.5 BCI	Mean	97.5 BCI
<i>Acer platanoides</i>	-10.918	12.977	36.649
<i>Acer pseudoplatanus</i>	1.272	25.373	49.333
<i>Carpinus betulus</i>	-9.569	14.034	38.254
<i>Fagus sylvatica</i>	-2.973	20.898	44.675
<i>Quercus petraea</i>	4.917	28.551	52.648
<i>Quercus robur</i>	1.771	25.543	49.512
Wildflower Species			
<i>Allium ursinum</i>	16.907	40.499	64.238
<i>Anemone nemorosa</i>	-8.603	15.288	38.582
<i>Anemone ranunculoides</i>	-5.891	17.459	40.899
<i>Corydalis cava</i>	-10.094	13.842	37.366
<i>Corydalis solida</i>	-18.657	5.05	29.134
<i>Hepatica nobilis</i>	-8.689	15.07	38.049

Table S7: Posterior estimated species-level random effects (means and 95% Bayesian credible intervals) for Eastern North American tree and wildflower species. Estimates are provided for the parameters derived from the JAGS model described in the main methods section.

Tree Species	Posterior estimates for JAGS model		
	2.5 BCI	Mean	97.5 BCI
<i>Acer rubrum</i>	-7.604	14.973	37.502
<i>Acer saccharum</i>	-6.973	15.713	38.429
<i>Carya glabra</i>	7.179	30.13	52.733
<i>Fagus grandifolia</i>	-4.443	18.569	41.082
<i>Quercus alba</i>	3.722	26.84	49.571
<i>Quercus rubra</i>	-1.691	20.884	43.75
Wildflower Species			
<i>Anemone quinquefolia</i>	5.866	28.665	51.847
<i>Dicentra canadensis</i>	0.89	23.615	46.774
<i>Dicentra cucullaria</i>	-3.67	19.123	42.092
<i>Erythronium americanum</i>	-5.344	17.539	40.383
<i>Hepatica americana</i>	-10.444	12.357	35.284
<i>Sanguinaria canadensis</i>	-11.023	11.935	34.784

Supplementary Figures

Figure S1: Maps of the 5,522 herbarium specimens collected between 1901 and 2020 across a) eastern Asia, b) western Europe, and c) eastern North America. Points represent observations of wildflower FFD (circles) and overstory LOD (crosses). Background color indicates average March-April temperatures in the current climate simulation (averaged from 2009-2018 using CRU TS v4.03 climate data).

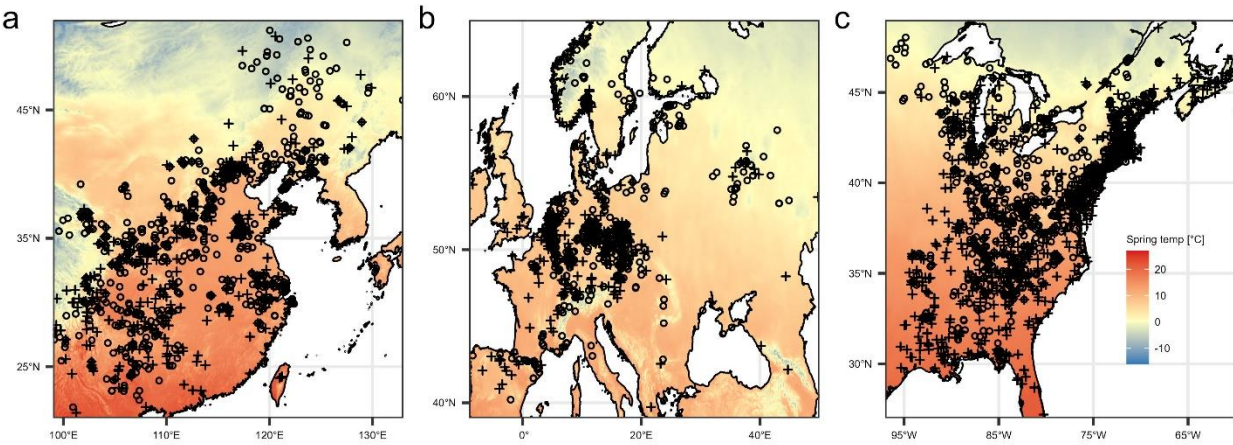


Figure S2: Posterior estimated means (left-hand panels) and standard deviations (right-hand panels) of spatial autocorrelation effects (in days) for (a-b) wildflower and (c-d) canopy tree phenology in East Asia. Positive and negative mean values indicate regions where phenology is expected to be delayed or earlier, respectively, compared to what is predicted from spring temperature and elevation alone. Maps are cropped to the extent of the Matérn meshes used to fit the models.

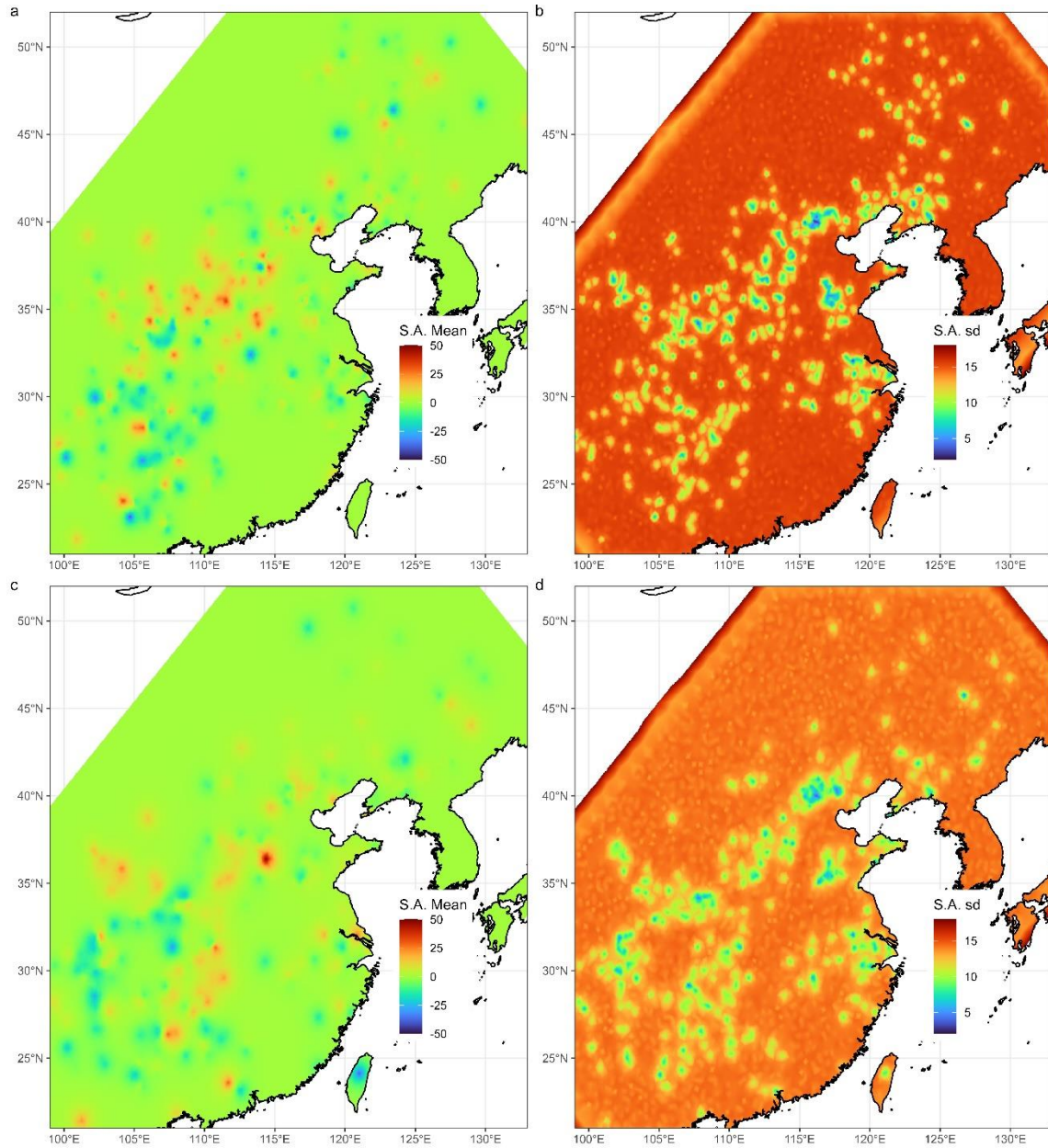


Figure S3: Posterior estimated means (left-hand panels) and standard deviations (right-hand panels) of spatial autocorrelation effects (in days) for (a-b) wildflower and (c-d) canopy tree phenology in Europe. Positive and negative mean values indicate regions where phenology is expected to be delayed or earlier, respectively, compared to what is predicted from spring temperature and elevation alone. Maps are cropped to the extent of the Matérn meshes used to fit the models.

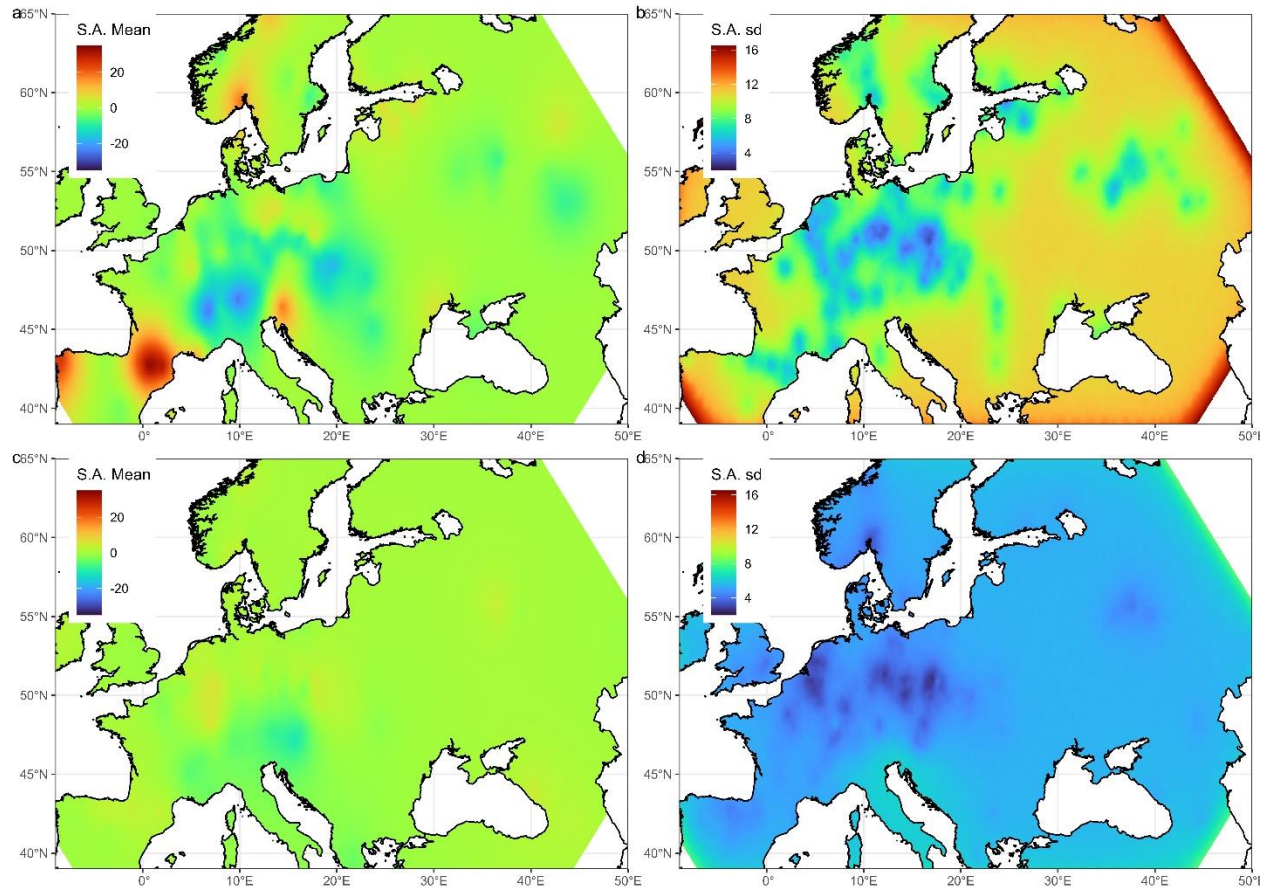
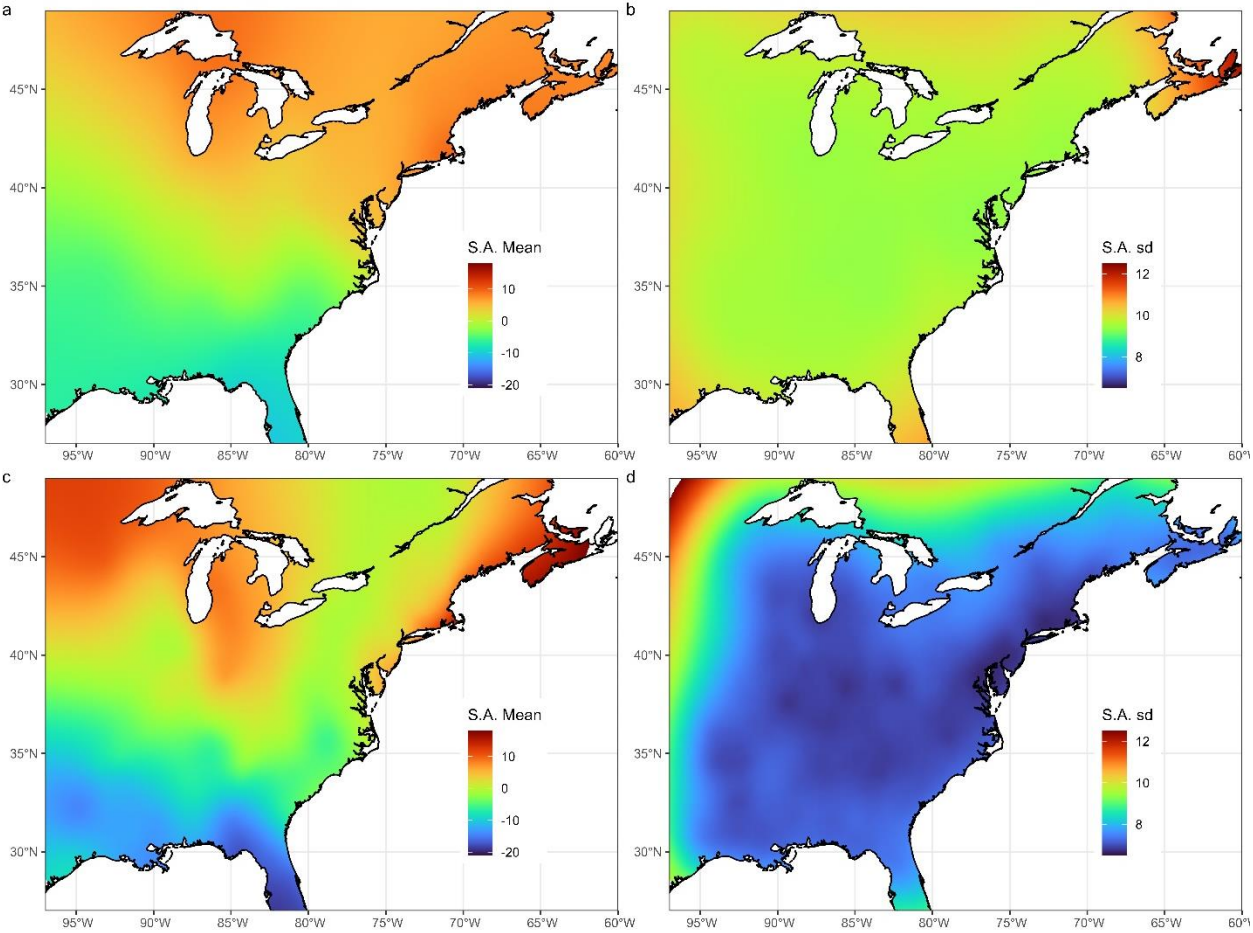


Figure S4: Posterior estimated means (left-hand panels) and standard deviations (right-hand panels) of spatial autocorrelation effects (in days) for (a-b) wildflower and (c-d) canopy tree phenology in eastern North America. Positive and negative mean values indicate regions where phenology is expected to be delayed or earlier, respectively, compared to what is predicted from spring temperature and elevation alone. Maps are cropped to the extent of the Matérn meshes used to fit the models.



166 **Figure S5:** Estimated wildflower FFD (top row) and canopy tree LOD (bottom row) under
167 current climate conditions (averaged from 2009-2018, see methods) in (a, d) Asia, (b, e) Europe,
168 and c, f) North America.

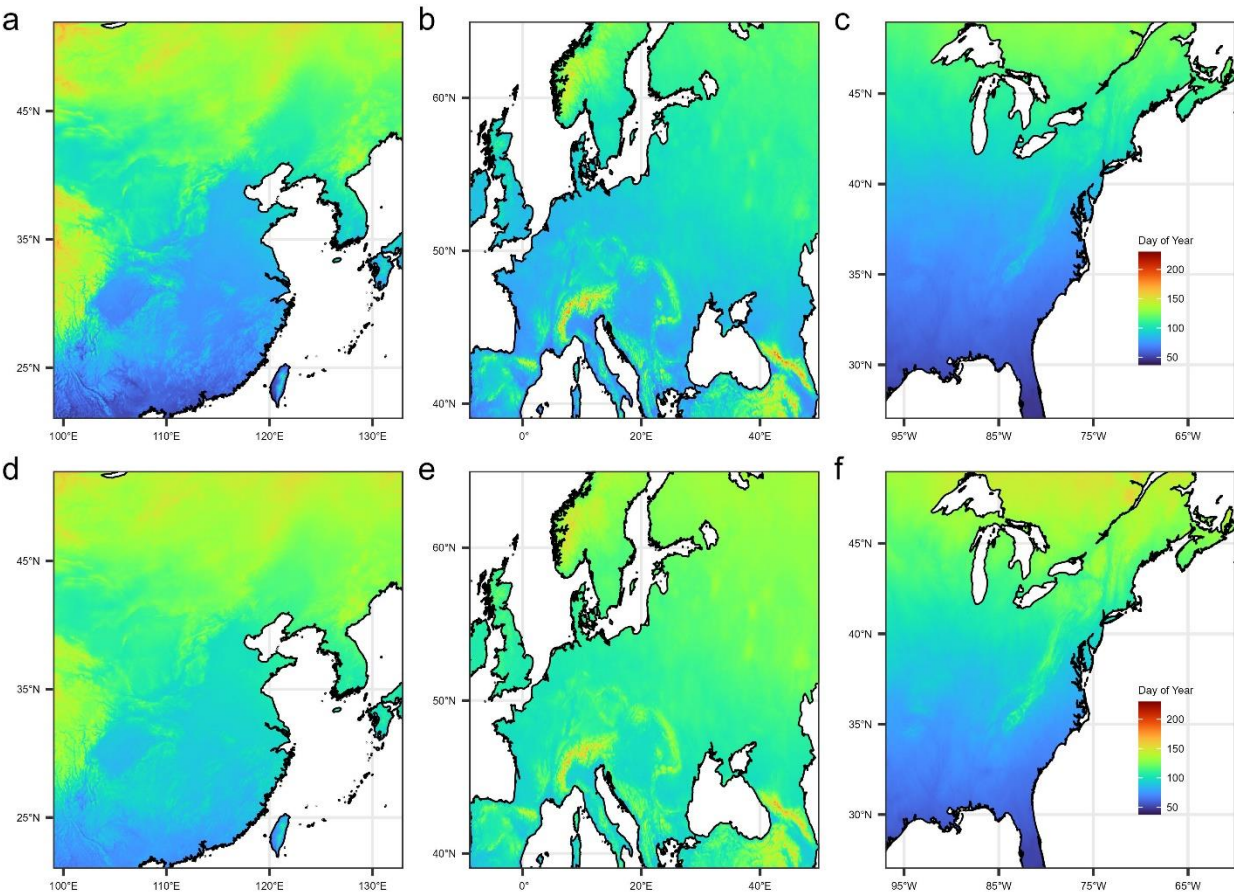


Figure S6: Projected wildflower FFD (top row) and canopy tree LOD (bottom row) under future climate conditions (estimated from the average projected climate conditions from 2081–2100, see methods) in (a, d) Asia, (b, e) Europe, and c, f) North America.

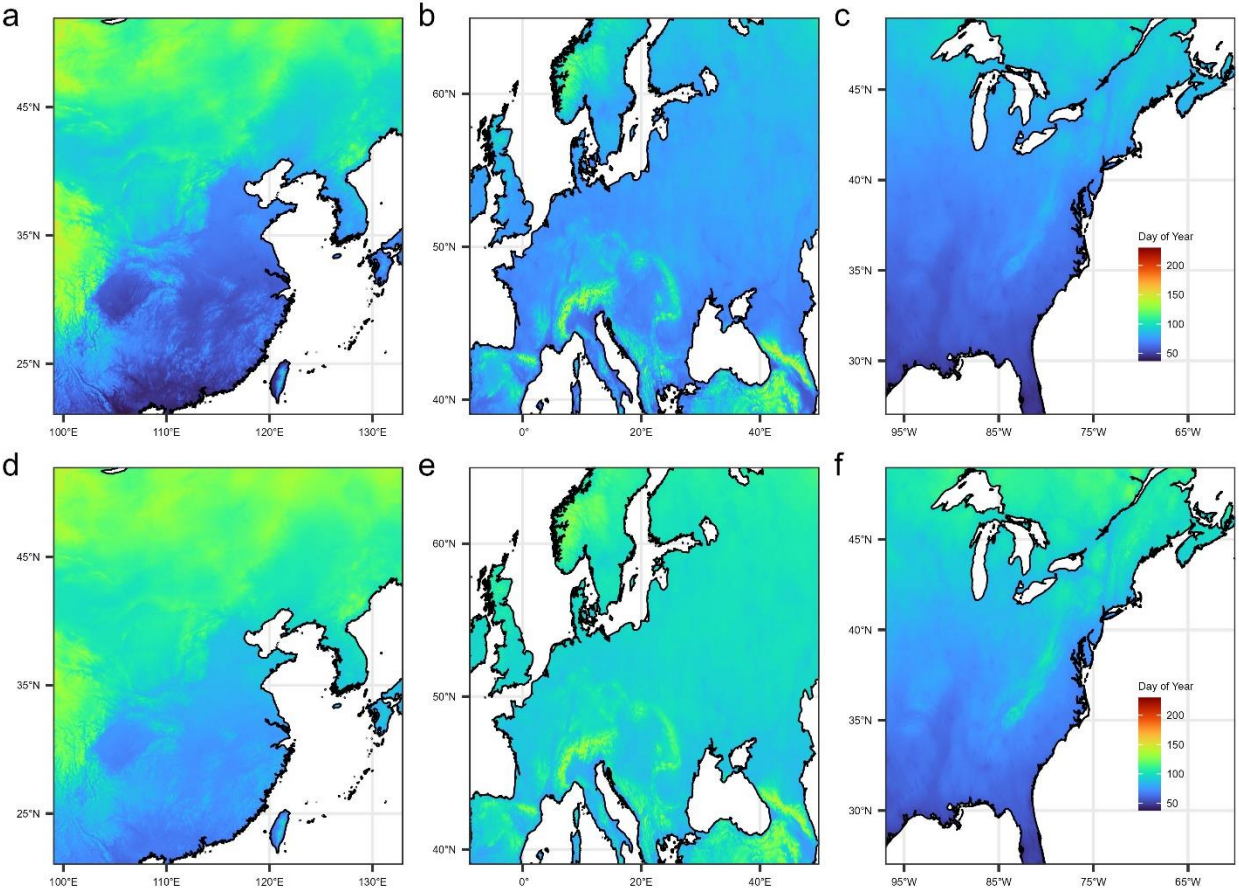


Figure S7: Projected mean difference between wildflower flowering (FFD) and canopy tree leaf out (LOD) (in days) under future climate conditions at the end of the century (see methods) in a) Asia, b) Europe, and c) North America. Negative values indicate LOD is estimated to occur before FFD.

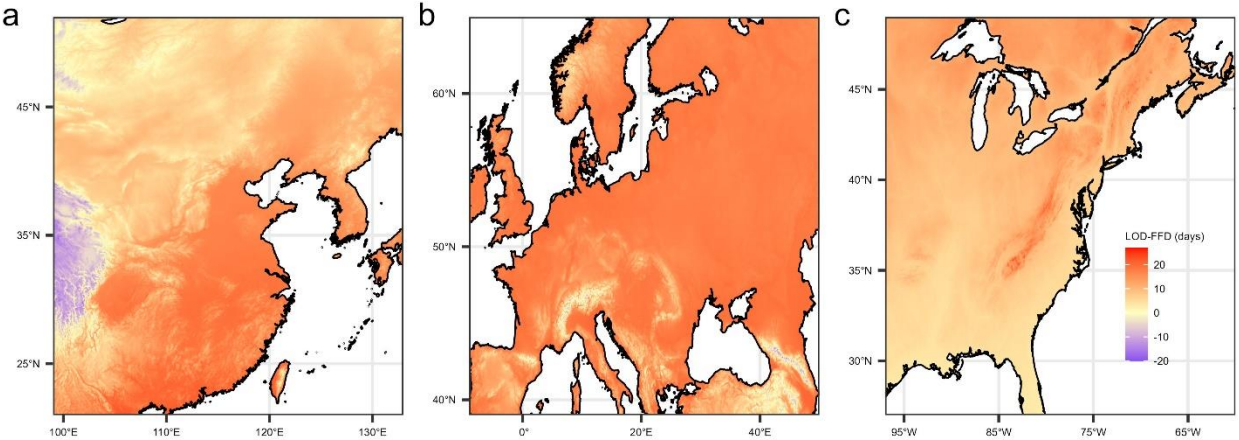


Figure S8: Difference in average spring temperature between current environmental conditions (averaged between 2009-2018) and future conditions (2080-2100) for a) Asia, b) Europe, and c) eastern North America. Dark gray regions indicate areas where the consensus land classification is < 1% deciduous or mixed deciduous forest cover.

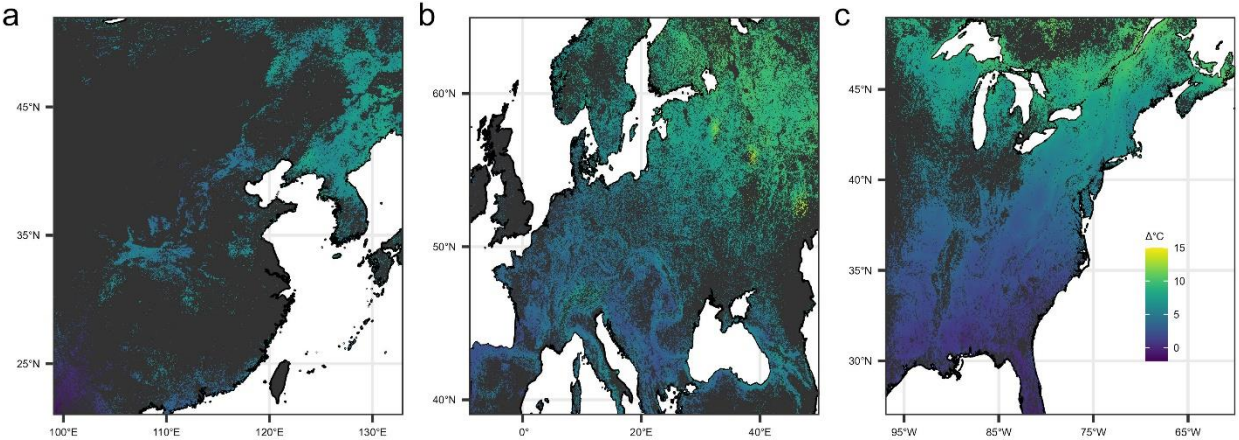


Figure S9: Correlation strengths (adjusted r^2 values) for linear regressions relating different one-, two-, and three-month aggregated spring temperature windows to observed wildflower First Flowering Date (FFD, blue) and tree Leaf Out Date (LOD, gold). Horizontal lines indicate the adjusted r^2 value for the relationship with average March-April temperature for ease of comparison with the other windows.

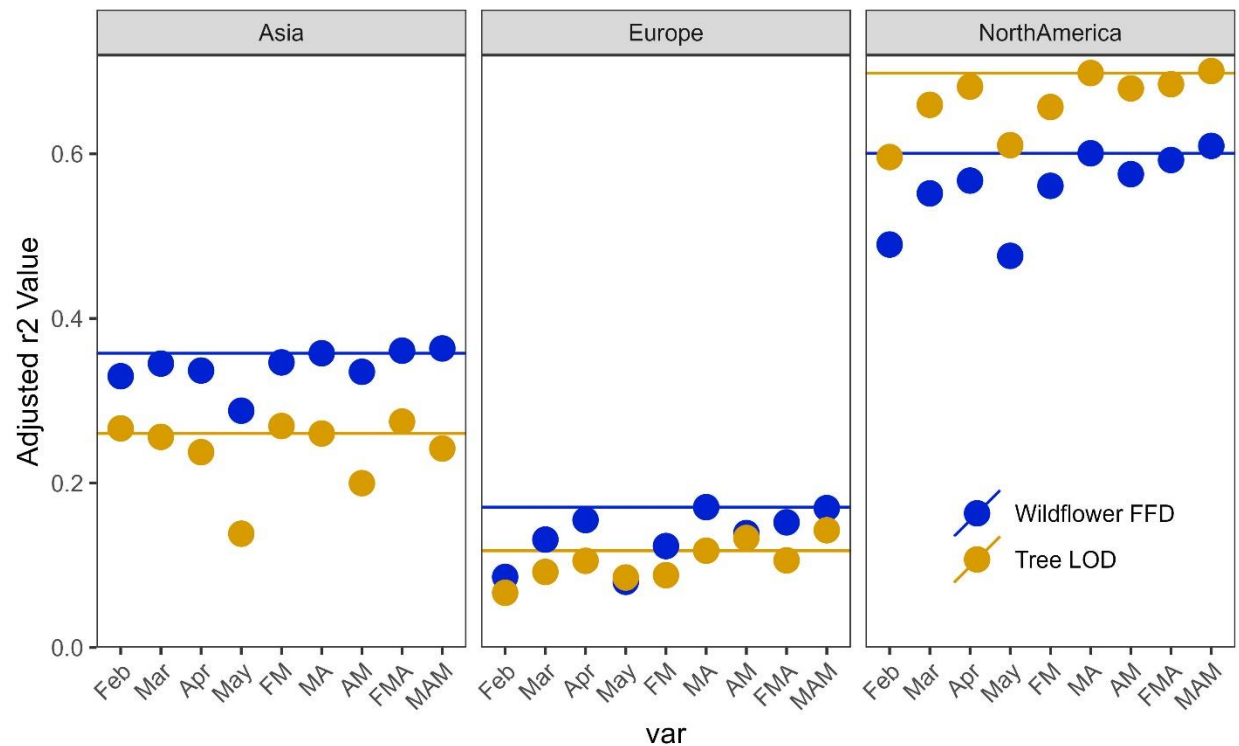
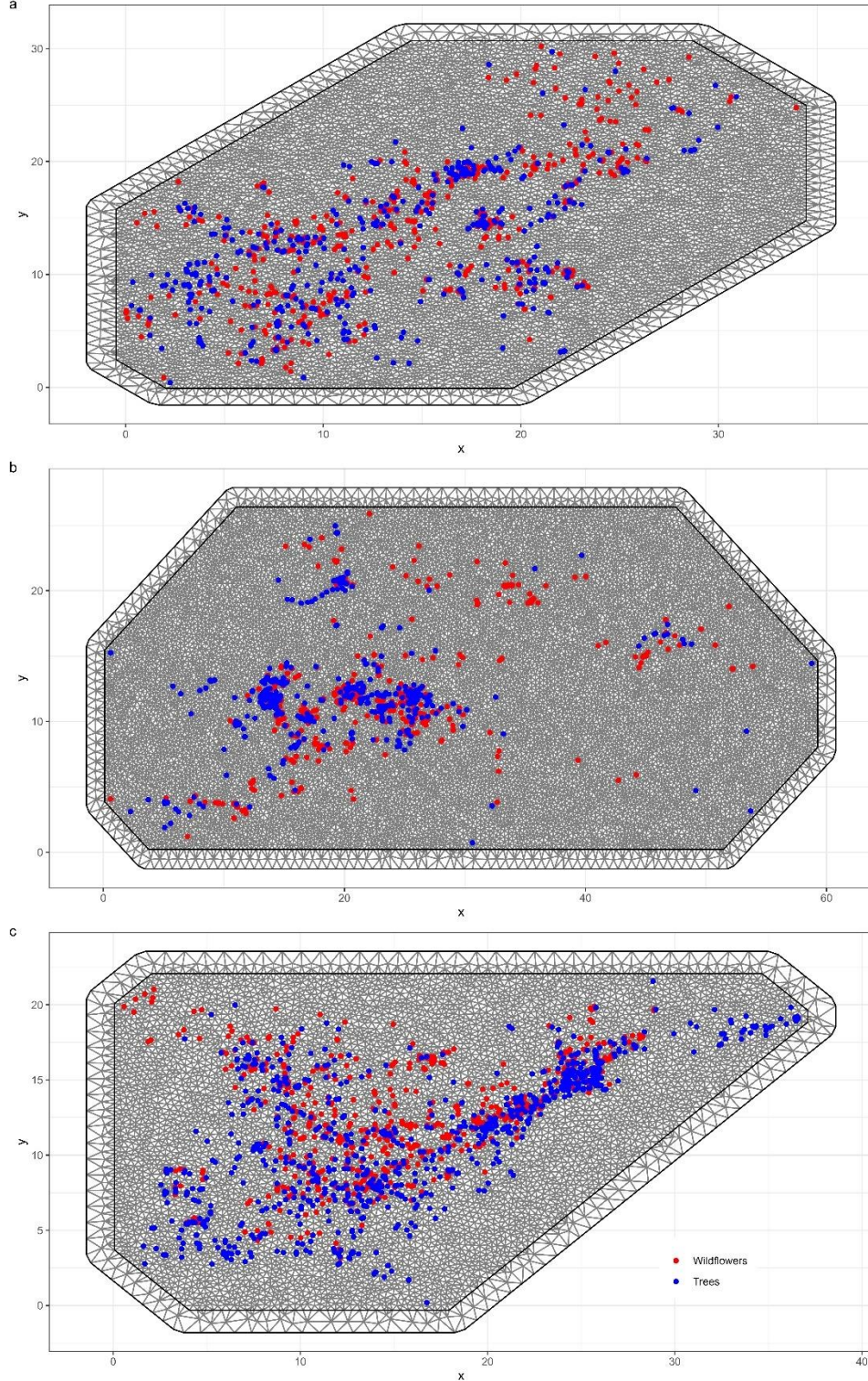
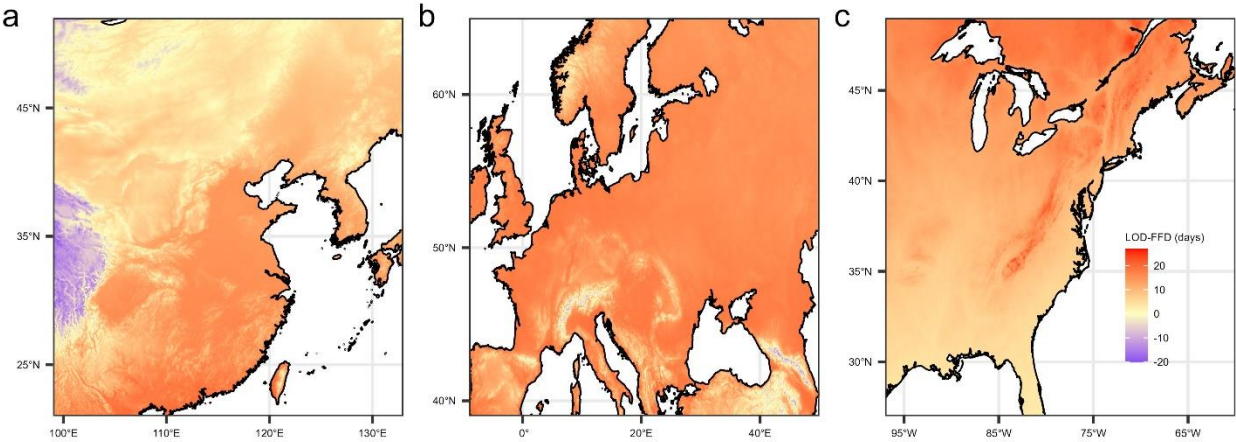


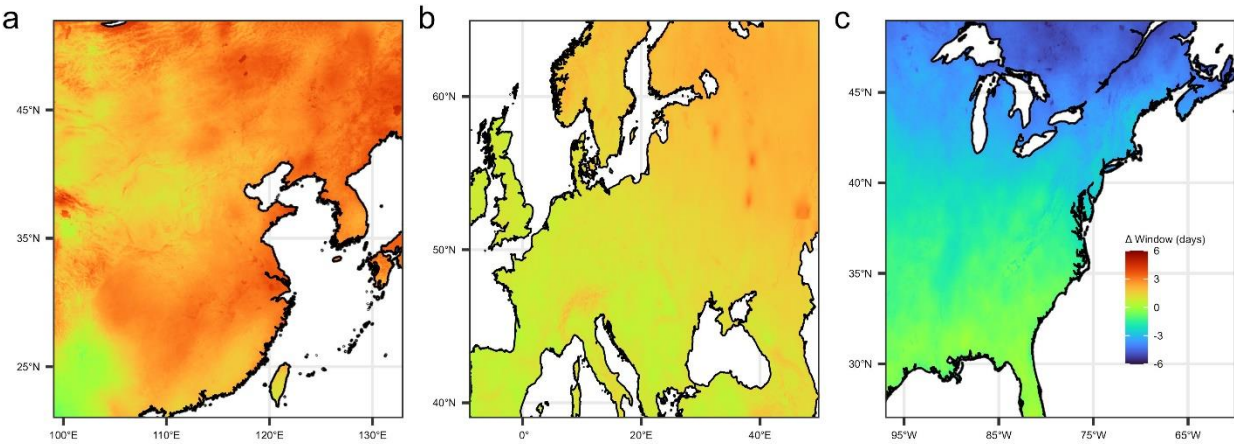
Figure S10: Matérn meshes used to fit INLA models that include spatial autocorrelation terms for a) East Asia, b) Europe, and c) Eastern North America. Red and blue points represent relative locations of observed wildflower and tree phenology, respectively. Coordinates are scaled from decimal degree coordinates so that all locations have positive latitude and longitude values.



201 **Figure S11:** Full, uncropped version of Figure 3.



204 **Figure S12:** Full, uncropped version of Figure 4.



207

208 **Supplementary Information References:**

209 1. Ettinger, A. K. *et al.* Winter temperatures predominate in spring phenological responses to

210 warming. *Nature Climate Change* **10**, 1137–1142 (2020).

211 2. Willems, F. M., Scheepens, J. F. & Bossdorf, O. Forest wildflowers bloom earlier as Europe

212 warms: lessons from herbaria and spatial modelling. *New Phytologist* **235**, 52–65 (2022).

213