Higher latitude spring-flowering herbs advance their phenology more than trees with warming temperatures

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Abstract

1) The phenologies of co-occurring trees and spring-blooming understory herbs in northeastern North American hardwood forests appear to be regulated by different environmental drivers—air temperature and soil temperature/snowpack, respectively. Accordingly, it has been hypothesized that climate change-driven asymmetry in the advancement of canopy leaf-out relative to the timing of understory growth could reduce photosynthetic rates and reproductive success of understory herbs through greater early-season shading.
2) To determine whether trees and spring-flowering forest herbs are advancing their phenologies at different rates with respect to increasing global temperatures, we examined the phenological responses to warming of 10 species of trees and 11 species of spring-flowering forest herbs (8,045 observations from 965 sites) in northeastern North America using 13 years of data collected by citizen scientists under the auspices of the USA-National Phenology Network.
3) Contrary to expectation, the degree of advancement of leaf-out as a function of temperature was greater in spring-flowering forest herbs than in trees, with a mean response rate of −4.9 days/˚C (95% BCI [−5.2, −4.6]) for spring-flowering forest herbs *vs.* −3.3 days/°C (95% BCI [−3.5, −3.1]) for trees. However, the response to temperature was not consistent across the latitudinal range, with spring-flowering forest herbs responding more strongly to warming than trees at middle (40–44˚N) and higher (45–48˚N) latitudes but not at lower latitudes (35–39˚ N).
4) *Synthesis:* In contrast to previous suggestions, our study shows spring-flowering forest herbs advancing their phenology at a higher rate than trees with respect to warming through most of the latitudinal range investigated, which could translate into a longer growing season and increased carbon uptake for spring-flowering forest herbs as spring temperatures rise.

1. Introduction

The timing of phenological events, such as flowering and leaf-out, affects the growth, competitiveness, reproductive success, and, ultimately, the fitness of plants (Chuine, 2010). Leaf-out date (defined as the timing of leaf emergence) determines the availability of daylight for photosynthetic carbon uptake and also affects the risk of frost damage (Kramer et al., 2010; Lenz et al., 2016) and herbivory (Pilson, 2000). Likewise, flowering time can influence plant reproductive success by affecting synchrony with pollinators (Rafferty & Ives, 2011), the time available for fruit development and seed dispersal (Chuine, 2010; Ettinger et al., 2018), rates of florivory and seed predation (Lacey et al., 2003; Pilson, 2000), and the risk of frost damage to flowers and fruits (Inouye, 2008). Consequently, the timing of emergence of leaf and flower buds is controlled by precise physiological mechanisms that respond to environmental triggers such as temperature, daylength, and precipitation (Flynn & Wolkovich, 2018; Jánosi et al., 2020; Korner & Basler, 2010; Linkosalo et al., 2006).

Several studies have demonstrated that different functional groups of plants have different environmental triggers for bud break (i.e., the timing of bud unfolding and start of leaf emergence), with temperate-zone woody species responding mainly to air temperature (Laube et al., 2014; Thomas et al., 2003; Zohner et al., 2016; Zohner & Renner, 2014), while perennial herbs appear to respond primarily to soil temperature and snow depth (Jánosi et al., 2020). If the phenologies of co-occurring trees and perennial herbs are indeed regulated by different environmental triggers, they could respond differently to global climate change. For example, canopy closure could advance at a faster rate than growth and development of perennial herbs, leading to increased shading, reduced photosynthetic rates and lower reproductive success for understory plants (Ge et al., 2015; Heberling, Cassidy, et al., 2019; Heberling, Fridley, et al., 2019).

A recent study of a woodland ecosystem in Massachusetts, USA, concluded that canopy tree species, including *Acer saccharum, Quercus alba,* and *Fagus grandifolia,* advanced their leaf-out timing by an average of nearly 2 weeks over a 160-year period, while spring-flowering herbs (i.e., understory perennial herbs that grow and bloom for a short period before canopy closure) advanced their first leaf-out date by less than a week, on average (Heberling, Fridley, et al., 2019). The authors predicted that the resulting change in temporal overlap between understory and canopy plants could reduce the carbon budget of the former by 12–26% by 2080, due to increased canopy shading. This loss of photosynthetic opportunity could be critical for spring-flowering herbs, which are a common and charismatic component of the understory of deciduous temperate forests, and which require high levels of sunlight reaching the forest floor to develop vegetative and reproductive parts before canopy closure. Reductions in carbon budgets via earlier canopy shading of these species could lead to population declines and eventual species replacement (Heberling, Fridley, et al., 2019; Lapointe, 2001).

Conversely, in a meta-analysis of phenological shifts among 112 species (including trees, shrubs, herbs, birds, amphibians, and insects) across various ecosystems in China, Ge et al. (2015) reached the opposite conclusion, finding that herbaceous species were exhibiting greater phenological advances than trees (5.7 days/decade, *vs.* 2.3 days/decade for trees). Clearly, there is no consensus yet on whether trees or perennial herbs are advancing their phenologies more strongly in response to climate change (Du et al., 2020; Ge et al., 2015; Heberling, Fridley, et al., 2019; Parmesan, 2007). One of the major challenges in answering this question is that phenological responses to warming vary interspecifically and geographically, making it difficult to generalize about entire functional groups (Buonaiuto et al., 2021; Nagahama & Yahara, 2019; Parmesan, 2007; Primack et al., 2009; Zhang et al., 2007).

Geography is likely to play a role in species' responses to climate change, for three largely separate reasons. First, certain areas, such as higher-latitude regions, are warming faster than others (2 to 3 times faster, depending on latitude; IPCC, 2018), which could lead to greater magnitudes of phenological change over time in those locations if species' phenologies are responding largely to temperature. Second, species or populations occurring in cooler regions may be more responsive to a given amount of warming, either because a given amount of warming represents a larger relative change (Prevéy et al., 2017), or because in cooler climates, a given amount of warming still allows chilling requirements to be met. For example, Zhang et al. (2007), using North American satellite and climate data from 1982 to 2005, found that species whose mid-range latitude is north of 40˚N showed greater advances in phenology over time than species with more southerly distributions. They hypothesized that this pattern was driven by the fact that chilling requirements were still being met at higher latitudes, where even a reduced number of chilling days owing to warming winter temperatures would still be sufficient to break winter dormancy, unlike at lower latitudes. Third, the unique environmental variables at a single site, such as precipitation, elevation, and edaphic factors (Du et al., 2020; Wielgolaski, 2001), all affect how species track a changing climate. For all these reasons, extrapolation from one location to another is problematic.

Overall, despite a large number of studies on the effects of warming temperatures on phenology, we still have little ability to predict where mismatches among functional groups are most likely—or even the direction of mismatches—because we lack studies that examine phenological responses across different sets of species that co-occur over wide geographical areas. We therefore asked whether: (1) eastern North American deciduous trees and spring-flowering forest herbs shift their leaf-out phenology at different rates with respect to temperature; (2) there is latitudinal variation in the response to temperature; and (3) leaf-out of trees and spring-flowering forest herbs has advanced (i.e., become earlier) over time. To answer these questions, we used data from the USA National Phenology Network to examine phenological responses to warming in 21 species (10 deciduous trees and 11 spring-flowering understory herbaceous perennials), over a broad latitudinal range (35˚ to 48˚ N) in this region.

2. Material and Methods

2.1 | Study system

The temperate deciduous hardwood forest is an ecosystem of major ecological and economic importance in eastern Canada and the northeastern US, dominated by tree genera such as *Acer*, *Quercus*, *Betula*, and *Fagus*. A key characteristic of this ecosystem is the changing light regime caused by seasonal variation in canopy cover as trees produce their leaves in spring and shed them in autumn. Maximum amounts of direct solar radiation reach the forest floor in early spring, accounting for over 90% of the total energy received in the understory during this period (Hutchison & Matt, 1977). In summer, following tree leaf-out, solar radiation in the understory decreases to 1–5% of that available above the canopy (Hicks & Chabot, 1985). Spring-blooming forest herbs (e.g., *Trillium grandiflorum, Claytonia virginica, Erythronium americanum*) are common in the understory of northeastern deciduous forests, taking advantage of the high luminosity before canopy closure to develop vegetative and reproductive parts.

2.2 | Phenology data

Data for this study were provided by the USA National Phenology Network (USA–NPN 2021, https://data.usanpn.org/observations/get-started; henceforth "NPN"). NPN data are collected by professional and citizen scientists. To ensure data quality, several protocols are applied, and volunteers go through extensive training. All protocols are standardized within plant functional types (e.g., deciduous trees, herbs). The accuracy of the volunteer-collected NPN plant phenology data was evaluated by Fuccillo et al., (2015), who found that professionals and volunteers had a 91% concordance rate, indicating that volunteers provide reliable observations.

We selected 10 species of trees and 11 species of spring-flowering forest herbs based on those with the greatest numbers of observations in the NPN dataset (Table S1). Spring-flowering forest herbs are defined here as early-flowering herbaceous species that emerge at the beginning of spring, taking advantage of the high levels of light in the understory to accumulate carbon reserves and reproduce (Lapointe, 2001). Their epigeous growth normally occurs from late March to late June; they then enter a period of hypogeous growth following canopy closure and seasonal (summer) temperature increases (Lapointe, 2001). We included only those species that the literature reports as developing their vegetative and reproductive parts before canopy closure (Augspurger & Salk, 2017; Augspurger & Zaya, 2020; R. L. Brown et al., 1985; Hall & Sibley, 1976; Heberling, Cassidy, et al., 2019; Jacques et al., 2015; Kricsfalusy & Ponomarenko, 2013; Muller, 1978; Reader & Bricker, 1992).

Species observations had to meet three criteria for inclusion: their geographical distribution had to encompass eastern North America, observations had to go back at least 10 years from 2021, and species needed to have a minimum of 50 observations (Table S1). For each selected species, we extracted individual phenometrics reports for the first day of the year (DOY) for which a phenophase (i.e., an observable stage or phase in the annual life cycle that can be defined by a start and end point) had a positive observation, focusing on the phenophases defined as "leaves" for both functional groups. The phenophase "leaves" for forbs includes both "above ground buds with green tips" and "fully unfolded leaves". Since forest herb leaf emergence occurs rapidly, we included both phenophase descriptions in our data, keeping only the earliest observation when both phenophases were available for the same individual. For trees, the phenophase "leaves" refers to "fully unfolded leaves". For both groups, only the first entry for "leaves" was kept, *i.e.*, the earliest positive observationoccuring after a "0"observation in the same calendar year, and it is possible that the true start of the phenophase occurred at some point before these first positive observations. However, it seems unlikely that any resulting bias in our estimates of first dates would be greater for one functional group than the other. Note that individual plants are defined differently for the two functional groups in this study: For trees, a unique identifier is provided for each individual, whereas for forbs, the unique identifier can represent a patch of individuals or a single plant (see Appendix for details).

We extracted all North American data available in the NPN portal for the 21 focal species. We filtered the data to retain observations from January 1, 2009, to July 31, 2021, and from latitudes 35° to 48.2° N and longitudes east of 91° W. These choices reflect the fact that there were few observations for spring-flowering forest herbs prior to 2009, below 35°, and above 48.2°, and to maintain observations within the geographical range of the eastern temperate forests (as described by Dyer 2006). We excluded records occurring after DOY 172 (June 21) for all species, and for trees, we also excluded records where budbreak occurred later than leaf-out, or where the interval between budbreak and leaf-out was greater than 30 days, reasoning that such observations were likely errors. After those restrictions were applied, the number of remaining observations was 8,045 (Figure 1 and Table S1).

2.3 | Spring phenology and temperature

To determine whether trees and spring-flowering forest herbs shift their leaf-out phenology at different rates with respect to temperature, we fitted a hierarchical Bayesian model in which the DOY was a function of temperature. DOY refers to the first day of the year at a given site in a given year on which the phenophase "leaves" was reported. Monthly mean temperatures for winter and spring were extracted for each site for the 2009–2021 period from the PRISM database (http://www.prism.oregonstate.edu). Mean spring temperatures were calculated by averaging the monthly mean temperatures for each location for the period from March 1 to May 31; mean winter temperatures were calculated for the period from December 1 to February 28.

We fitted separate models for trees and spring-flowering forest herbs, and then to assess whether trees and spring-flowering forest herbs differed in their response to warming, we calculated the estimate of the difference between the distributions of the slope for each functional group using 3,000 samples from the posterior distributions.

The models take the following form:

$$Day\ of\ the\ year_{[i]} = \alpha_{jk[i]} + \beta_{j[i]} \times temperature_{[i]} \quad (1)$$

where α is the intercept and β is the slope, both including a group-level interaction (*j*) between species and site (analogous to random effects in the frequentist literature). Since species are expected to vary in their mean leaf-out day and in their response to temperature, and because this response also varies with geographical location, we allowed the intercept and the slope to vary, meaning the effect of temperature could vary by the interaction between species and site. We also allowed the intercept to vary by year (*k*) to account for the non-independence of observations taken in the same year. We did not include plant individual as a group-level term since most observations are single observations rather than repeated measures across the years. For population-level effects (analogous to fixed effects in the frequentist literature), the prior distributions were: $\alpha \sim Normal(100, 33)$; $\beta \sim Normal(0, 1000)$. The correlations between varying intercepts and slopes were also estimated using $lkj(2)$ (Lewandowski-Kurowicka-Joe distribution, Lewandowski et al., 2009) as a prior for the correlation matrix. The intercept priors were weakly informative to speed convergence by preventing the Markov chain from sampling highly unlikely values, such as negative values for mean leaf-out date. Since the data were centred (to speed convergence), the choice of $\mu_\alpha = 100$ is equivalent to a mean DOY of 100 (April 10), which is a reasonable value given the latitudinal range of the data and the values normally reported in the literature for the leaf-out day of trees and spring-flowering forest herbs (Diez et al., 2012; Morin et al., 2009; Park et al., 2019; Willems et al., 2021). For the slope, we applied a zero-centred non-informative prior. Since models using mean spring and mean winter temperatures produced similar results, we focus on the results using spring temperatures; however, we also present results based on other time-windows for temperature calculation (see section 2.5 and Table S3).

To assess whether individual species advanced their phenology with warming, we also fitted separate hierarchical Bayesian models of the same form as model (1) for each species. To account for variation in the mean and the rate of change due to geographical location, we allowed the intercept and slope to vary for each site. The priors were chosen as described for the previous model.

2.4 | Changes in spring phenology throughout the latitudinal range

To assess whether spring-flowering forest herbs and trees differ in their response to temperature as a function of latitude, we fitted a multilevel Bayesian model where latitude was treated as categorical, such that separate models were fitted for each of three categories: equal or greater than 35° and lower than 40°, greater or equal to 40° and lower than 45°, and greater or equal to 45° and up to 48.2° (for simplicity, henceforth, 35–39°, 40–44°, and 45–48° N). The model takes the same form as model (1), and prior distributions were as described above. Similar to model (1), we allowed the intercept to vary for each year and for the interaction between each species and site, and the slope to vary for the interaction between each species and site.

To test whether these results were driven by our choice of the March 1 to May 31 time-window for the temperature data (which might be later than the period of peak temperature sensitivity for low-latitude populations and earlier for high-latitude populations), we repeated all the temperature models using different time-windows for the calculation of mean spring temperature—an earlier time-window, from February to April; and a later time-window, from April to June.

2.5 | Change in spring phenology with time

To determine whether leaf-out dates of trees and spring-flowering forest herbs have advanced since 2009, we fitted a multilevel Bayesian model, in which the first day of the year on which an observation occurred (DOY) was a function of year, treated as continuous. A separate model was fitted for each functional group (trees and spring-flowering forest herbs), and since species are expected to have different spring phenologies, and because their phenologies also vary with geographical location, we allowed the intercept and the slope to vary, allowing the effect of year to vary by the interaction between species and site:

$$Day\ of\ the\ year_{[i]} = \alpha_{j[i]} + \beta_{j[i]} \times year_{[i]} \quad (2)$$

Here, α is the intercept, and β is a random slope, both including a group-level interaction (j) between species and site. Because the magnitude of directional change in temperature in our study region over the study period (2009–2021) has been modest compared to among-year variation (see Results 3.3), we also ran a similar set of models with year treated as categorical to assess year-to-year variation in leaf-out dates This model takes the following form:

$$Day\ of\ the\ year_{[i]} = \alpha_{[i]} + \beta_{jyear[i]} \quad (3)$$

where α is the intercept, and β is a second intercept including a group-level interaction (j) between species and site.

The prior distributions were the same as described previously. For both models, we fitted separate models for each functional group and for species.

For all models, we obtained the parameters' posterior distributions using the Hamiltonian MCMC method (Betancourt & Girolami, 2013). We ran all chains for a minimum of 4,000 iterations, adopting a warm-up of 1,000 iterations. We monitored convergence by running four different chains with different start values and calculating Rubin's R (Gelman & Rubin, 1992), where convergence is assumed when R is close to 1. By sampling from the posterior distribution, we computed the mean and Bayesian credible intervals (BCI) for all parameters using 3,000 draws from the posterior. As a measure of model fit, we also computed the Bayes-R^2 for each (Gelman et al., 2019). All analyses were performed using the package brms (Bürkner, 2017), which allows the implementation of Stan in R (R Core Team, 2020).

3. Results

3.1 | Spring phenology and temperature

Overall, the spring phenology of both trees and spring-flowering forest herbs tended to be earlier when temperatures were warmer. Slopes describing each functional group were negative and did not overlap zero (trees: $\mu_\beta = -3.3$ days/˚C, 95% BCI [−3.5, −3.1]; spring-flowering forest herbs: $\mu_\beta = -4.9$ days/˚C, 95% BCI [−5.2, −4.6]; Table 1 and Figure 2). Contrary to expectation, the 95% BCI of the estimated difference between posterior distributions of the slopes for spring-flowering forest herbs and trees was negative and did not overlap zero, indicating that spring-flowering forest herbs responded more strongly to warmer temperatures than did trees ($\mu_\beta = -1.6$ days/˚C, 95% BCI [−1.9, −1.2]). Therefore, on average, spring-flowering forest herbs advanced their spring phenology by 1.6 days more than trees for each degree increase in temperature. This pattern was similar for the model using winter temperature data, with spring-flowering forest herbs also advancing their spring flowering phenology more than trees. Using different time-windows for calculation of spring temperature did not change the results: spring-flowering forest herbs still exhibited greater responsiveness to temperature than trees (Table 1).

3.2 | Changes in spring phenology throughout the latitudinal range

For lower latitudes (35–39˚ N), there was no detectable difference between the functional groups in responsiveness of spring phenology to temperature, regardless of the time-window over which mean spring temperature was calculated. At middle (40–44˚ N) and higher latitudes (45–48˚ N), spring-flowering forest herbs advanced leaf-out more strongly than trees with respect to temperature, regardless of time-window (Figure 3, Table 2). To address the possibility that the observed phenological trends across the latitudinal range could have been driven by an outlier species, we re-ran the latitudinal analysis removing the most abundant species within each latitudinal band, and also restricting the analysis to species that occur throughout the latitudinal range, and, in both cases, our results were unchanged (see R code provided).

The phenological response of spring-flowering forest herbs to temperature differed among the latitudinal bands, with these species advancing their phenology more strongly with warmer temperatures at middle latitudes than at lower or higher latitudes (Figure 3, Tables 2 and S4). Conversely, the magnitude of the trees' phenological response decreased from the lowest- to the highest-latitude band, except when mean spring temperature was calculated over the period of April to June, i.e., the later time-window (Figure 3, Tables 2 and S4). We found no pattern of greater responsiveness to temperature at higher latitudes (45–48˚ N), for spring-flowering forest herbs or trees, independent of the time-window used to calculate mean spring temperatures.

3.3 | Change in spring phenology with time

Contrary to our expectation, mean spring temperatures in our dataset decreased slightly over the timespan analysed (Figure 4A; see Figure S1 for separate temperature trends for each latitudinal band). This trend was largely due to an exceptionally warm spring in 2012 (mean spring temperature of 11.9 ˚C; in comparison, the coolest year, 2014, had a mean spring temperature of 7.8 ˚C), which leveraged the early end of the regression line upward (Figure 4A and S1). In accordance with the modest cooling trend observed in the dataset as a whole, the model revealed slight overall delay in spring phenology of trees and spring-flowering forest herbs between 2009 and 2021 (Table 3). There is no evidence that the functional groups differed in their rate of phenological shift with time, since the 95% BCI of the difference of the slope estimates overlapped zero (Table 3; mean and 95% BCI of the difference between the posterior distributions of the slope: 0.3 days/year [−0.2, 0.9]). For several species, there was no detectable directional change in phenology over the timespan analysed, and therefore no evidence that their spring phenology has advanced or delayed in our study region over the last 13 years (Table 3).

In 2012, the warmest year of the study period (Figure 4A), spring-flowering forest herbs exhibited an earlier spring phenology than trees—to the extent that leaf-out of spring-flowering forest herbs occurred 10 days earlier than tree leaf-out (mean and 95% BCI of the difference between posterior distributions of means for trees and spring-flowering forest herbs: −10.0 [−17.2, −3.0]). Conversely, both trees and spring-flowering forest herbs exhibited delayed spring phenology in 2014 (Figure 4B), the coolest year in the time-series analysed, resulting in overlapping leaf-out dates for the two functional groups in that year (mean and 95% BCI of the difference between posterior distributions of means for trees and spring-flowering forest herbs: 2.2 [−4.3, 8.6], Figure 4B).

4. Discussion

Using a plant phenology dataset that spans 13 years and 21 species, with 8,045 data points from 965 locations, we show that, overall, spring leaf-out is advancing more strongly with temperature for spring-blooming forest herb species than it is for trees in North America's eastern hardwood forest ecosystems. However, this trend varies with latitude, with no detectable difference between functional groups for lower latitudes (35–39° N), and spring-flowering forest herbs responding more strongly to temperature than trees at middle and higher latitudes (40–44° N and 45–48° N). Furthermore, both functional groups vary in their phenological response to warmer temperatures across the latitudinal range, with spring-flowering forest herbs at middle latitudes advancing their leaf-out date more than those at lower and higher latitudes, and trees at lower latitudes advancing their spring phenology more than those at middle and higher latitudes. In contrast to what has previously been reported in the literature, our study shows spring-flowering forest herbs advancing their phenology more strongly with temperature than deciduous trees throughout most of our North American study region.

4.1 Phenological responses of trees and spring-flowering forest herbs

Our finding that both trees and spring-flowering forest herbs advanced their spring phenology in response to warming temperatures is consistent with previous studies and suggests that the response of plants to rising temperatures could increase the length of the growing season in deciduous temperate forests (Jacques et al., 2015; Menzel et al., 2006; Zohner & Renner, 2014; although see Zani et al., 2020). For spring-flowering forest herbs, earlier emergence relative to tree leaf-out could increase fitness since they produce most of their photosynthates in spring before canopy closure (Dion et al., 2017; Heberling, Cassidy, et al., 2019; Jacques et al., 2015). Those photosynthates are used not only for vegetative growth and reproduction but also for rhizomal resource storage (Ida & Kudo, 2008). Thus, an earlier spring growing season could influence fitness both by increasing seed production and by increasing resource storage for future growth. Spring-flowering forest herbs are known for being slow colonizers, and there is concern that these species will not shift their geographic ranges poleward fast enough to respond to climate change (Augspurger & Salk, 2017; De Frenne et al., 2011). If spring-flowering forest herbs can respond to temperature changes through temporal shifts, they may adjust well to climate change over the short term, i.e., via phenotypic plasticity. Additional studies are needed to evaluate whether the phenotypic plasticity we observed would serve as an adaptive response to a warming climate (Duputié et al., 2015).

The different responses of trees and spring-flowering forest herbs to temperature in our study may occur because co-occurring trees and spring-flowering forest herbs in northeastern temperate deciduous forests sense temperature in different ways, even if the phenologies of both functional groups are mainly regulated by temperature. The main trigger for tree leaf-out is thought to be the accumulation of warm air temperatures (forcing), but tree phenology also responds to photoperiod and chilling (Basler & Korner, 2014; Laube et al., 2014; Zohner et al., 2016, 2017; Zohner & Renner, 2015), while spring-flowering herbs respond largely to soil temperature and snow depth (Jánosi et al., 2020; Pardee et al., 2019). However, the relationship between air temperatures, soil temperature, and snow depth is not straightforward because higher air temperatures are linked to decreased snow depth, and snow acts to insulate soil from temperature oscillations during winter. Thus, warmer air temperatures can lead, paradoxically, to colder soil temperatures, if soil remains frozen but not snow-covered (P. J. Brown & DeGaetano, 2011; Zhu et al., 2019). Therefore, higher temperatures could allow spring-flowering forest herbs to fulfill their chilling requirements (Augspurger & Salk, 2017) due to still-cold below-ground temperatures through the winter, and to experience warm temperatures in early spring due to the lack of insulating snow (P. J. Brown & DeGaetano, 2011; Zhu et al., 2019), which could explain their stronger response to warmer temperatures.

Despite general agreement that phenological responses to temperature are likely to vary across latitudes, there is still no consensus as to whether populations at higher latitudes are indeed more sensitive to temperature. Previous studies of herbaceous plants have reported more responsiveness to temperature for populations at higher latitudes or lower latitudes (Park et al., 2019; Parmesan, 2007; Prevéy et al., 2017; Routhier & Lapointe, 2002; Zhang et al., 2007). For trees, there is no consensus either way, with studies reporting higher latitudes responding more than middle and lower latitudes (Morin et al., 2009), or a similar response across latitudes (Phillimore et al., 2012). However, the studies mentioned above vary widely in terms of methodologies, geographical location, and latitudinal range analysed, which could contribute to the differences reported. Here, we found that spring-flowering forest herbs at middle latitudes (40–44° N) were more responsive to warmer temperatures than those at lower (35–39° N) or higher latitudes (45–48°

N). On the other hand, trees' response to temperature was higher at lower latitudes (35–39˚ N) relative to middle and high latitudes.

We hypothesize that the divergent results of our study across the latitudinal range could lie in factors other than temperature, such as snowpack, precipitation, or even solar radiation. As mentioned above, temperature is regarded as a crucial driver of spring phenology. However, phenological responses are mechanistically complex, and temperature, photoperiod, and other variables correlated with latitude interact with each other. Changes in air temperature and precipitation with warming likely vary from one location to another, with mid-latitudes experiencing a larger number of days when the ground is not covered by snow during the winter relative to higher latitudes, and, consequently, earlier snowmelt (Zhu et al., 2019). As discussed, reduced snow cover when the soil is still frozen could allow spring-flowering forest herbs to fulfill their chilling requirements and respond rapidly to forcing, perhaps explaining the stronger response of spring-flowering forest herbs at these locations. As for trees, their response to warming temperatures is mediated by interactions with chilling and photoperiod (Basler & Korner, 2014; Laube et al., 2014; Zohner et al., 2016; Zohner & Renner, 2015). In particular, the shorter day lengths in late winter may prevent leafing out in response to warmer temperatures, and this photoperiodic constraint may be particularly acute at high latitudes (Flynn & Wolkovich, 2018; Fu et al., 2012, 2015, 2019; Zohner et al., 2017; Zohner & Renner, 2014, 2015). Our results reinforce the need for further research into how environmental variables and local adaptation interact to produce different phenological responses across geographic and environmental gradients.

Our finding that spring-flowering forest herbs advanced their phenology more than trees with warmer temperatures at middle latitudes (40–44˚) directly contradicts the findings of an earlier study, conducted within the same latitudinal range, but in a single location (Heberling, Fridley, et al., 2019). Specifically, Heberling et al. (2019) reported that trees were advancing their phenology more strongly in response to warming than spring-flowering forest herbs, resulting in a shorter period for the latter to accumulate carbon before canopy closure, which the authors suggested could jeopardize fitness. To ensure that differences between the two studies were not due to differences in the time-window used to define spring, we re-analyzed our data using temperatures from the same date range used by Heberling et al. (2019), i.e., from March 1 to April 30. This change did not qualitatively affect our results, which still showed spring-flowering forest herbs advancing their phenology more than trees by –1.5 days/˚C on average (or by −0.9 days/˚C if we include only observations coming from the latitudinal range of 40–44˚N; see Table S2). Therefore, the discrepancy between the two studies could be a consequence of three non-mutually exclusive factors. First, the two studies, despite having some overlap in the tree species selection (six species out of the 15 in the Heberling's study), have no overlap in the set of herbaceous species studied. Species-specific responses to temperature variation could therefore be driving the different results. Secondly, the studies differ in their geographical scopes. Heberling et al. (2019) studied a single geographical location, while our dataset spans 965 locations across northeastern North America. The specific environmental conditions at a single site, such as precipitation, elevation, and edaphic factors, can affect phenology at a small scale (Ge et al., 2015; Wielgolaski, 2001), making it unwise to extrapolate from a single site to larger areas. Third, despite encompassing a broader geographical range, our study covered a relatively short time-period (2009–2021), whereas Heberling et al. (2019) analyzed contemporary data (2004–2018) and historical observations (1850s) together. We re-analyzed their data for the contemporary period only and found no difference in the rate of change between trees and spring-flowering forest herbs, suggesting that the findings of Heberling et al. (2019) were largely driven by the historical observations, which encompassed cooler temperatures than those observed today. It is therefore possible that differences in the results were driven by the differences in the time-period analysed (see Dose & Menzel, 2004; Ge et al., 2015; Rutishauser et al., 2007). Past and future temperatures beyond the range of conditions observed in our dataset could yield phenological shifts that would not be predicted by our model results, if, for example, phenological responses to temperature are actually non-linear—as is expected if factors other than forcing temperatures also influence phenology, as discussed by Wolkovich et al. (2021), Flynn & Wolkovich (2018) and Iler et al. (2013). The differences between the studies reinforce the need for more large-scale phenological syntheses encompassing long-term observations of multiple species (Gallinat et al., 2021).

4.2 | Implications of warmer temperatures for the hardwood forest ecosystem

There are still several unanswered question about the implications of warmer temperatures for the fitness of spring-flowering forest herbs and trees. For instance, warmer temperatures during spring can hinder bulb growth (Lapointe, 2001; Nault & Gagnon, 1993), but we lack studies investigating how such changes to hypogeous growth caused by warming affect plant fitness. Also, earlier leaf senescence under warmer temperatures has been reported in spring-flowering forest herbs and has been attributed to reduced bulb growth (Heberling, Cassidy, et al., 2019; Lapointe, 2001; McKenna & Houle, 2000); however, this response varies widely among individuals and species (Jacques et al., 2015; McKenna & Houle, 2000). Furthermore, species could be affected differently by warmer temperatures given their different carbon gain strategies (Augspurger & Salk, 2017; Heberling, Cassidy, et al., 2019; Jacques et al., 2015). Again, more studies are needed to address how warmer temperatures influence rhizome growth and forest herb fitness over the long term.

For trees, earlier leaf-out and longer growing season could also be beneficial if they increase the time available for carbon uptake. In contrast to spring-flowering forest herbs, most of the energy used by trees in temperate deciduous forests for the development of flowers and fruits comes from previously stored nutrients, since most flower before leaf-out (Augspurger & Zaya, 2020). Thus, consistently earlier leaf-out could translate into more stored resources for reproduction in subsequent years. However, increased photosynthetic productivity by trees at the beginning of the growing season can also cause earlier leaf senescence, which in turn shortens the growth period (Zani et al., 2020). More studies are needed to address how changes in the length of the growing season due to higher temperatures will affect carbon uptake by trees in the future.

Earlier emergence and leaf-out could expose both spring ephemerals and trees to unpredictable frost events, since warmer springs may not be accompanied by parallel increases in winter temperatures. Climate change is also expected to increase the frequency of extreme weather events (Marino et al., 2011; Solomon, 2007). Late frost can cause significant damage and fitness loss to plants (Augspurger, 2009; Gu et al., 2008; Inouye, 2008; Lenz et al., 2013; Pardee et al., 2019). For instance, in 2007, a major frost event took place in Illinois, USA, and as a result, the leaf expansion period was extended by 16–34 days for refoliating species (Augspurger, 2009). Leaf or leaf-bud loss to frost represents a significant cost for deciduous trees, affecting growth, reproduction, canopy expansion and nutrient reserves, as refoliation to compensate for damage demands extra resources, despite a shorter growing season in which to acquire them. However, spring-flowering forest herbs might benefit from such frost events if trees suffer the brunt of the damage from exposure to the cold night sky while sheltering the understory plants (Man et al., 2009), which can then profit from the decreased shading.

Furthermore, to fully assess the consequences of warmer temperatures for plant fitness it is necessary to consider their interactions with herbivores and pollinators. For instance, shifts in timing of herbivore emergence relative to plant phenology, as well as changes in the frequency or severity of herbivore outbreaks (independent of phenology), could have major impacts on understory shading and carbon budgets of trees and understory plants (Fabina et al., 2010; Pureswaran et al., 2018; Ren et al., 2020). Also, if plants and insects do not respond at the same rate to warming, mismatches between flowers and flower-visitors could occur (Kharouba et al., 2018; Kudo & Ida, 2013). Most tree species in temperate deciduous forests are wind-pollinated; warmer temperatures would therefore not affect their fitness through interactions with insect visitors. However, bees are known to visit and collect pollen from wind-pollinated trees in early spring when other pollen sources are scarce (Saunders, 2018); how earlier leaf-out of wind-pollinated trees would affect the fitness of these species is unknown. Spring-flowering forest herbs are generally insect-pollinated, and given the short flowering period of these species, phenological mismatches between these plants and their pollinators are possible (Kudo & Cooper, 2019). Also, since different phenophases can respond to warming at different rates (Buonaiuto et al., 2021), wind-pollinated trees could suffer reductions in pollination through mechanical interference if leaf-out shifts more dramatically than flowering.

4.3 | Conclusions

Our study demonstrates that spring-flowering forest herbs advance their phenology more strongly than trees in response to higher temperatures in throughout much of the range of deciduous temperate forests in North America. This greater responsiveness to warming could translate into a longer growing season for these understory wildflowers. However, predicting how warmer temperatures will affect individual species over the long term is challenging. As we demonstrated, the phenological response to temperature varies with latitude, with functional groups differing in how their responses vary throughout the latitudinal range. We are still a long way from a comprehensive understanding of the complex mechanisms regulating the phenologies of trees and spring-flowering forest herbs, and how those drivers differ not only between functional groups, but also among species within those functional groups. Furthermore, the short-term and presumably plastic responses to temperature observed in this study do not tell us about the capacity for these long-lived plant species to adapt to climate change over evolutionary time scales. Finally, it will be important to investigate the generality of our results by testing whether the observed pattern holds for deciduous temperate forests in Europe and Asia.

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Author contribution

JF devised the original manuscript idea, which was subsequently refined through discussions with the other authors. EFA performed the data preparation and analysis. EFA wrote the manuscript with input and revisions from the other authors.

Conflict of Interest Statement

The authors declare no conflict of interest.

Data availability statement

The data that support the findings of this study are available in http://doi.org/10.5066/F78S4N1.

R code supplementing the article is available in 10.5281/zenodo.6525427.

Table 1: Relationships between spring phenology and temperature for 10 tree species and 11 forest herb species at 965 temperate deciduous forest sites in eastern North America. Mean spring temperatures were calculated by averaging the monthly mean temperatures from March 1 to May 31. Sample sizes for each species are shown in Table S1. Values shown are slope estimates (in days per °C) and Bayes-R^2 followed by their 95% BCI for the following model: $DOY = \alpha + \beta * temperature$. Separate models were fitted for each species and functional group. Overall estimates for trees and spring-flowering forest herbs are shown at the top of the table. A negative BCI that does not overlap zero indicates an earlier spring phenology with higher temperatures.

	Species	**95% BCI**	**Bayes-R^2**
	Spring-flowering forest herbs	-4.9 [-5.2, -4.6] *	87.1 [86.4, 87.6]
	Trees	-3.3 [-3.5, -3.1] *	87.3 [86.9, 87.6]
Spring-flowering forest	*Arisaema triphyllum*	-4.8 [-6.1, -3.5] *	69.3 [60.4, 75.9]
	Claytonia virginica	-4.6 [-6.7, -2.5] *	55.0 [44.3, 63.7]
	Clintonia borealis	-4.2 [-6.0, -2.6] *	82.4 [79.4, 84.7]
	Cornus canadensis	-3.4 [-4.4, -2.2] *	78.3 [72.1, 82.9]
	Erythronium americanum	-4.7 [-5.3, -4.0] *	71.7 [66.7, 75.6]
	Maianthemum canadense	-4.0 [-4.9, -3.0] *	90.1 [88.9, 91.2]
	Mertensia virginica	-4.9 [-6.4, -3.3] *	70.6 [63.2, 76.3]
	Podophyllum peltatum	-3.4 [-4.8, -2.1] *	63.9 [54.9, 70.9]
	Sanguinaria canadensis	-5.4 [-6.7, -4.1] *	64.8 [53.8, 73.5]
	Trillium erectum	-3.6 [-4.3, -2.9] *	73.8 [66.5,79.2]
	Trillium grandiflorum	-3.0 [-5.5, -0.1] *	70.8 [48.6, 88.4]
Trees	*Acer rubrum*	-3.8 [-4.1, -3.4] *	87.7 [86.8, 88.6]
	Acer saccharum	-3.2 [-3.8, -2.6] *	85.2 [83.1, 87.6]
	Betula alleghaniensis	-1.3 [-2.9, 0.7]	83.8 [81.0, 85.9]
	Fagus grandifolia	-2.8 [-3.2, -2.4] *	89.5 [88.4, 90.4]
	Fraxinus americana	-3.4 [-5.5, -1.3] *	94.7 [91.3, 96.5]
	Juglans nigra	-2.6 [-3.9, -1.1] *	73.8 [66.8, 78.6]
	Liriodendron tulipifera	-3.3 [-4.0, -2.7] *	64.9 [61.1, 67.9]
	Populus tremuloides	-3.3 [-4.4, -2.3] *	59.0 [48.0, 66.9]
	Prunus serotina	-3.9 [-4.8, -2.9] *	85.4 [83.2, 87.0]
	Quercus rubra	-3.5 [-4.4, -2.6] *	83.3 [79.5, 86.0]

*95% BCI does not overlap zero

Table 2: Relationships between spring phenology and temperature for 10 tree species and 11 forest herb species at 965 temperate deciduous forest sites in eastern North America. Mean spring temperatures were calculated by averaging the monthly mean temperatures from March 1 to May 31. Values shown are slope estimates (in days per °C) and 95% BCI for the following model: $DOY = \alpha + \beta * temperature$. The difference among models is the time period over which the mean spring temperature was calculated. Separate models were fitted for each functional group. Overall estimates for trees and spring-flowering forest herbs are shown followed by the 95% BCI, and by the mean and 95% BCI of the difference between the estimates of the slopes. A negative BCI that does not overlap zero indicates an earlier spring phenology with higher temperatures. A negative value for the difference of the slope estimates indicates that spring-flowering forest herbs are advancing their phenology more than trees in response to temperature, and a positive value indicates that trees are advancing their phenology more in response to temperature.

Model	Mean and 95% BCI		Mean and 95% BCI of the difference between the slopes
	Spring-flowering forest herbs	Trees	
February - April			
Overall	-4.5 [-4.8, -4.2]*	-2.6 [-2.8, -2.4]*	-1.9 [-2.2, -1.6]*
35°- 39°	-3.1 [-4.5, -1.6]*	-3.4 [-3.9, -2.8]*	0.3 [-1.3, 1.8]
40°- 44°	-3.9 [-4.7, -3.1]*	-2.3 [-2.7, -2.0]*	-1.5 [-2.4, -0.7]*
45°- 48°	-1.1 [-2.2, 0.0]	0.4 [-0.2, 1.0]	-1.6 [-2.8, -0.3]*
March - May			
Overall	-4.9 [-5.2, -4.6]*	-3.3 [-3.5, -3.1]*	-1.6 [-1.9, -1.3]*
35°- 39°	-2.7 [-4.4, -1.0]*	-3.7 [-4.3, -3.1]*	1.0 [-0.8, 2.9]
40°- 44°	-4.9 [-5.7, -4.0]*	-3.5 [-4.0, -3.0]*	-1.4 [-2.4, -0.4]*
45°- 48°	-3.4 [-4.5, -2.2]*	0.4 [-0.6, 1.5]	-3.8 [-5.3, -2.3]*
April - June			
Overall	-5.3 [-5.6, -5.0]*	-3.5 [-3.8, -3.2]*	-1.8 [-2.2, -1.3]*
35°- 39°	-2.1 [-4.0, -0.2]*	-2.5 [-3.5, -1.4]*	1.7 [-0.4, 3.7]
40°- 44°	-5.0 [-6.0, -4.0]*	-2.7 [-3.5, -1.9]*	-2.2 [-3.5, -1.0]*
45°- 48°	-4.3 [-5.6, -3.0]*	-2.3 [-3.1, -1.3]*	-2.0 [-3.6, -0.5]*

*95% BCI does not overlap zero

Table 3: Relationships between spring phenology and year for 10 tree species and 11 spring-flowering forest herb species at 965 temperate deciduous forest sites in eastern North America. Sample sizes for each species are shown in Table S1. Values shown are slope estimates and Bayes-R^2 followed by their 95% BCI for the following model: $DOY = \alpha + \beta * year$. Separate models were fitted for each species and functional group. Overall estimates for trees and spring-flowering forest herbs are shown at the top of the table. A positive BCI that does not overlap zero indicates that spring phenology became later over the time period analysed here; a negative BCI indicates that spring phenology became earlier.

	Species	**95% BCI**	**Bayes-R^2**
	Spring-flowering forest herbs	0.6 [0.1, 1.0]	83.3 [82.5, 84.2]
	Trees	0.2 [0.0, 0.5]	83.5 [83.0, 84.0]
Spring-flowering forest herbs	*Arisaema triphyllum*	1.1 [-0.3, 2.6]	54.4 [42.0, 63.3]
	Claytonia virginica	1.0 [-1.3, 3.5]	49.4 [38.8, 57.9]
	Clintonia borealis	-0.1 [-1.0, 0.8]	72.4 [67.5, 76.1]
	Cornus canadensis	0.6 [-0.9, 2.0]	63.9 [54.7, 70.6]
	Erythronium americanum	0.2 [-0.7, 1.0]	58.8 [50.7, 65.1]
	Maianthemum canadense	0.6 [-0.3, 1.5]	84.6 [82.9, 86.0]
	Mertensia virginica	-0.3 [-1.3, 0.8]	62.0 [54.0, 58.0]
	Podophyllum peltatum	0.1 [-1.2, 1.3]	51.4 [41.2, 59.7]
	Sanguinaria canadensis	-2.2 [-4.5, -0.1]	56.1 [41.2, 67.0]
	Trillium erectum	0.7 [-0.2, 1.7]	63.2 [53.2, 70.5]
	Trillium grandiflorum	-0.8 [-2.3, 1.2]	64.3 [45.6, 75.2]
Trees	*Acer rubrum*	0.2 [-0.2, 0.7]	79.4 [78.4, 80.3]
	Acer saccharum	-0.8 [-1.4, -0.2]	82.0 [80.8, 83.1]
	Betula alleghaniensis	1.9 [0.3, 3.6]	82.2 [80.0, 84.0]
	Fagus grandifolia	1.3 [0.6, 2.0]	85.7 [84.4, 86.7]
	Fraxinus americana	2.8 [-0.9, 6.7]	87.4 [84.4, 89.4]
	Juglans nigra	0.4 [-0.5, 1.3]	52.4 [43.5, 59.6]
	Liriodendron tulipifera	-0.2 [-0.7, 0.3]	49.0 [45.3, 52.3]
	Populus tremuloides	1.2 [-0.1, 2.7]	60.4 [52.0, 66.8]
	Prunus serotina	-0.2 [-1.2, 0.8]	79.0 [77.7, 80.8]
	Quercus rubra	-0.4 [-1.3, 0.3]	63.5 [59.6, 66.8]

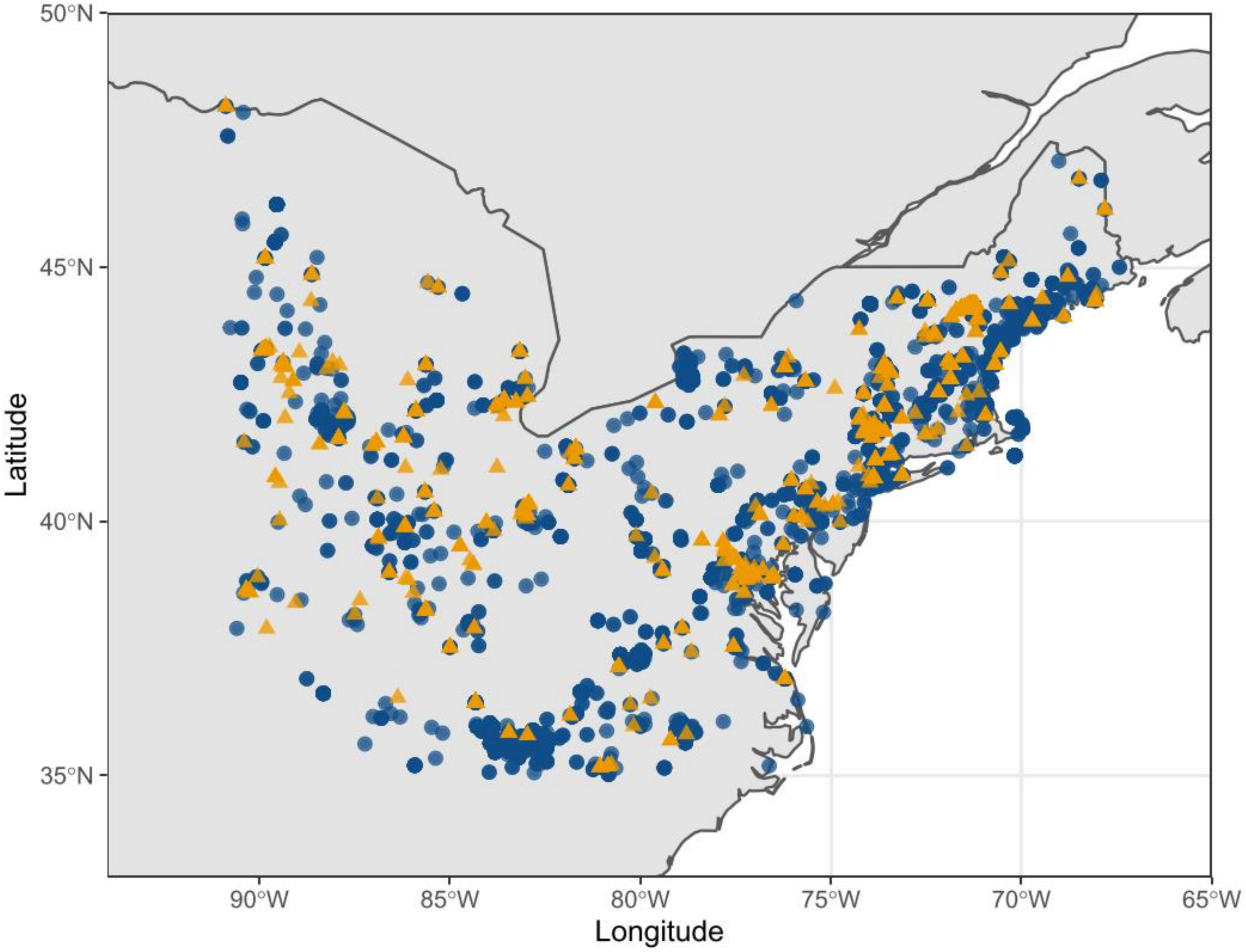

Figure 1: Map of eastern North America showing the locations of the 965 temperate deciduous forest sites for 10 tree species (blue dots) and 11 forest herb species (yellow triangles).

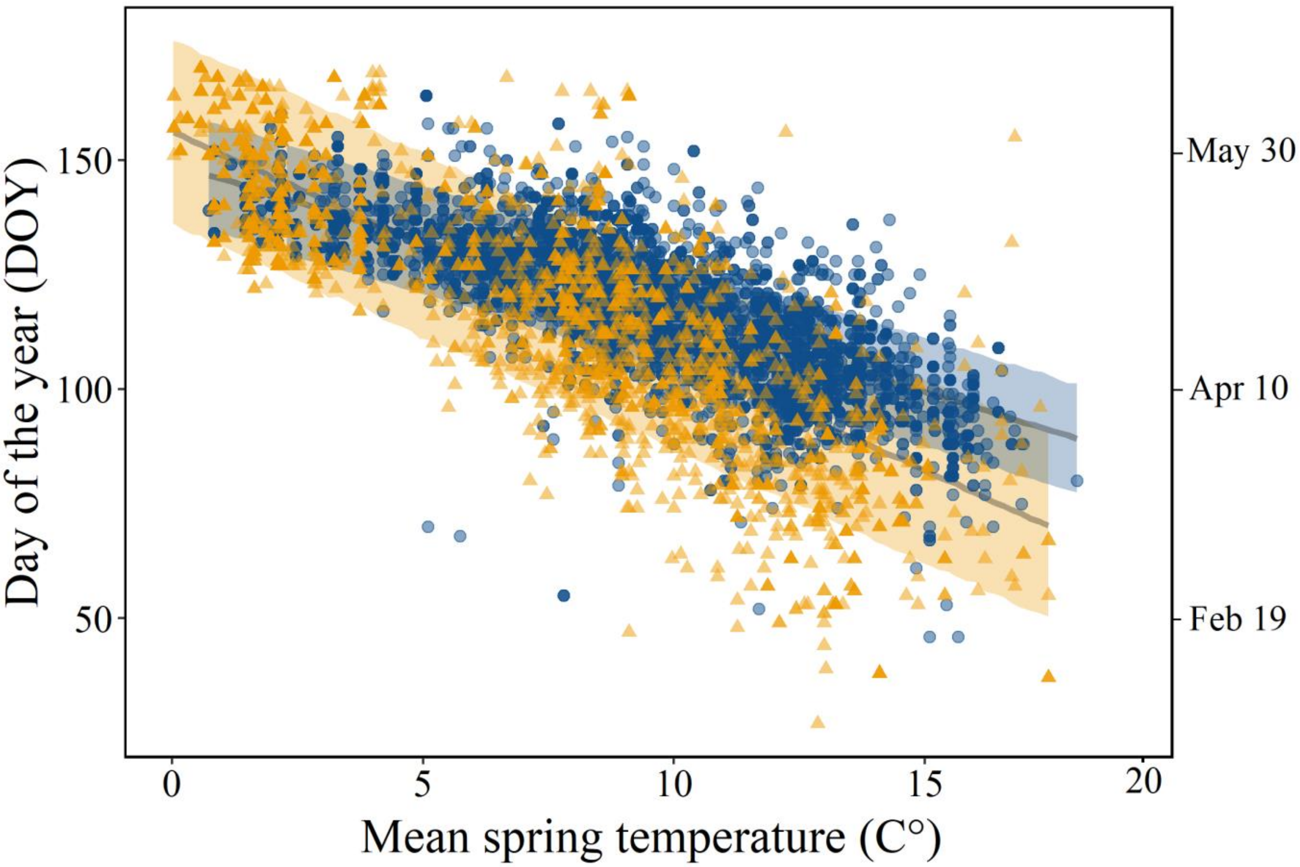

Figure 2: Relationship between spring phenology (day of year of leaf-out) and temperature for 10 tree species (blue dots) and 11 forest herb species (yellow triangles) (N = 6,040 tree observations, 2,005 forest herb observations) at 965 temperate deciduous forest sites in eastern North America. Separate models were fitted for each functional group. Solid lines show predicted relationships ($DOY = \alpha + \beta * temperature$), blue and yellow shading indicate the 95% BCI. Mean spring temperatures were calculated by averaging the monthly mean temperatures from March 1 to May 31.

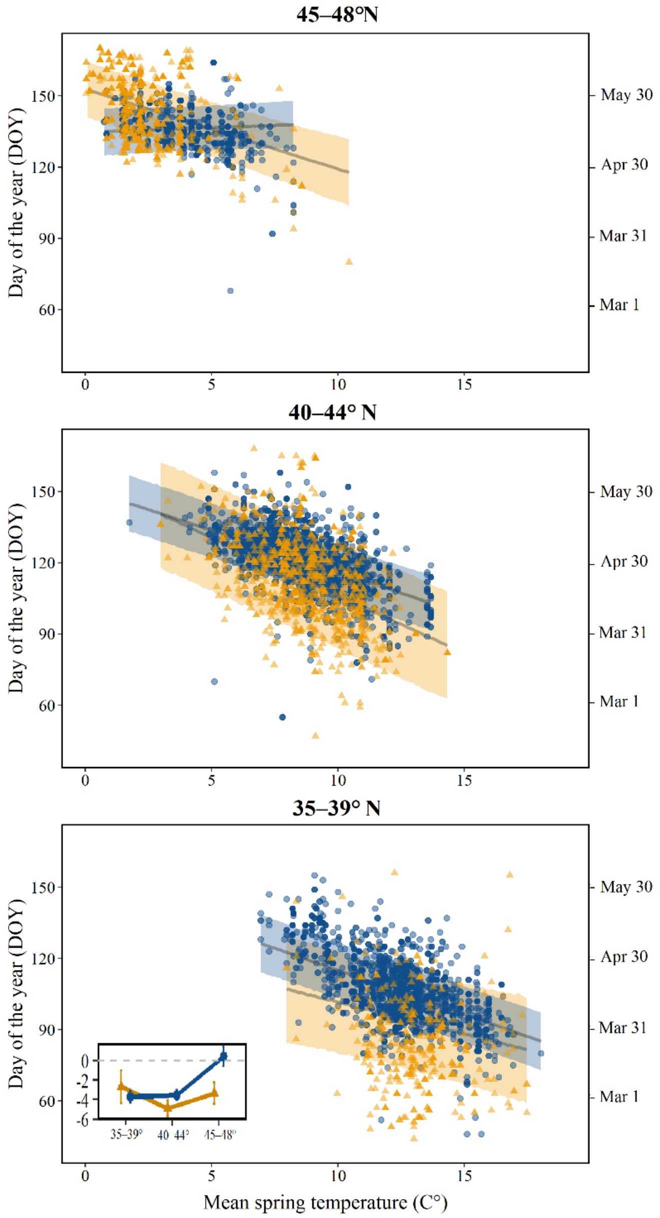

Figure 3: Predicted relationships between leaf-out day and temperature (solid lines) for different latitudinal bands, from the model $DOY = \alpha + \beta \times temperature$, for trees (blue dots) and spring-flowering forest herbs (yellow triangles). Blue and yellow shading indicate the 95% BCI. Inset figure shows the response to temperature (days/˚C) of both functional groups for each of the latitude categories (35–39˚, 40–44˚, 45–48˚ N). Mean spring temperatures were calculated by averaging the monthly mean temperatures from March 1 to May 31.

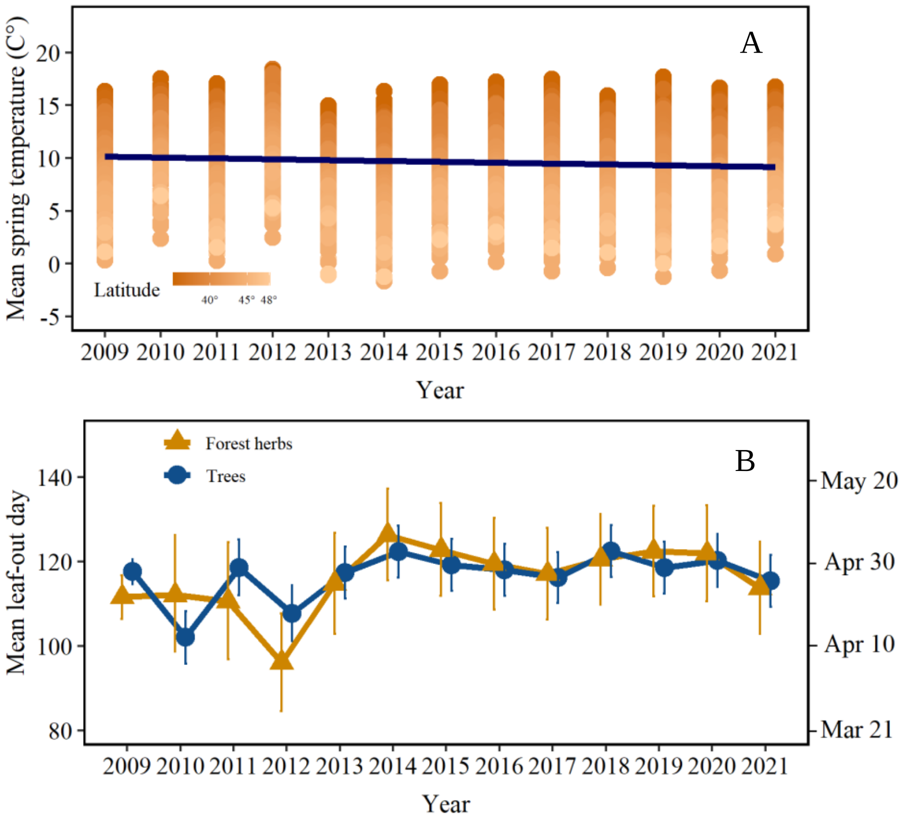

Figure 4: A) Mean spring temperature (March 1 to May 31, calculated by averaging the monthly mean temperatures) from 2009 to 2021 for 965 temperate deciduous forest sites in eastern North America. The decrease in mean spring temperature (shown by the dark blue line, representing the linear trend over time across all sites) was caused by a warm 2012. **B)** Estimates and 95% BCI for the mean leaf-out dates for 10 tree species and 11 spring-flowering forest herb species at 965 temperate deciduous forest sites in eastern North America ($DOY = \alpha + \beta * year$, where year is categorical).

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