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RESEARCH ARTICLE

Leveraging Natural History Collections to Understand the Impacts of Global Change

# Warmer temperatures are linked to widespread phenological mismatch among native and non-native forest plants

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## Abstract

1. Deciduous trees, shrubs and forest wildflowers may be advancing their leaf-out phenology at different rates in response to a warming climate. A mismatch between understory and overstory phenology may lead to a reduction of understory light levels in the early spring, which is a critical period when many spring-blooming wildflowers achieve highest photosynthetic rates. However, the extent of this phenomenon beyond a single site or region is largely unknown.
2. Using 3083 herbarium specimens collected between 1870 and 2019 across eastern North America, we assessed leaf-out and flowering times of 10 tree species (6 native, 4 non-native), 4 shrub species (2 native, 2 non-native) and 7 wildflower species (6 native, 1 non-native). We paired phenological data with historical climate data to quantify differences in phenological sensitivity to spring temperature across canopy strata, across species' geographical ranges and between native and non-native species.
3. Predicted phenological mismatches between native trees and wildflowers differed across large spatial scales, with wildflower populations in warmer regions of North America more likely to be affected. Overall, native tree species leafed out 3.6 days earlier per °C spring warming, while native wildflower species advanced their flowering times by 3.2 days per °C, resulting in phenological mismatch as wildflowers experience fewer days before tree leaf-out at warmer temperatures. Native trees and wildflowers in the warmer, southern part of their ranges advanced their spring phenology 2 and 1.5 times faster, respectively, than those in colder, northern locations. The phenological sensitivity of non-native plants was less variable across their ranges. Non-native trees and shrubs exhibited greater phenological sensitivity than native wildflowers. Notably, phenological sensitivities differed substantially among wildflower species, suggesting that certain species are more likely to be affected by phenological mismatch as climate warming progresses.
4. *Synthesis*: Our results provide new insight into novel phenological responses within and among species across a wide geographical range and the potential impact of competition and interactions with non-native invasive species. This research highlights the value of newly-available digitized museum collections

in phenological research to cover longer time periods, wider spatial areas and a greater diversity of species than otherwise possible.

**KEYWORDS**
climate change, eastern deciduous forest, herbaceous layer, herbaria, invasive plants, museum specimens, phenological sensitivity, spring ephemerals

## 1 | INTRODUCTION

Plants are important indicators of climate change, as plant species in temperate ecosystems demonstrate a strong trend of shifting their spring phenology—or timing of seasonal events—earlier with warmer temperatures (Bertin, 2008; Cleland et al., 2007; Ellwood et al., 2019; Everill et al., 2014; Menzel et al., 2006; Miller-Rushing & Primack, 2008; Panchen et al., 2012; Polgar et al., 2013; Primack et al., 2004; Stuble et al., 2021). Species vary in their phenological sensitivity, with some species demonstrating greater or lesser shifts with each degree of spring warming (Heberling, McDonough MacKenzie, et al., 2019; Lee & Ibáñez, 2021a; Park et al., 2018; Reeb et al., 2020). These different rates of response could lead to phenological mismatches, where alignment in the timing of ecological relationships is disrupted (Kharouba et al., 2018; Kharouba & Vellend, 2015; Mayor et al., 2017; Renner & Zohner, 2018).

A recent study in Concord, Massachusetts, USA, building on the observations of environmental philosopher Henry David Thoreau from the 1850s, found that canopy trees are advancing their leaf-out times faster than understory wildflowers are in response to warming temperatures (Heberling, McDonough MacKenzie, et al., 2019). Many early-blooming forest wildflowers rely on the period of full sunlight exposure before canopy trees leaf out in order to perform most of their photosynthesis and carbon gain for the year (Augspurger & Salk, 2017; Heberling, Cassidy, et al., 2019; Kudo et al., 2008; Lapointe, 2001). This difference in phenological sensitivity is resulting in a shrinking period of full early-spring sunlight for wildflowers, and thus a likely decline in their ability to photosynthesize and store carbon (Heberling, McDonough MacKenzie, et al., 2019). However, it remains untested if this phenological mismatch is widespread across eastern North America. As climate warming intensifies, it is important to understand how the phenology of different plant species will respond, and if different responses correspond to understory plants receiving more or less sunlight. Wildflowers are important for their ecological roles in cycling key nutrients in the ecosystem, contributing to forest species diversity and providing nutrition to pollinators and animals (Gallinat et al., 2020; Gilliam, 2007; Whigham, 2004).

Phenological mismatches resulting from different rates of change have been documented across trophic levels (Kharouba et al., 2018; Kharouba & Vellend, 2015; Mayor et al., 2017; Post & Forchhammer, 2008). However, few studies have compared phenological mismatches among plants occupying different forest layers (but see Heberling, McDonough MacKenzie, et al., 2019; Lee & Ibáñez, 2021a; Routhier & Lapointe, 2002, suggesting that such mismatches may be common but understudied), and most studies of phenological mismatches have been limited to small geographic areas (Heberling, Cassidy, et al., 2019; Kharouba & Vellend, 2015; Post & Forchhammer, 2008). Early spring light is also important for tree seedling survival (Lee & Ibáñez, 2021b), and a recent study found earlier leaf out in seedlings under climate change to be critical to tree recruitment (Lee & Ibáñez, 2021a).

Long-term data necessary to study these dynamics are limited, though herbaria are increasingly being used to study how phenology is changing in response to climate change (Davis et al., 2015; Heberling, Prather, et al., 2019; Lang et al., 2019; Meineke et al., 2018; Reeb et al., 2020; Zohner & Renner, 2014). Recent mass digitization of herbarium specimens has enabled easy access to millions of records of plant occurrence and phenology through time (Daru et al., 2017; Heberling, Prather, et a., 2019; Panchen et al., 2019; Soltis, 2017; Yost et al., 2018). Researchers can now use this vast, digital resource to conduct studies of changing phenology across large geographic ranges for thousands of species with an efficiency not previously possible (Ellwood et al., 2019; Heberling & Isaac, 2017; Meineke et al., 2018; Willis, Ellwood, et al., 2017). Park et al. (2018) showed that for widely-distributed plant species, populations had greater phenological sensitivity in the southeastern USA compared with the northeastern USA. Kopp et al. (2020) found that phenological sensitivity was greater at western latitudes and lower elevations in the Pacific Northwest region of North America. Song et al. (2021) found greater phenological sensitivity at lower latitudes in eastern Asia. These prior studies indicate that species frequently differ in phenological sensitivity across their ranges. Such within-species variation further suggests that phenological mismatch may vary across regions, but this has rarely been studied (but see Routhier & Lapointe, 2002).

Deciduous forests are commonly invaded by shade-tolerant woody shrubs (Martin et al., 2009), which also form a canopy over wildflowers. Non-native plants that have been introduced to new regions have evolved in different climate conditions and thus may have unique sensitivities to environmental cues that differ from native plants (Zohner & Renner, 2014). For example, many non-native plant species in North America occupy different phenological niches compared with native plants (Fridley, 2012; Gallinat et al., 2018; Gallinat et al., 2020; Reeb et al., 2020), and Reeb et al. (2020) found that native and non-native species had different phenological sensitivities to temperature and precipitation in Pennsylvania, USA. These changing dynamics could impact whether non-native species outcompete and shade out native wildflowers. However, it is yet untested whether non-native species are also contributing to or affected by phenological mismatch among forest layers.

In this study, we use herbarium specimens to examine a potential phenological mismatch between overstory trees and understory wildflowers in temperate deciduous forests of eastern North America. This ecosystem is currently heavily invaded by non-native plants (Martin et al., 2009) with predicted increases in introductions of new non-native plants (Allen & Bradley, 2016; Seebens et al., 2017). Therefore, we also investigate the phenological sensitivity of non-native invasive trees, shrubs and wildflowers and compare these with native species. We hypothesize the following:

1. Native understory wildflowers across eastern North America are at risk of reduced early-spring sunlight exposure due to phenological mismatches with shrubs and overstory trees.
2. Non-native species have greater phenological sensitivity to warming temperatures than native species, further contributing to mismatches.
3. Plant species in North America have greater phenological sensitivity to temperature in warmer locations than in colder locations.
4. The order in which species leaf out or flower changes as spring temperatures increase.

Overall, we ask whether understory native wildflowers across eastern North America are losing early-spring light access due to phenological mismatches with overstory native or non-native woody species and will continue to be shaded out earlier with ongoing warming.

## 2 | MATERIALS AND METHODS

### 2.1 | Herbarium specimens

We assessed leaf-out date (LOD) or flowering date (FD) from herbarium specimens collected in eastern North America for 21 species that are common in deciduous forests and have large ranges spanning much of the eastern half of the continent (Table 1). In this study, LOD and FD are proxies of phenological events assessed using herbarium specimens, and we use these terms to mean the date of collection for a specimen that was assessed to be in early-leafing condition (trees) or with open, functional flowers (shrubs, wildflowers). We do not use these terms to mean onset or first date. We selected species which are widespread and common across much of the Eastern Deciduous Forest Biome of North America and well represented in the herbarium record: six native overstory tree species (*Acer rubrum*, *Acer saccharum*, *Carya glabra*, *Fagus grandifolia*, *Quercus alba*, *Quercus rubra*), two native midstory shrub species (*Lindera benzoin*, *Vaccinium corymbosum*) and six native perennial herbaceous, spring-blooming wildflower species (*Anemone quinquefolia*, *Dicentra canadensis*, *Dicentra cucullaria*, *Erythronium americanum*, *Hepatica americana*, *Sanguinaria canadensis*). We chose non-native species which are considered invasive in at least ten U.S. states (EDDMapS, 2021) that also span forest strata: four invasive tree species (*Acer platanoides*, *Populus alba*, *Pyrus calleryana*, *Ulmus pumila*), two invasive midstory shrub species (*Berberis thunbergii*, *Euonymus alatus*) and one invasive understory wildflower (*Ficaria verna*).

We sought to capture when plants leaf out to determine the implications of potential phenological mismatch for plants' photosynthetic capacity in the early spring. We assessed LOD for trees, as we found that it was possible to distinguish young leaves from mature leaves in pressed herbarium specimens. However, we did not evaluate shrub and wildflower species directly for leaf-out times, as it is not possible on most specimens to distinguish young leaves from mature leaves, owing in part to the smaller size of shrub and herb leaves relative to tree leaves. Instead, we assessed FD for shrubs and wildflowers. We selected species which leaf out at around the same time as they flower (see Everill et al., 2014 for trees; shrubs and wildflowers were selected based on authors' field knowledge of these characteristics). For our analyses, we assume that the gap between leaf out and flowering (and therefore, their responses to climate) is small enough that it does not affect the results. Therefore, for shrubs and wildflowers, our phenological evaluations for flowering status also capture leaf-out times. In fact, many of the shrub and wildflower specimens had young leaves on them.

From spring 2019 through summer 2020, we accessed all available digitized specimen records (with images) of study species from the Consortium of Northeastern Herbaria (https://portal.neherbaria.org), the New York Botanical Garden William and Lynda Steere Herbarium (https://sweetgum.nybg.org), the Mid-Atlantic Herbaria Consortium (https://midatlanticherbaria.org), the Southeast Regional Network of Expertise and Collections (https://sernecportal.org), the Consortium of Midwest Herbaria (https://midwestherbaria.org), Canadensys (https://data.canadensys.net) and the Acadia University E.C. Smith Herbarium (https://procyon.acadiau.ca).

Tree species were evaluated for early, young leaves. Early leaves were determined using a combination of characteristics, including size, translucency, visual texture and the presence or absence of flowers (Everill et al., 2014). Shrub and wildflower species were evaluated for functional flowers using a combination of characteristics, including shape, openness, colour and the absence of fruits. For specimens included in the study, we recorded the date, location, collector and herbarium. We used geographic coordinates provided with the specimens, or if they were not available, we georeferenced the specimens to the centroid of the most precise geographic unit provided (address, then city or town, then county; Ellwood et al., 2019) using 'geocode' in R package GGMAP (Kahle & Wickham, 2013). We evaluated a total of 3797 herbarium specimens in early-leafing or flowering condition from over 100 herbaria across the eastern United States and Canada. However, we eventually excluded 714 evaluated specimens because we were unable to find matching climate data, leaving us with 3083 specimens in the final analysis. Data from all 3797 specimens are available in Supplemental Table S1.

Specimens dated from 1870 to 2019 and were collected from Florida, USA, to Quebec, Canada (Figure 1). The collection years of herbarium specimens were similar among native trees, shrubs and

**TABLE 1** The scientific names, common names, sample sizes (*n*), growth form classification and native/non-native classification of the 21 study species. Latitudinal range describes the lowest and highest latitude of a collected herbarium specimen in the study

| Scientific name | Common name | *n* | Growth form | Origin | Latitudinal range (°N) |
|---|---|---|---|---|---|
| *Acer rubrum* | Red maple | 310 | Tree | Native | 29.7–46.8 |
| *Acer saccharum* | Sugar maple | 141 | Tree | Native | 30.2–48.6 |
| *Carya glabra* | Pignut hickory | 110 | Tree | Native | 27.2–43.0 |
| *Fagus grandifolia* | American beech | 153 | Tree | Native | 29.7–46.2 |
| *Quercus alba* | White oak | 163 | Tree | Native | 29.8–44.5 |
| *Quercus rubra* | Red oak | 124 | Tree | Native | 33.3–47.0 |
| *Lindera benzoin* | Northern spicebush | 255 | Shrub | Native | 28.6–44.5 |
| *Vaccinium corymbosum* | High-bush blueberry | 262 | Shrub | Native | 27.3–46.1 |
| *Anemone quinquefolia* | Wood anemone | 181 | Wildflower | Native | 33.0–47.4 |
| *Dicentra canadensis* | Squirrel corn | 141 | Wildflower | Native | 34.9–46.9 |
| *Dicentra cucullaria* | Dutchman's breeches | 176 | Wildflower | Native | 34.5–46.7 |
| *Erythronium americanum* | Yellow trout lily | 188 | Wildflower | Native | 32.3–46.8 |
| *Hepatica americana* | Round-lobed hepatica | 147 | Wildflower | Native | 32.4–47.7 |
| *Sanguinaria canadensis* | Bloodroot | 216 | Wildflower | Native | 30.2–48.0 |
| *Acer platanoides* | Norway maple | 65 | Tree | Non-native | 34.5–46.8 |
| *Populus alba* | White poplar | 20 | Tree | Non-native | 32.6–45.5 |
| *Pyrus calleryana* | Callery pear | 55 | Tree | Non-native | 30.4–41.8 |
| *Ulmus pumila* | Siberian elm | 28 | Tree | Non-native | 35.0–46.9 |
| *Berberis thunbergii* | Japanese barberry | 132 | Shrub | Non-native | 32.9–45.5 |
| *Euonymus alatus* | Burning bush | 99 | Shrub | Non-native | 34.9–43.2 |
| *Ficaria verna* | Lesser celandine | 117 | Wildflower | Non-native | 34.8–44.5 |

wildflowers, and similar among non-native trees, shrubs and wildflowers in the study, with non-native specimens skewing later in time than native specimens (Figure S1). We collected an average of seven specimens per species from each state or province, with the number of specimens ranging from 0 to 80 across our study region. Greater sample sizes for some species were due to the inclusion of data from existing datasets (Ellwood et al., 2019; Everill et al., 2014). Herbarium datasets often include common geographic and temporal herbarium specimen collection biases, such as an overrepresentation of specimens collected near roads and herbaria and peak collection of specimens occurring during the 1900s in North America (Daru et al., 2017; Meineke & Daru, 2021).

## 2.2 | Climate data

We collected historic climate data for each specimen from the National Oceanic and Atmospheric Administration's Global Historical Climatology Network. We extracted temperature data for each specimen in the year it was collected from the nearest weather station within a 25-km radius using the R packages GGMAP (Kahle & Wickham, 2013) and RNOAA (Chamberlain, 2017). We calculated monthly average temperatures for all months in the dataset by averaging daily minimum and maximum temperatures for all days in a month. We excluded herbarium specimens with incomplete temperature records from the analysis. We used $R^2$ values to determine that average March and April temperature was the best or among the best predictors of early-spring phenology for all of our subgroups of data (including native species, non-native species, trees, shrubs, wildflowers and Cold, Medium and Warm-temperature subdivisions). We used mean spring temperature because of its documented correlation with plant phenology (Miller-Rushing & Primack, 2008; Panchen et al., 2012) and our ability to directly compare results with those of previous phenological studies in the eastern United States (e.g. Ellwood et al., 2013; Heberling, McDonough MacKenzie, et al., 2019; Park et al., 2018; Willis, Law, et al., 2017).

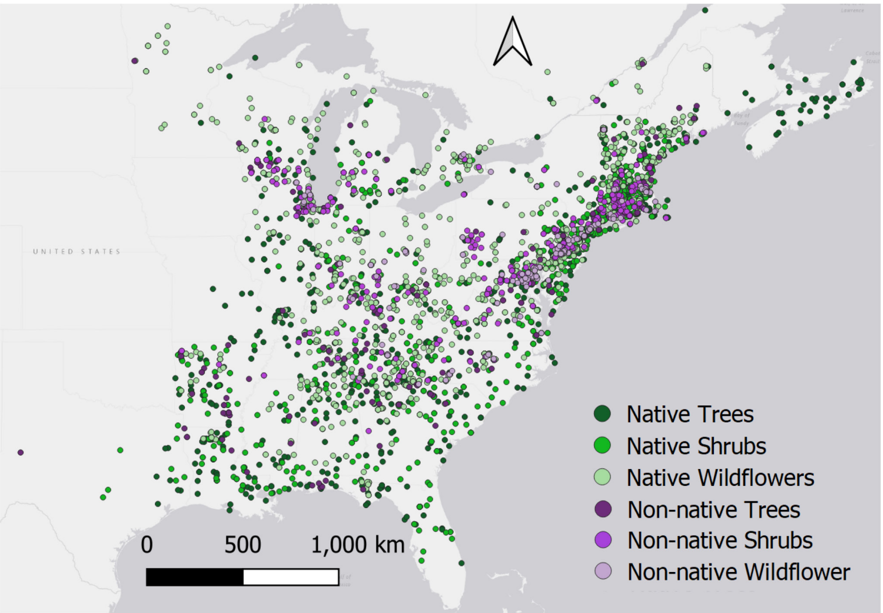


**FIGURE 1** Map of herbarium specimen collection locations in eastern North America by growth form and origin.

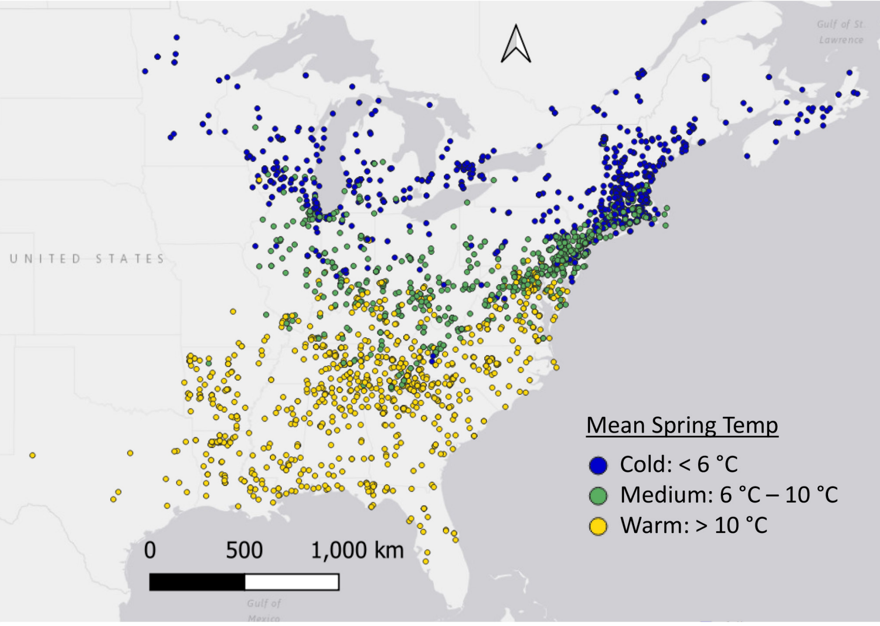


**FIGURE 2** Map of herbarium specimen collection locations in eastern North America by mean spring (March/April) temperature groups.

## 2.3 | Dividing specimens by spring temperature

Plants from warmer climates sometimes respond differently to climatic variation than plants from colder climates (Kopp et al., 2020; Park et al., 2018; Song et al., 2021). Because our collected specimens spanned a large temperature gradient across eastern North America, we wanted to control for the effect of climatic differences on plant temperature sensitivity. To compare phenological sensitivity across climates, we divided our specimens into three spring temperature groupings (Cold, Medium and Warm) based on the average spring (March and April) temperature in the year a specimen was collected. This analysis also addresses the different geographic spread of specimens by comparing specimens in similar locations to each other. In a method similar to Love and Mazer (2021), we split the specimens into three equal-sized groups of those with the coldest, medium and warmest temperatures, then determined the temperature cut-offs dividing those groups and rounded to the nearest whole degree. This division of the dataset resulted in the Cold temperature group as locations with an average spring temperature of less than 6°C, the Medium temperature group as locations with an average spring temperature of greater than or equal to 6°C and less than or equal to 10°C, and the Warm temperature group as locations with an average spring temperature of greater than 10°C. The Cold, Medium and Warm temperature groups had similar sample sizes among native species (mean sample size 285) and non-native species (mean sample size 57). There is some geographical overlap among the temperature groups due to the presence of some colder high elevation sites further south, some warmer coastal sites further north, and due to interannual temperature variation, with occasional cold springs further south and warm springs further north (Figure 2).

## 2.4 | Data analysis

All analyses were conducted using R statistical software, version 3.5.1 (R Core Team, 2018). We used Bayesian linear regression, performed in JAGS (Plummer, 2003) using *r2jags* (Su & Yajima, 2015), to model relationships between average spring temperature (which we define throughout as the mean of March and April temperatures in the year the specimen was collected) and the day of year of early-spring phenology (leaf-out for trees and flowering for shrubs and wildflowers). To determine the best temperature predictor variable for early-spring phenology of our specimens, we compared linear regressions of day of year for leaf-out or flowering phenology (LOD or FD) and different combinations of average monthly temperatures (Heberling, McDonough MacKenzie, et al., 2019; Supplemental Table S2).

We performed regressions separately for native trees, native shrubs, native wildflowers, non-native trees, non-native shrubs and non-native wildflower, including random intercepts for species and year (Table 2). We also modelled phenological responses of trees, shrubs and wildflowers to temperature separately for subdivisions by temperature grouping (i.e. Cold, Medium and Warm) and for each individual species, including year as a random effect (Iler et al., 2017). We used these models to estimate changes in the sequence of phenological events across groups and species at spring temperatures of 0°C, 10°C and 20°C. We conducted analyses to confirm that our conclusions were robust to different time periods. All prior distributions were non-informative. Normal distribution priors with mean zero and variance $10^5$ were used for fixed-effect parameters, and random-effect standard deviations were sampled from a uniform prior (0, 100). We ran our final models with three parallel Markov chain Monte Carlo (MCMC) chains for 50,000 iterations, discarding the initial 10,000 for burn-in. Trace plots and the Gelman–Rubin diagnostic (<1.1) were used to confirm convergence (Gelman & Hill, 2007). Across models, we consider two groups to be statistically significant if the 95% credible intervals from parameter posterior distributions do not overlap.

# 3 | RESULTS

## 3.1 | Native trees shift phenology more with spring warming than native wildflowers

Native trees advanced their LODs significantly faster than native wildflowers advanced their FDs in response to warmer spring temperatures. The six native tree species leafed out 3.6 days earlier per °C increase in mean spring temperature, while the six native wildflower species flowered 3.2 days/°C earlier (Figure 3). The models predict that native wildflowers flower 16 days earlier than native trees leaf out at average spring temperatures of 0°C, but only 7 days earlier at average spring temperatures of 20°C. We compare phenology at 0°C and 20°C to capture the range of spring temperatures in the dataset and highlight how phenology may shift as the climate warms.

Individual species differed in their sensitivity to spring temperature. *Fagus grandifolia* and *A. rubrum* were the most-sensitive native tree species, advancing their leaf-out 4.0 and 3.7 days/°C, respectively (Figure 4). *Quercus alba* and *A. saccharum* were the least-sensitive native tree species, advancing leaf-out 3.2 and 3.3 days/°C, respectively. *E. americanum* and *S. canadensis* were the most-sensitive native wildflower species, both advancing their flowering 3.5 days/°C. *A. quinquefolia*, *D. canadensis* and *D. cucullaria* were the least-sensitive native wildflower species, advancing their flowering only 2.6, 2.8 and 2.8 days/°C, respectively.

## 3.2 | Phenological sensitivity across species' ranges

Native trees in the Warm spring temperature group advanced their leaf-out phenology about two times faster for each degree of warmer spring temperature compared with native trees in the Medium or Cold temperature groups (Figure 5). Native wildflowers in the Warm and Medium spring temperature groups were more sensitive to spring temperature than those in the Cold temperature group, although modelled slope $\beta_{LOD}$ or $\beta_{FD}$ credible intervals overlap. Native shrubs were more sensitive in the Medium temperature group, but not significantly so. Non-native trees and the non-native wildflower did not differ significantly in their sensitivity across Cold, Medium and Warm spring temperature groups, although the non-native wildflower did exhibit a trend of increasing sensitivity from Cold to Warm temperature groups. Non-native shrubs were more than two times more sensitive in the Medium compared with the Cold temperature group and had intermediate sensitivity in the Warm temperature group. Native trees were significantly about 1.5 times more sensitive to spring temperature than native wildflowers in the Warm spring temperature group, but there was no significant difference between native trees and wildflowers in the Cold temperature group.

## 3.3 | Non-native species phenological sensitivity

Non-native trees, shrubs and wildflowers did not differ significantly in their phenological sensitivity to spring temperature compared with their native counterparts; although non-native trees were slightly more sensitive than native trees, native shrubs were slightly more sensitive than non-native shrubs and the non-native wildflower was slightly more sensitive than native wildflowers (Figure 3). Non-native plants had much greater variability in their phenological sensitivity.

Individual non-native species also differed in their phenological sensitivity, although the credible intervals were large and only one difference was statistically significant (Figure 4). *Pyrus calleryana* was the most-sensitive non-native tree species, advancing its leaf-out 4.4 days/°C of spring warming. *Quercus alba* was the least-sensitive

**TABLE 2** Bayesian regression model results of slope (β1) and intercept (β0) estimates with 2.5 and 97.5 credible intervals (CI) and standard deviations (*SD*)

| Origin | Growth form | Species | Temperature group | β1 mean | β1 2.5 CI | β1 97.5 CI | β1 sd | β0 mean | β0 2.5 CI | β0 97.5 CI | β0 *SD* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Native | Trees | NATIVE TREES | All | −3.607 | −3.755 | −3.458 | 0.075 | 150.558 | 147.364 | 153.802 | 1.653 |
| | | *Acer rubrum* | All | −3.743 | −4.022 | −3.449 | 0.148 | 144.621 | 137.377 | 152.043 | 3.498 |
| | | *Acer saccharum* | All | −3.286 | −3.586 | −2.989 | 0.148 | 143.469 | 135.839 | 151.578 | 3.866 |
| | | *Carya glabra* | All | −3.693 | −4.155 | −3.218 | 0.238 | 159.339 | 149.638 | 168.720 | 4.682 |
| | | *Fagus grandifolia* | All | −3.979 | −4.366 | −3.613 | 0.193 | 151.544 | 141.194 | 161.527 | 4.962 |
| | | *Quercus alba* | All | −3.196 | −3.521 | −2.851 | 0.171 | 152.593 | 143.850 | 160.550 | 4.061 |
| | | *Quercus rubra* | All | −3.500 | −3.873 | −3.125 | 0.189 | 151.003 | 143.422 | 158.384 | 3.562 |
| | Shrubs | NATIVE SHRUBS | All | −4.258 | −4.486 | −4.026 | 0.118 | 147.890 | 140.756 | 155.082 | 3.666 |
| | | *Lindera benzoin* | All | −3.783 | −4.111 | −3.444 | 0.172 | 131.951 | 126.903 | 137.149 | 2.566 |
| | | *Vaccinium corymbosum* | All | −4.546 | −4.853 | −4.257 | 0.152 | 161.796 | 152.636 | 170.877 | 4.346 |
| | Wildflowers | NATIVE WILDFLOWERS | All | −3.222 | −3.382 | −3.063 | 0.081 | 135.177 | 132.052 | 138.498 | 1.632 |
| | | *Anemone quinquefolia* | All | −2.561 | −2.991 | −2.120 | 0.221 | 139.334 | 132.545 | 146.266 | 3.386 |
| | | *Dicentra canadensis* | All | −2.845 | −3.267 | −2.434 | 0.211 | 137.143 | 132.082 | 142.290 | 2.542 |
| | | *Dicentra cucullaria* | All | −2.843 | −3.236 | −2.452 | 0.197 | 131.852 | 125.420 | 138.869 | 3.248 |
| | | *Erythronium americanum* | All | −3.538 | −3.866 | −3.196 | 0.171 | 136.297 | 128.705 | 143.982 | 3.747 |
| | | *Hepatica americana* | All | −3.303 | −3.839 | −2.744 | 0.280 | 129.168 | 123.219 | 135.121 | 3.064 |
| | | *Sanguinaria canadensis* | All | −3.484 | −3.723 | −3.239 | 0.127 | 130.823 | 121.430 | 140.598 | 4.594 |
| Non-native | Trees | NON-NATIVE TREES | All | −3.682 | −4.110 | −3.256 | 0.220 | 143.482 | 136.672 | 150.116 | 3.404 |
| | | *Acer platanoides* | All | −3.028 | −3.502 | −2.560 | 0.239 | 140.543 | 135.185 | 146.514 | 2.815 |
| | | *Populus alba* | All | −2.925 | −4.134 | −1.706 | 0.592 | 145.063 | 119.761 | 170.819 | 12.750 |
| | | *Pyrus calleryana* | All | −4.359 | −5.270 | −3.485 | 0.449 | 138.635 | 121.056 | 155.959 | 8.809 |
| | | *Ulmus pumila* | All | −3.979 | −4.970 | −2.992 | 0.497 | 148.640 | 135.995 | 160.302 | 6.149 |
| | Shrubs | NON-NATIVE SHRUBS | All | −3.933 | −4.390 | −3.502 | 0.227 | 157.880 | 151.315 | 164.730 | 3.406 |
| | | *Berberis thunbergii* | All | −4.258 | −4.767 | −3.730 | 0.262 | 151.887 | 145.746 | 157.487 | 2.943 |
| | | *Euonymus alatus* | All | −3.731 | −4.484 | −2.993 | 0.373 | 164.598 | 156.436 | 172.738 | 4.175 |
| | Wildflower | NON-NATIVE WILDFLOWER | All | −3.638 | −4.355 | −2.931 | 0.367 | 135.824 | 123.374 | 147.340 | 5.755 |
| | | *Ficaria verna* | All | −3.638 | −4.355 | −2.930 | 0.367 | 135.824 | 123.374 | 147.340 | 5.755 |

(Continues)

**TABLE 2** (Continued)

| Origin | Growth form | Species | Temperature group | β1 mean | β1 2.5 CI | β1 97.5 CI | β1 sd | β0 mean | β0 2.5 CI | β0 97.5 CI | β0 *SD* |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Native | Trees | NATIVE TREES | Cold | −2.616 | −3.154 | −2.062 | 0.276 | 145.670 | 141.882 | 149.478 | 1.929 |
| | | NATIVE TREES | Medium | −3.129 | −4.470 | −1.773 | 0.685 | 148.295 | 137.120 | 159.264 | 5.608 |
| | | NATIVE TREES | Warm | −4.943 | −5.388 | −4.495 | 0.230 | 168.987 | 161.438 | 176.181 | 3.789 |
| | Shrubs | NATIVE SHRUBS | Cold | −2.764 | −3.697 | −1.853 | 0.466 | 142.067 | 133.587 | 150.306 | 4.168 |
| | | NATIVE SHRUBS | Medium | −4.659 | −6.246 | −3.026 | 0.821 | 151.940 | 136.273 | 167.645 | 7.996 |
| | | NATIVE SHRUBS | Warm | −3.781 | −4.510 | −3.072 | 0.372 | 140.378 | 126.045 | 154.653 | 7.332 |
| | Wildflowers | NATIVE WILDFLOWERS | Cold | −2.422 | −2.902 | −1.935 | 0.249 | 132.366 | 128.763 | 136.158 | 1.879 |
| | | NATIVE WILDFLOWERS | Medium | −3.513 | −4.396 | −2.627 | 0.443 | 138.203 | 130.604 | 145.509 | 3.815 |
| | | NATIVE WILDFLOWERS | Warm | −3.505 | −4.364 | −2.633 | 0.438 | 138.351 | 125.951 | 151.117 | 6.459 |
| Non-native | Trees | NON-NATIVE TREES | Cold | −1.674 | −3.022 | −0.300 | 0.687 | 137.571 | 129.354 | 145.311 | 4.095 |
| | | NON-NATIVE TREES | Medium | −3.151 | −5.029 | −1.202 | 0.973 | 140.646 | 124.713 | 155.865 | 7.842 |
| | | NON-NATIVE TREES | Warm | −2.580 | −3.729 | −1.416 | 0.599 | 129.581 | 112.538 | 146.552 | 8.907 |
| | Shrubs | NON-NATIVE SHRUBS | Cold | −2.614 | −4.189 | −1.041 | 0.802 | 152.371 | 141.697 | 162.712 | 5.265 |
| | | NON-NATIVE SHRUBS | Medium | −5.909 | −7.516 | −4.385 | 0.807 | 172.612 | 159.069 | 186.591 | 7.017 |
| | | NON-NATIVE SHRUBS | Warm | −4.126 | −6.668 | −1.695 | 1.278 | 160.989 | 129.885 | 192.003 | 16.043 |
| | Wildflower | NON-NATIVE WILDFLOWER | Cold | −1.818 | −5.081 | 1.330 | 1.629 | 129.004 | 102.431 | 156.525 | 13.314 |
| | | NON-NATIVE WILDFLOWER | Medium | −3.308 | −6.375 | −0.084 | 1.570 | 133.488 | 104.498 | 160.935 | 14.172 |
| | | NON-NATIVE WILDFLOWER | Warm | −3.534 | −6.356 | −0.751 | 1.454 | 132.515 | 93.036 | 171.134 | 19.660 |

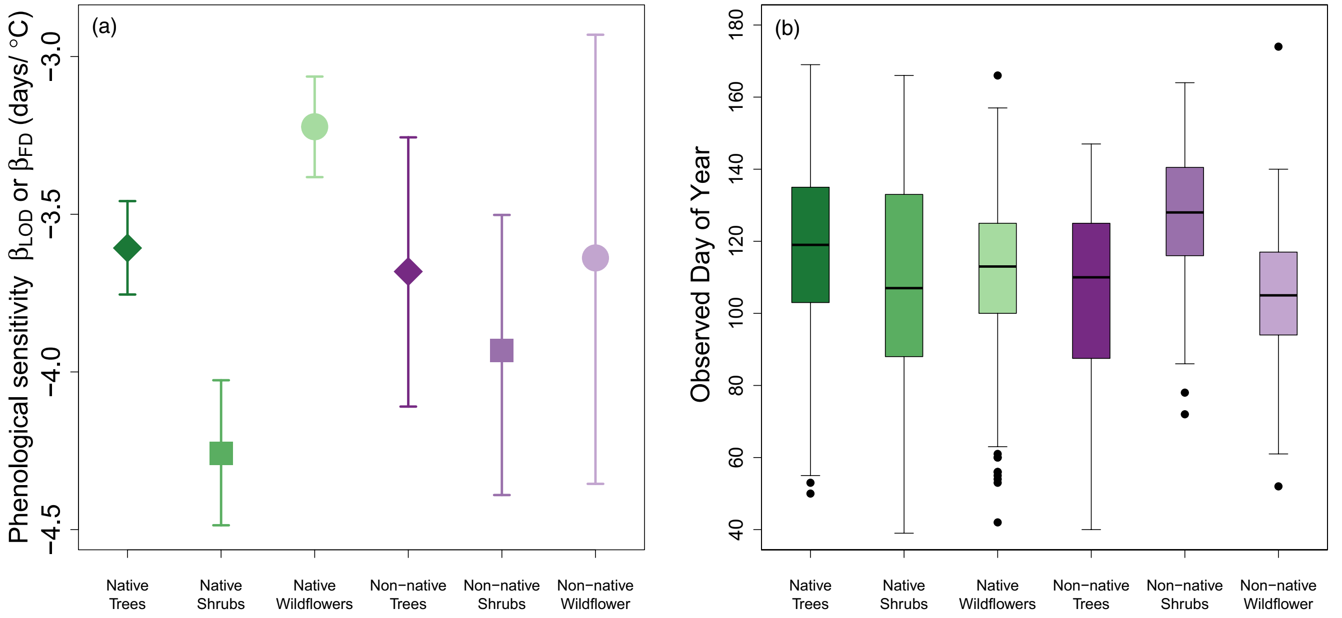
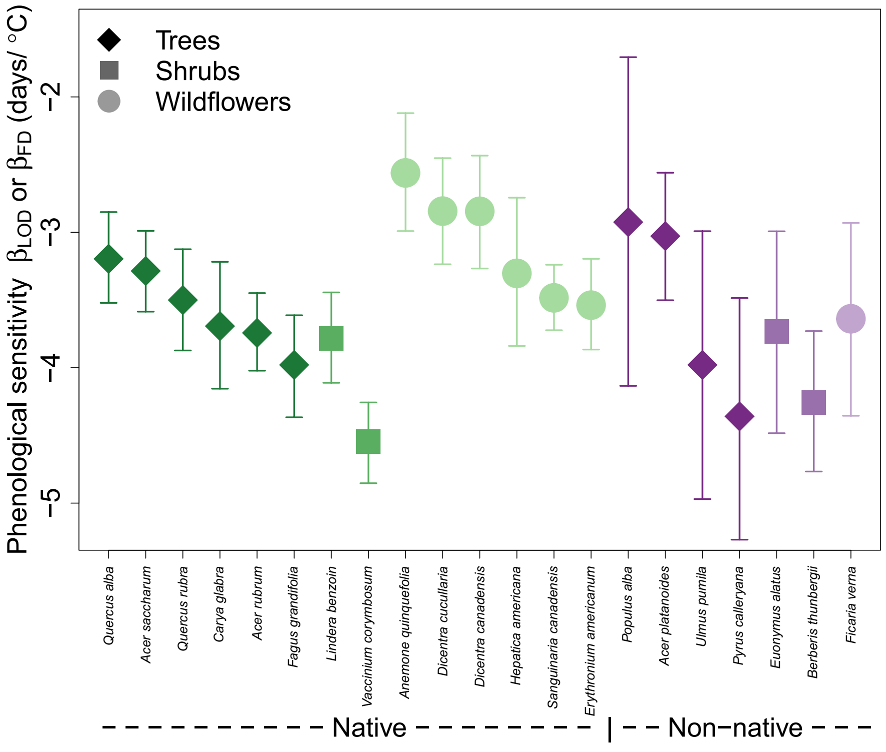


**FIGURE 3** Forest plant species exhibited different modelled phenological sensitivity (leaf-out date for trees, flowering date for shrubs and wildflowers) to mean spring temperature (a) and different observed mean dates and ranges of leaf out or flowering (b) based on their growth form (overstory tree, midstory shrub or understory wildflower) and their origin (native or non-native) using herbarium records across eastern North America. Points in 3A represent the model slope estimates for $\beta_{LOD}$ or $\beta_{FD}$. Non-overlapping 95% credible intervals in 3A indicate model results which are statistically significantly different. Green colours represent native species and purple colours represent non-native species.

**FIGURE 4** Individual forest plant species exhibited different phenological sensitivity to warming temperatures. Points represent the slope estimates (with 95% credible intervals) for $\beta_{LOD}$ (trees) or $\beta_{FD}$ (shrubs, wildflowers) from species-specific models. Non-overlapping credible intervals indicate parameter posterior estimates which are statistically significantly different. Green colours represent native species and purple colours represent non-native species.



non-native tree species, advancing leaf-out 2.9 days/°C of warmer spring temperature. Of the non-native shrubs, *B. thunbergii* was more sensitive than *E. alatus*, advancing their flowering times 4.3 and 3.7 days/°C, respectively. The non-native wildflower *F. verna* advanced its flowering 3.6 days/°C.

### 3.4 | Order of early-spring phenology changes with warming

Based on fitted model estimates, the order of early-spring phenological events—leaf-out and flowering—changed at different

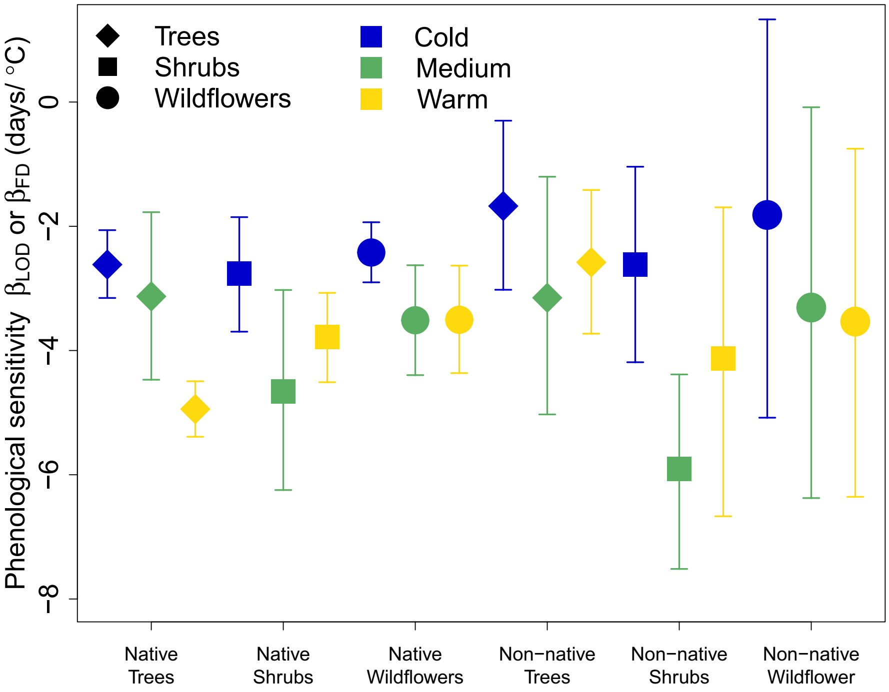


**FIGURE 5** Forest plant species had different phenological sensitivity to warming temperatures based on their collection location's average spring temperature (Cold, Medium or Warm), growth form (canopy tree, midstory shrub or understory wildflower) and origin (native or non-native) in a study of herbarium records collected across eastern North America. Points represent slope estimates $\beta_{LOD}$ or $\beta_{FD}$ (with 95% credible intervals) by sites grouped by long-term mean spring temperatures. Non-overlapping credible intervals indicate parameter posterior estimates which are statistically significantly different.

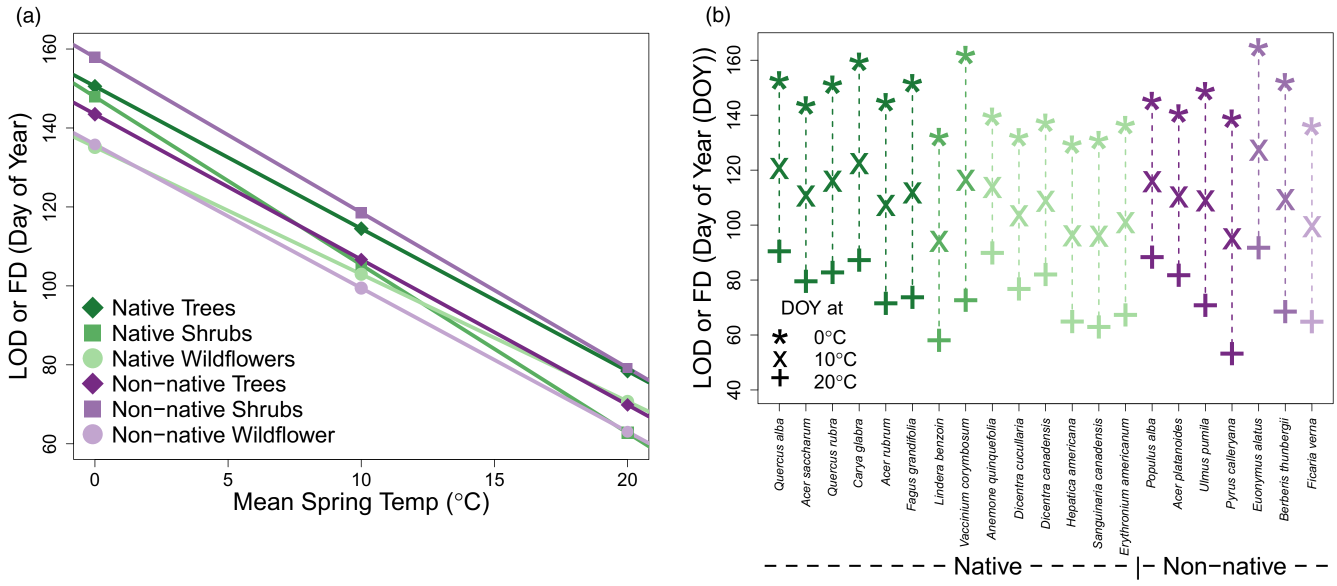


**FIGURE 6** The order of early-spring phenology for forest plant species by growth form and origin groups (a) and individual species (b) changed across different average spring temperatures. Points represent fitted model estimates of LOD (trees) and FD (shrubs, wildflowers) at spring temperatures of 0°C, 10°C and 20°C. Green colours represent native species and purple colours represent non-native species.

spring temperatures. At colder average spring temperatures (0 °C), the native wildflowers were the first to flower, followed by the leaf-out and flowering of the non-native wildflower, non-native trees, native shrubs, native trees, and then non-native shrubs (Figure 6a). Non-native shrubs flowered on average 23 days later than native wildflowers and 7 days later than native trees. At warmer average spring temperatures (20°C), native shrubs were the first to leaf out, followed by the leaf-out and flowering of the non-native wildflower, non-native trees, native wildflowers, native trees and then non-native shrubs. Non-native shrubs flowered on average 16 days later than native shrubs and 1 day later than native trees.

From 0°C to 20°C, the gap between native wildflowers' flowering and native trees' leafing out decreased from 15 to 8 days. The gap between native wildflowers' and non-native trees' early phenology decreased with warmer spring temperatures. Native wildflowers flowered about 8 days before non-native trees at 0°C, but non-native trees leafed out about 1 day before native wildflowers at 20°C. Non-native shrubs flowered about 22 days after native wildflowers at 0°C, and this gap decreased to about 9 days at 20°C.

At the species level, the order of phenology also changed at different spring temperatures, based on the fitted model estimates for individual species. *Vaccinium corymbosum* (native shrub) shifted from being one of the latest species to flower at 0°C to being in the middle at 20°C (Figure 6b). *Populus alba* (non-native tree) shifted from being in the middle at 0°C to being one of the latest species at 20°C. *P. calleryana* (non-native tree), *L. benzoin* (native shrub), *H. americana* (native wildflower) and *F. verna* (non-native wildflower) remained four of the earliest species across temperatures. Three of the native wildflowers—*A. quinquefolia*, *D. canadensis* and *D. cucullaria*—shifted to being later in the order at higher temperatures.

## 4 | DISCUSSION

### 4.1 | Native trees shift phenology more with warmer spring temperatures than native wildflowers

We evaluated over 3000 digitized herbarium specimens to assess differences in spring leaf out and flowering sensitivities and resulting changes to spring phenology order across forest layers and across the ranges of 21 species. We found that native trees advanced their leaf-out times with increased spring temperatures faster than native wildflowers advanced their flowering times. Although interesting regional variation exists, this study demonstrates that earlier findings at a single site in Concord, Massachusetts (Heberling, McDonough MacKenzie, et al., 2019) are consistent with a general phenomenon across eastern North America. This phenological mismatch means that wildflowers are likely to experience reduced sunlight access for photosynthesis in the early spring in coming decades, and these impacts may lead to declines in the abundance of native wildflower populations as the climate warms (Augspurger & Salk, 2017; Heberling, McDonough MacKenzie, et al., 2019; Nault & Gagnon, 1993). It is unclear whether small changes of a few days in this early-season light window meaningfully affect fitness. Further studies should examine the impacts of this phenological mismatch on wildflower growth, reproduction and survival.

A loss of wildflower species from the forest understory would have widespread ecological and conservation impacts. Wildflowers comprise a key component of the species-diverse herbaceous forest layer, impact the regeneration and success of overstory plants, mediate carbon cycling, maintain key nutrients in the ecosystem (e.g. nitrogen, phosphorus) and provide nutrition to many animals (Gallinat et al., 2020; Gilliam, 2007, 2014; Whigham, 2004). In addition to their ecological roles, spring-blooming wildflowers are important for food, medicine, nature appreciation and cultural heritage, particularly for Indigenous communities (Applequist, 2010; Burkhart & Jacobson, 2009; Foster & Duke, 2000; Herrick, 1995; Hirsch, 2018; Kuhnlein & Turner, 1991; Meeker & Elias, 1993).

Therefore, it is important to quantify the different responses to climate change among species in order to better understand the extent of mismatches and which species might be more or less successful as the climate warms. Wildflower species that are more sensitive to temperature (e.g. *E. americanum*) may be less impacted by advancing tree canopy leaf out than wildflower species which are less sensitive (e.g. *A. quinquefolia*). In addition, a wildflower population located in a forest where the dominant tree species is less sensitive to temperature (e.g. *Q. alba*) may have more sunlight access and ability to photosynthesize than if the wildflowers were in a forest area where the dominant tree species is more sensitive (e.g. *F. grandifolia*) and thus, shades them over sooner.

Overall, we did find the same general pattern and similar rates of sensitivity to temperature variation as the earlier Heberling, McDonough MacKenzie, et al. (2019) study from Concord. Our study and Heberling, McDonough MacKenzie, et al. (2019) found a consistent pattern of sensitivity among species: for example, of the six native tree species, *Q. alba* was the least sensitive and *A. rubrum* was the most or second-most sensitive in both studies. However, these two studies found slightly different phenological sensitivities for trees and wildflowers. Heberling, McDonough MacKenzie, et al. (2019) found that native tree species advanced their leaf-out times by 4.4 days/°C spring warming on average and wildflower species advanced their flowering times by 2.2 days/°C, whereas we found that, at the broader continental scale, native tree species advanced their leaf-out times by 3.6 days/°C spring warming on average and wildflower species advanced their flowering times by 3.2 days/°C. These differences in magnitude of sensitivity suggest that, within this patten, there is important species-level variation. Heberling, McDonough MacKenzie, et al. (2019) included nine additional native tree species, and *A. quinquefolia* was the only native wildflower species in both studies. Nevertheless, given that our two studies used different types of data (field observations vs. herbarium specimens) and covered different geographical regions (Concord, Massachusetts vs. eastern North America), species and time periods, it is striking that the overall pattern and direction of sensitivity are similar. This consistency in the pattern of phenological sensitivity for native trees and spring-blooming wildflowers indicates that these results may be generalizable for these growth forms in temperate North American deciduous forests. Furthermore, we found that native shrub phenological sensitivity was similar to that of native trees. This is consistent with results from other studies which found that woody understory plant phenology is equally as or more sensitive to spring temperature compared with that of canopy trees (Lee & Ibáñez, 2021a, 2021b). We are not sure if our results are generalizable to other species of non-native trees, shrubs and wildflowers, due to the smaller number of species in our analyses, and in particular, the greater variability of the phenological responses in non-native species.

### 4.2 | Phenological sensitivity across species' ranges

Phenological sensitivity differed across native species' latitudinal ranges in eastern North America. Native trees and wildflowers were more sensitive to temperature in the Warm temperature group (predominantly in the southeastern USA) in comparison with the Cold temperature group (predominantly in the northeastern USA), although this difference was not significant for wildflowers. This implies that phenological mismatches will be greater for native wildflowers in the southeastern United States—wildflowers in the warmer, southern locations will have fewer days of full sunlight access before they are shaded over, compared with wildflowers in the colder, northern sites. Other studies have found similar trends of species phenological sensitivity increasing at lower latitudes (Park et al., 2018; Song et al., 2021; Zhang et al., 2015). Both Park et al. (2018) and Zhang et al. (2015) suggest that plants in southern regions may have adapted greater phenological sensitivity because the climate is more stable and less variable, and thus there is a greater payoff of tracking spring temperatures when there is less risk of late-spring frost damage. Differences in species' phenological sensitivity across latitudinal ranges could also be influenced by changes in community composition and competition.

In contrast to native trees, non-native species did not differ in phenological sensitivity across their latitudinal range. One reason for this may be that all the non-native plants in our study were intentionally introduced by humans as ornamental plants. Human selection may have reduced genetic variability or selected for individuals with specific phenological timing. Thus, these non-native species may not have adapted to the highly-variable northeastern U.S. climate and may have maintained similar phenological sensitivity across their range (Ebeling et al., 2011). An alternative reason is that the ranges of our non-native species are more limited, with fewer occurrences in the Southeast (EDDMapS, 2021), which may have reduced our ability to detect latitudinal differences.

### 4.3 | Non-native species phenological sensitivity

We did not find significant differences between the phenological sensitivity of native and non-native plants. Our results differ from other studies, which largely found that non-native species have more plastic phenology and are advancing more with warming temperatures than are native species (Calinger et al., 2013; Willis et al., 2010; Wolkovich et al., 2013; Wolkovich & Cleland, 2014; Zettlemoyer et al., 2019; but see Wilsey et al., 2018 for greater phenological sensitivity in native species). However, many of these studies differed from ours in methodology (experimental field or twig warming studies) and geographic scope. We also had smaller sample sizes of non-native plants relative to native plants. Further work is needed to determine if the comparability we found in phenological sensitivity between native and non-native plants is due to genuine similarity or due to our choice of species, methods or sample size. Non-native trees have greater phenological sensitivity than native wildflowers, thus posing a threat to native wildflower fitness, particularly in areas where non-native trees are the dominant canopy trees. In addition, the greater sensitivity of non-native shrubs compared with native wildflowers suggests that in warmer climates the impact of non-native shrub shading may increase with warming.

### 4.4 | Order of early-spring phenology changes with warmer spring temperatures

The order of early-spring phenology changed from colder to warmer temperatures, with the more-sensitive groups advancing in the order, and the less-sensitive groups falling back in the order. The two native shrubs shifted from fourth- to first-earliest of the six groups. The native wildflowers shifted from first to fourth in the order.

In general, species which are more sensitive and advance in the order are likely to benefit from increased access to sunlight. The species which advanced the most in the order are *V. corymbosum*, *P. calleryana*, *B. thunbergii*, *F. grandifolia*, *U. pumila*, *L. benzoin*, *A. rubrum*, *C. glabra* and *E. alatus*. It is possible that these species will have the competitive advantage of earlier and longer access to sunlight in the early spring under conditions of climate warming (Alexander & Levine, 2019; Cleland et al., 2012; De Frenne et al., 2011; Willis et al., 2008; Willis et al., 2010). *Pyrus calleryana* and *L. benzoin* are two of the earliest-leafing and earliest-flowering species, so their phenology may become comparatively even earlier at warmer temperatures. This may be an advantage, or it is possible that these earliest species will suffer from increased frost damage (Augspurger & Salk, 2017; Inouye, 2008) and herbivory (Meineke et al., 2021). Zohner et al. (2020) suggest that late spring frost risk is decreasing in North America, but increasing in Europe and Asia. These dynamics should be considered when projecting which species are likely to thrive or decline under future climate change conditions.

The species that moved back the most in the order of spring activity are *A. quinquefolia*, *D. canadensis*, *D. cucullaria*, *P. alba* and *A. platanoides*. It is possible that these species will suffer competitively under warming climate conditions. They may have less access to early-spring sunlight and less ability to synthesize and store carbon.

## 5 | CONCLUSIONS

The results of this study may be used to inform recommendations for conserving native wildflower populations. Wildflower species that are less phenologically sensitive to spring temperature and flower later are more likely to be at risk of decline (e.g. *A. quinquefolia*, *D. canadensis*, *D. cucullaria*), and tree and shrub species that are more phenologically sensitive and leaf out early in the spring (e.g. *A. rubrum*, *F. grandifolia*, *P. calleryana*, *U. pumila*, *L. benzoin*) are more likely to shade out wildflowers. This dynamic is likely to be particularly salient in the Southeastern United States where conservation professionals and managers may seek out further resources to guide management options, which may include thinning out trees and shrubs to maintain early sunlight access for wildflowers (e.g. Maynard-Bean & Kaye, 2019 for non-native shrub removal) or managed relocation for wildflower species threatened by shading (Karasov-Olson et al., 2021).

Our results provide new insight into phenological responses within and among species across a wide geographical range and the potential impact of competition and interactions with non-native invasive species. This research highlights the value of newly-available digitized museum collections in phenological research to cover longer time periods, wider spatial areas and a greater diversity of species than otherwise possible. This field of study would benefit from further analyses to determine how generalizable these results are to other species, regions and ecosystems. It remains unclear if these phenological patterns are similar in other temperate deciduous forests of the world, as these patterns may differ due to biogeography (Zohner et al., 2017). Similar studies could also be conducted in different ecosystems to assess if these trends in phenological sensitivity and mismatch also apply to other ecosystems, such as chaparral or boreal forests, or are controlled by other climatic variables like moisture (Keatley et al., 2002; Kramer et al., 2000; Song et al., 2020). Furthermore, to elucidate the mechanisms of these phenological mismatches, physiological experiments could be conducted to test whether different levels of the canopy are responding to different temperature cues, such as air or soil temperature, or are relying more on photoperiod. Understanding differences in the temperature cues for different levels of the canopy could help us anticipate future mismatches as climate conditions continue to change. Further, understanding the changes in other ecosystems and the roles of other climate variables can help us to understand the magnitude of the potential mismatches and plan conservation responses.

## AUTHOR CONTRIBUTIONS

Richard B. Primack and Tara K. Miller designed the research. Tara K. Miller and Richard B. Primack contributed to data collection. Tara K. Miller analysed data with assistance from J. Mason Heberling, and Tara K. Miller, J. Mason Heberling, Sara E. Kuebbing and Richard B. Primack interpreted data. Tara K. Miller wrote the manuscript with contributions from J. Mason Heberling, Sara E. Kuebbing and Richard B. Primack.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest.

## PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/1365-2745.14021.

## DATA AVAILABILITY STATEMENT

Data are archived on Open Science Framework: https://doi.org/10.17605/OSF.IO/YMHJR (Miller, 2022).

## NATIVE LAND ACKNOWLEDGEMENT

This research studies plants found in deciduous forest ecosystems across the eastern United States. We acknowledge that our institutions and study sites are located within the ancestral and unceded homelands of many Indigenous communities. Below, we recognize the specific location where we work and the specific communities who first called this site their home. We also recognize that land acknowledgements are not enough to rectify the violence, forcible displacement and treaty violations by early European colonists and US federal, state and governments on Indigenous peoples. However, we hope our land acknowledgement will offer recognition and respect to the people who lived and worked on these lands, create public awareness about the history of where we work, promote the decolonization of ecology and conservation biology and serve as a call that more work needs to be done to promote social justice in our profession and in our nation.

**SUFFOLK COUNTY, MASSACHUSETTS** The Boston University main campus in Boston, MA is located on lands once occupied by the Massachusett (*Mass-adchu-es-et*) people, the Pawtucket people and the Wampanoag people (Wôpanâak). English colonizers and the United States and Massachusetts Commonwealth governments decimated the Indigenous people through forcible removal, forced assimilation, land grabbing and genocide. Many people of these and other Indigenous Nations still live in Massachusetts today.

**ALLEGHENY COUNTY, PENNSYLVANIA** The University of Pittsburgh main campus and the Carnegie Museum of Natural History (CMNH) in Pittsburgh, PA are located on lands once occupied by the Monongahela people (autonym unknown), the Seneca (*O-non-dowa-gah*) people--one of the Six Nations of the Haudenosaunee (hoe-den-ah-show-nee)--and the Lenape (*Lenni-Lenape* or Delaware) people, the Wyandot (*Wandat*) people, the Shawnee (*Shaawanwaki*) people and the Osage Nation (*Wahzhazhe*). These lands are home to many nations and peoples, in part, because of continued colonial expansion that forced entire nations to move westward to avoid violence and extirpation. European colonists violated multiple treaties and used the Indian Removal Act of 1830 to forcibly remove the Seneca (now the Seneca-Cayuga Nation), Lenape (now the Delaware Nation and Delaware Tribe of Indians), Wyandot (now the Wyandotte Nation) and Shawnee (now the Absentee-Shawnee Tribe of Indians of Oklahoma, Eastern Shawnee Tribe of Oklahoma and Shawnee Tribe) to what is now Oklahoma, where many of their descendants live today. A related group of Seneca are the Seneca Nation of Indians who today live in Salamanca, New York. We encourage our readers to use the Native Land Digital map (https://native-land.ca/) that seeks to map the Indigenous territories, treaties and languages from around the world.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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