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ARTICLE

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# Phenological response to climate variation in a northern red oak plantation: Links to survival and productivity

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## Abstract

In a changing climate, the future survival and productivity of species rely on individual populations to respond to shifting environmental conditions. Many tree species, including northern red oak (*Quercus rubra*), exhibit phenotypic plasticity, the ability to respond to changes in environmental conditions at within-generation time scales, through varying traits such as leaf phenology. Phenotypic plasticity of phenology may vary among populations within a species' range, and it is unclear if the range of plasticity is adequate to promote fitness. Here, we used a 58-year-old common garden to test whether northern red oak populations differed in phenological sensitivity to changes in temperature and whether differences in phenological sensitivity were associated with differences in productivity and survival (proxies of fitness). We recorded 8 years of spring leaf emergence and autumn leaf coloration and loss in 28 distinct populations from across the species' full range. Across the 28 populations, spring leaf out consistently advanced in warmer years, but fall phenology was less responsive to changes in temperature. Southern, warm-adapted populations had larger shifts in phenology in response to springtime warming but had lower long-term survival. Moreover, higher phenological sensitivity to spring warming was not strongly linked to increased productivity. Instead, fitness was more closely linked to latitudinal gradients. Although springtime phenological sensitivity to climate change is common across northern red oak populations, responses of productivity and survival, which could determine longer-term trajectories of species abundance, are more variable across the species' range.

**KEYWORDS**
adaptation, climate change, climate gradients, common garden, fitness, growth, phenology, phenotypic plasticity, survival

## INTRODUCTION

Recent and projected rates of climate change present a vexing challenge for biodiversity. Mechanisms through which species respond to climate change, such as adaptation to novel environments and migration to more suitable habitat, require long periods of time, especially for sessile species such as trees (Corlett & Westcott, 2013; Fei et al., 2017; Kokko et al., 2017). Rates of adaptation and migration are limited by generation times and are typically observed at decadal to millennial scales for tree species (Fei et al., 2017; Lenoir et al., 2008; Woodall et al., 2009; Zhu et al., 2012). Given that projected rates of climate change exceed these rates (Corlett & Westcott, 2013; Kokko et al., 2017; Loarie et al., 2009), species' future success depends on more rapid responses to climate change at daily to annual time scales.

Phenotypic plasticity—the ability of genotypes (individuals or populations) to vary phenotypes (traits) in response to environmental change—provides a mechanism for species to respond to climate change more rapidly (within generations). Phenology—the timing of recurring biological events such as leaf out in spring and leaf senescence in autumn—is phenotypically plastic, allowing species to respond to variation in environmental conditions on daily to seasonal time scales (Cleland et al., 2007; Fu et al., 2015; Piao et al., 2019). Shifts in phenology in response to warming have been observed across many tree species, and these responses are hypothesized to improve individual fitness by extending the growing season and increasing productivity (Cleland et al., 2007; Fu et al., 2015; Piao et al., 2019; Polgar & Primack, 2011; Richardson et al., 2010). However, other factors, including photoperiod (day- and night-length cues) and/or chilling requirements (for dormancy release), could limit or confound responses to climate warming (Ford et al., 2017; Harrington & Gould, 2015; Singh et al., 2017; Zohner et al., 2016). In addition, phenological shifts can also strongly influence ecosystem processes including plant-insect synchrony, nutrient and water cycling, and climate-productivity feedbacks, among others, resulting in the alteration of ecosystem functioning and service provision (Cleland et al., 2007; Fu et al., 2015; Pan et al., 2011; Piao et al., 2019).

Common garden studies, which transplant trees from a wide variety of historic climate conditions to a new location, act as pseudo-climate change experiments. Space-for-time substitutions in common garden studies include both warming and cooling scenarios when the common garden is placed near the center of the species' range (Liang, 2016; Steiner et al., 2021; Vitasse et al., 2010; Zohner & Renner, 2014). The spatial transfer to a common garden allows researchers to study the range-wide plasticity of phenology (i.e., the scale often detected by remote sensing) at a local scale. This can be used to distinguish adaptations to seed source conditions (via thermal accumulation and/or photoperiod requirements across the species' range) that lead to variation in population-level responses to interannual temperature variability at the common garden (Ford et al., 2017; Gerst et al., 2017; Liang, 2016; Savolainen et al., 2007; Zohner & Renner, 2014). Differences in phenological sensitivity, defined here as the magnitude of shifts in phenology per unit change in environmental condition (e.g., days per degree of warming, Wolkovich et al., 2021), may indicate whether certain populations exhibit a greater range of phenotypic plasticity that can promote fitness in response to climate change. The detection of spatial patterns of phenological sensitivity and fitness within a common garden study can help identify whether the relocation of populations (via natural dispersal, climate-driven range shifts, or human-assisted migration) will notably affect their ability to persist in novel conditions.

Quantifying patterns of phenology at a common garden can help identify whether the range of phenotypic plasticity among populations will allow certain populations to better respond to changing environmental conditions (Liang, 2016, 2019) and whether a greater range of phenotypic plasticity (higher phenological sensitivity) can promote fitness. Here, we utilized a 58-year-old common garden of the widespread North American species northern red oak (*Quercus rubra*) to (i) quantify phenological responses to variation in environmental conditions over an 8-year period, (ii) assess links in phenological sensitivity to seed source climate, and (iii) test whether phenological sensitivity is reflected in measures of fitness (productivity and survival).

## METHODS

### Common garden design and phenology observations

In the early 1960s (1962–1964), a common garden of northern red oak was established at Martell Forest near West Lafayette, IN, USA (40.438, −87.038). The original study aimed to quantify the effects of transplanting northern red oak trees for timber production (Kriebel et al., 1988, 1976). The common garden contained populations of northern red oak from 32 locations across most of the native range in eastern North America (35.6° N to 47.3° N and 96.5° W to 68.5° W; Appendix S1: Figure S1; see Kriebel et al. [1976] for more information about study design). Each population was replicated three times (96 plots) in a randomized complete block design, and each plot originally contained 16 trees sourced from an average of eight parent trees. Due to mortality over the 58 years

since establishment of the common garden, the median number of remaining trees at the end of the study period was four per plot. Additionally, one population had missing seed source information, one population (Ogle County, IL) had no remaining trees across all plots at the start of the study period, and 10 plots contained no remaining trees. Therefore, we removed a population from our analysis if it had fewer than three trees or two plots remaining at the end of the study period, leaving a total of 398 trees across 28 populations and 83 plots. The final list of seed source locations is available in Appendix S1: Table S1, and their spatial distribution is in Appendix S1: Figure S1.

Beginning in autumn 2013 and continuing through spring 2020, we observed phenology every 2–7 days (depending on weather and weekend access to Martell Forest) during the spring and autumn seasons. Observations were made at the plot level and represented the average across all live trees in the plot because tree height (many >25 m) made it difficult to distinguish the canopy of some trees from each other and because within-tree (branch-to-branch) variability was sometimes as large as between-tree variability. Observations were made visually by eye or with binoculars as the stages necessitated (Liang, 2015). We recorded spring phenology in four phenophases: (1) buds beginning to swell, (2) buds beginning to open, (3) small immature leaves unfolding and becoming visible, and (4) leaves growing to their final size. We recorded the first three phenophases at 10%, 50%, and 90% thresholds and the fourth phenophases at 25%, 50%, 75%, and 100% thresholds (due to the more linear growth rate of leaves). We observed autumn phenology as two simultaneous (as opposed to progressive) stages: leaf coloration (percentage of leaves changed color) and leaf fall (percentage of leaves lost from the canopy). Both autumn phenophases were recorded at 10%, 50%, and 90% thresholds, with the addition of full (100%) leaf coloration. Full leaf fall was not recorded because northern red oak often retains a small portion of leaves throughout the winter. On average, we recorded spring phenology 20 times per season and autumn phenology 24 times per season.

There are two main types of models for phenology: models to assess the progression of a phenological time series within years and, as used in this study, models to assess interannual shifts of the day of year (DOY) of observed phenological transitions for comparison across years (Liang, 2019; Yu et al., 2016). Here, we were interested in the DOY of the beginning and end of the growing season. Although bud burst (buds swelling and opening) indicates the end of dormancy, few trees in our study had low branches to accurately judge these early stages, so we instead focused this study on the timing of leaf out, the beginning of the growing season when the carbon balance switches from negative (using carbon reserves) to positive (capturing a sufficient amount of carbon for leaf development; Keel & Schädel, 2010). We defined leaf out as the DOY of the first observation when >90% of leaves had unfolded (final threshold of the third spring phenophase) because it was the most reliable measurement; before leaf unfolding, bud swell and bud opening can be difficult to distinguish, and after leaf unfolding, estimating leaf growth relative to the expected final leaf size can also be difficult. In autumn, we were interested in the timing of senescence as the end of the growing season and beginning of the winter dormant season. Because senescence is a long, multistage process (Fracheboud et al., 2009), we used three indicators of senescence, an early measure based on leaf color (first DOY when leaf color was >10%), a late measure based on leaf fall (first DOY when leaf fall was >90%), and a hybrid measure incorporating the simultaneous nature of the leaf color and leaf fall phenophases (the first DOY when both leaf color was >50% and leaf fall was >10%, hereafter "senescence"), to account for the high correlation between leaf color and leaf fall (Spearman's rank correlation $\rho = 0.89$, $S$-value > 1000, df = 14,445, $p < 0.001$). Occasionally, plots did not reach 90% leaf fall by the end of the data collection season. For these cases, we used a linear extrapolation by adding the median time between observations (3 days) for each threshold level below 90% leaf fall on the last observation (i.e., the final DOY for the data collection season with 3 days added if the observed leaf fall was >50% or 6 days added if the observed leaf fall was >10%) following an approach similar to that of Liang (2015). For each phenological event, we calculated the difference between the observed DOY and the mean within-population DOY across all years to represent the shift in phenology due to climate change and other variables.

## Climate and weather data

We aimed to assess the effects of local environmental conditions on the timing of phenological events. Gridded temperature data from Daymet (1-km resolution, acquired using the R package daymetr; Hufkens et al., 2018; Thornton et al., 2016) allowed us to compare how warm each day during the study period was relative to a 30-year normal. We extracted $T_{max}$ and $T_{min}$ from the Daymet pixel centered on the common garden site to compute a 60-day preseason window mean temperature prior to the timing of each phenological event (following Wang et al., 2014). To do so, we calculated the mean day of leaf out across all years for each population. Then we calculated mean temperature (using Daymet data) of the preseason window ending at this DOY for each

population in each year of the study period. We centered the data by subtracting each preseason mean temperature during the study period from the equivalent 60-day average from historic (1980–2009) Daymet data. Although this calculation could include temperature data from after a phenological event occurred (i.e., for replicates with phenological events occurring earlier than the mean across replicates of the same population), it allowed us to standardize across years to estimate how warm/cool any DOY of the study period was relative to the historic average. We also applied a similar approach using local weather station data but found a high correlation with Daymet data; therefore, we only present the analysis using Daymet hereafter (see Appendix S1).

We used historic climate at the seed source as a proxy for local adaptations that may limit the sensitivity of phenological events. Bioclimatic variables (BIOCLIM) are biologically relevant variables commonly used to identify differences in the climatic niches of populations of widespread species (Fick & Hijmans, 2017). There are many BIOCLIM variables—19 in the WorldClim data set (Fick & Hijmans, 2017)—that represent precipitation and temperature magnitude and variability and the interaction between precipitation and temperature. We accessed WorldClim BIOCLIM variables using the R package raster (Hijmans, 2018). A full list and description of BIOCLIM variables is available in Appendix S1: Table S4, with more details available in O'donnell and Ignizio (2012).

We also aimed to test whether average springtime accumulated growing degree days (GDD) at the seed source was a better predictor of phenology than BIOCLIM variables. We used daily gridded temperature data (daily maximum and minimum temperature, $T_{max}$ and $T_{min}$) from Daymet (Thornton et al., 2016) at each of our 28 seed sources for years 1980–2009 (the earliest available Daymet data) to calculate GDD during spring months (March through May) using the formula

$$\mathrm{GDD} = \max\left(\frac{T_{max} + T_{min}}{2} - T_{base}, 0\right), \quad (1)$$

where $T_{base}$ is a fixed value of −0.6°C, and GDD is given a value of 0 when the average of $T_{max}$ and $T_{min}$ is less than $T_{base}$ (Liang, 2015; Zhang et al., 2014). Daily GDD were summed for spring (March through May) and averaged across the 30-year data set (Liang, 2015).

## Quantifying sensitivity of phenology to climate change

Differences in environmental conditions (thermal accumulation) are hypothesized to shift phenology (Wang et al., 2014). We assessed the sensitivity of northern red oak using linear regression models fit in a hierarchical fashion (Larue et al., 2019; Ratcliffe et al., 2017). First, we modeled the shift in a phenological event (e.g., shift in the DOY for population $j$ in year $i$ relative to the mean DOY for all populations across all years) as a function of environmental conditions (e.g., shift in preseason mean temperature relative to the 30-year average at the common garden, hereafter "phenological sensitivity"). To account for potential pseudoreplication (multiple replicates of the same seed source treatment), we included block (replicate number) as an indicator variable in our phenological sensitivity models. Then we modeled the slope of the phenological sensitivity models as a function of seed source climate (19 BIOCLIM variables and mean annual accumulated GDD from Daymet temperature data) to identify which populations from different climatic conditions had higher/lower sensitivity to climate variation during the study period. Because many BIOCLIM variables are correlated, we fit models with each variable individually and compared all models using a corrected Akaike information criterion ($AIC_c$).

## Assessing impact of shifting phenology on short- and long-term fitness

We quantified two measures of fitness, one short-term (i.e., during the study period) and one long-term (i.e., since the establishment of the common garden). Specifically, we measured periodic annual increment (PAI) of basal area during the study period as a proxy for short-term fitness and survival (number of trees remaining at the end of the study period) since the establishment of the common garden as a proxy for long-term fitness. Measures of change in basal area such as PAI are commonly used to measure tree growth and serve as a proxy for aboveground biomass accumulation and carbon sequestration (Domke et al., 2012; Jenkins et al., 2003). PAI was estimated using dbh measurements taken in January 2013 before the study period and remeasurements taken in February 2020 near the end of the study period. Some trees had negative or abnormally large growth rates that were due to measurement errors such as the growth/removal of vines and decisions about where to measure multitrunk trees (most trees had growth rates <1.1 cm dbh year$^{-1}$, but a few had growth rates >2.7 cm dbh year$^{-1}$, which is abnormally large relative to the rest of the common garden). Therefore, we removed trees with negative or >2.7 cm dbh year$^{-1}$ growth, leaving a total of 346 trees in our estimates of PAI (Appendix S1: Table S1). We converted dbh to basal area and calculated PAI using the equation

$$\mathrm{PAI} = \frac{\pi \times \left(\frac{\mathrm{dbh}_{2020}}{2}\right)^2 - \pi \times \left(\frac{\mathrm{dbh}_{2013}}{2}\right)^2}{N_{\mathrm{year}}}, \quad (2)$$

where $\mathrm{dbh}_{2020}$ and $\mathrm{dbh}_{2013}$ are our two dbh measurements for each tree and $N_{\mathrm{year}} = 7$ growing seasons between measurements. We then averaged this value across all trees in the plot to standardize PAI ($\mathrm{cm}^2\ \mathrm{tree}^{-1}\ \mathrm{year}^{-1}$). We also calculated change in diameter and found it to be highly correlated with PAI of basal area (Pearson's correlation $r = 0.96$, $t$-value $= 16.6$, df $= 26$, $p < 0.001$), so we focused the rest of the analyses on the PAI of basal area.

We assessed the relationship between phenological sensitivity and our proxies for fitness using a general linear model for PAI and a generalized linear model (GLM) with a Poisson error distribution and log-link function for survival. We tested for nonlinear relationships by including quadratic terms in the models because we hypothesized that there might be an optimal sensitivity for fitness. All analyses were performed in R version 4.0.1 (R Core Team, 2020) using the packages rgdal (Bivand et al., 2018) and raster (Hijmans, 2018) for geospatial analysis and stats (R Core Team, 2020), car (Fox & Weisberg, 2019), and MuMIn (Bartoń, 2018) for regression and assessing model fit.

# RESULTS

## Phenological shifts in response to warmer temperature

Leaf out (the first date when 90% of leaves had unfolded) consistently advanced in warmer years in our common garden study during the 8-year study period. The date of leaf out at the common garden varied from year to year across populations (Figure 1), with leaf out ranging from the 105th DOY to the 139th DOY (April 15–May 19 in non-leap years). Leaf-out sensitivity (the slope of the relationship between interannual population-level shifts in leaf out DOY as a function of preseason mean temperature, days $^{\circ}\mathrm{C}^{-1}$) was negative among all populations and

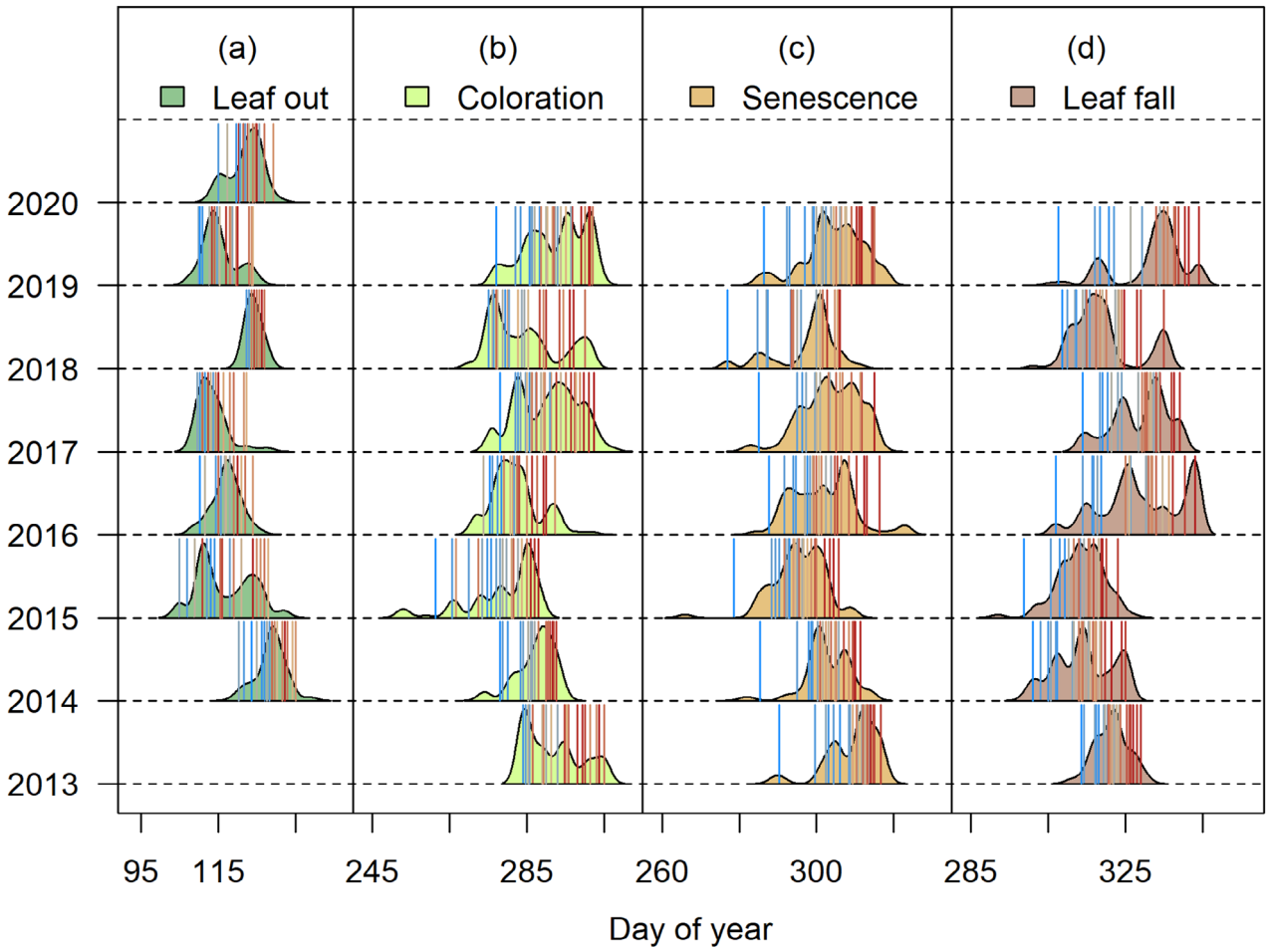


**FIGURE 1** Timing of phenological events across 8 years of phenological observations. Smoothed relative density curves indicate distribution of phenological events in spring (a) 90% leaf out and, in autumn, (b) 10% leaf color, (c) 50% leaf color and 10% leaf fall (leaf senescence), and (d) 90% leaf fall. Vertical lines indicate population means, and color scale indicates population latitude (blue = north, red = south).

significant at $\alpha = 0.05$ for all but two populations, which indicated that a warmer spring temperature led to an advancement of leaf out (earlier DOY) (Figure 2a, Appendix S1: Tables S2, S3 and Figures S2–S5). Populations shifted, on average, 2 days earlier per degree Celsius warming (range: −1.5 to −2.6 days $°C^{-1}$, Appendix S1: Table S3). This equated to a maximum leaf-out shift of 11.7 days earlier in warmer years to 13.4 days later in cooler years relative to the population mean DOY across the study period (Appendix S1: Table S2).

Despite consistent spring responses to warming, autumn phenology showed weaker responses to changing autumn weather. Leaf coloration, leaf fall, and senescence all varied from year to year, but only end-of-season leaf fall showed consistent shifts across populations (Figure 2 and Appendix S1: Table S2 and Figures S3–S5). Leaf fall was generally delayed in warmer years (consistent positive relationship with preseason temperature, 0.5–2.3 days $°C^{-1}$), but slopes were only significant (at $\alpha = 0.05$) for two northern populations (Figure 2d and Appendix S1: Table S3 and Figure S5). Leaf coloration and senescence showed inconsistent (both positive and negative) and nonsignificant responses to warmer fall temperature (−3.3 to 4.7 days $°C^{-1}$ and −1.8 to 2.0 days $°C^{-1}$ for leaf coloration and leaf senescence, respectively), except for one population (Pop.1, Anderson, TN), which had approximately 2 days $°C^{-1}$ delay in autumn senescence (Figure 2 and Appendix S1: Figures S3 and S4).

## Factors influencing spring phenological sensitivity

Spring phenological sensitivity was associated with local adaptations to seed source climate. We modeled leaf-out sensitivity as a function of bioclimatic variables (BIOCLIM) (Fick & Hijmans, 2017) and average springtime accumulated GDD (Thornton et al., 2016) at each seed source using individual bivariate linear models due to collinearity of the predictor variables. Because autumn phenophases did not show consistent significant responses to warmer temperature, we performed this analysis for autumn sensitivity for display purposes only (background gradient in Figure 2). Historic temperature gradients, such as isothermality and annual mean temperature, were the best predictors of leaf-out sensitivity (Figure 3a and Appendix S1: Table S4 and Figure S6). We also tested models with quadratic terms but found none to be statistically significant, that is, lack of a nonlinear relationship (Steiner et al., 2021). Generally, populations from warmer areas with higher isothermality (the ratio between monthly and annual temperature range, a measure of temperature evenness, which is generally correlated with annual mean temperature, Pearson's correlation $r = 0.79$, $t$-value $= 6.63$, df $= 26$, $p < 0.001$) had higher leaf-out sensitivity to warming (BIOCLIM 3, isothermality; background color in Figure 2a; slope $= -0.17$ days $°C^{-1}$ per SD increase in isothermality, $t$-value $= -3.03$, df $= 26$, $p = 0.006$, $R^2 = 0.26$, Appendix S1: Table S4). Leaf-out sensitivity had nonsignificant associations with precipitation and temperature–precipitation interaction BIOCLIM variables (Figure 3b,c and Appendix S1: Table S4). Populations from areas with higher average springtime accumulated GDD had significantly higher leaf-out sensitivity (slope $= -0.15$ days $°C^{-1}$ per SD increase in GDD, $t$-value $= -2.61$, df $= 26$, $p = 0.015$, $R^2 = 0.21$), which was consistent with the relationship between other temperature-related BIOCLIM variables and leaf-out sensitivity (Appendix S1: Table S4 and Figure S6). Although average springtime GDD is generally considered to be more relevant for predicting interannual variation in phenology than BIOCLIM, it was not better than the best BIOCLIM predictor (isothermality) at explaining interpopulation differences in phenological sensitivity when compared via corrected $AIC_c$ weights or $R^2$ ($AIC_c$ weight $= 0.73$ and 0.27, and $R^2 = 0.26$ and 0.21, for isothermality and GDD, respectively; Burnham et al., 2011).

## Phenology sensitivity versus fitness

Spring phenological sensitivity showed weak links to fitness (Figure 4, Appendix S1: Table S5). Populations that leafed out earlier in response to warmer temperature (higher leaf-out sensitivity) had lower long-term survival—Exp(slope) $= 1.62$ live trees per unit decrease in sensitivity, $z$-value $= 2.86$, df $= 26$, $p = 0.004$, $R^2 = 0.24$, Figure 4a and Appendix S1: Table S5—and had no significant differences in short-term growth of surviving trees over the study period (PAI, slope $= -3.36$ $cm^2$ $tree^{-1}$ $year^{-1}$ per unit increase in leaf-out sensitivity, $t$-value $= -0.91$, df $= 26$, $p = 0.37$, $R^2 = 0.03$, Figure 4b and Appendix S1: Table S5). These relationships may be indirectly influenced by spatial transfer: Survival, growing season length, and leaf-out sensitivity were significantly associated with latitude, with populations from further north having higher survival but lower leaf-out sensitivity and shorter growing seasons (Appendix S1: Table S5; slope $= -1.08$ days of growing season per degree latitude, $t$-value $= -6.75$, df $= 26$, $p < 0.001$, $R^2 = 0.64$, Figure 2e; Exp[slope] $= 1.65$ live trees per degree latitude, $z$-value $= 3.01$, $p = 0.003$, $R^2 = 0.27$, Figure 2f; slope $= 0.047$ days $C^{-1}$ sensitivity per degree latitude, $t$-value $= 2.86$, df $= 26$, $p = 0.008$, $R^2 = 0.24$, Figure 4d).

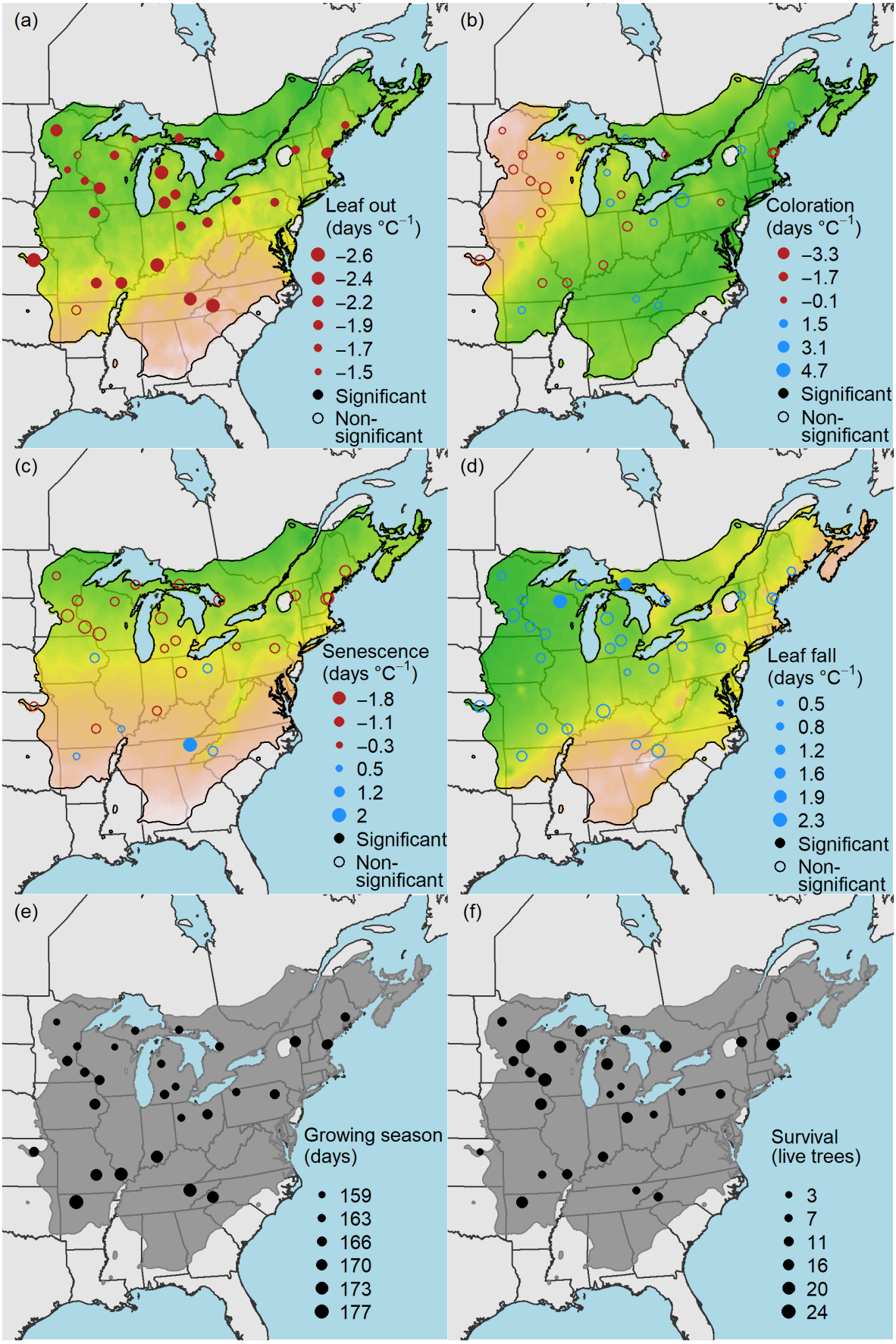


**FIGURE 2** Legend on next page.

## DISCUSSION

Our results suggested that populations are limited in their ability to use phenology to rapidly respond to climate change. Insensitivity of autumn phenology to interannual temperature variability indicated that populations were unable to take advantage of warmer autumn weather. In warmer years, populations tended to hold onto leaves longer (delayed leaf fall), but earlier stages of the senescence process showed both positive and negative relationships with autumn warming. Inconsistent responses to autumn warming have been observed for other species, so it was not surprising that northern red oak senescence did not exhibit a strong relationship with warming temperatures (Fu et al., 2018; Gallinat et al., 2015; Gunderson et al., 2012; Menzel et al., 2006). A lack of temperature sensitivity of senescence may indicate stronger photoperiod cues, a fixed leaf lifespan, or declining carbon balance (Liang, 2016; Way & Montgomery, 2015; Yu et al., 2016), which, in combination with other stressors such as drought and frost before and during the autumn season, can override the benefits of delayed leaf fall in response to warmer autumn temperatures (Gunderson et al., 2012; Xie et al., 2018).

Although populations did respond to warmer spring conditions, they were limited by adaptations to their seed source climates. Northern populations generally experienced climate warming during the establishment of the common garden, which limited their ability to respond to interannual variability in temperature. In contrast, populations sourced from warmer (southern) locations experienced climate cooling and were less limited—allowing more room for phenotypic plasticity. A potential nonlinear response is reflected by two hypothesized challenges that populations faced due to pseudo-climate manipulation via spatial transfer: (1) potential for inadequate chilling, which could lead to delayed dormancy release, thereby producing a weakened response in warmer temperatures (Brunner et al., 2014; Cooke et al., 2012; Liang, 2019, but note that warming may increase the amount of chilling experienced for some populations from very cold locations if their minimum temperature threshold for chilling accumulation is met more frequently or if chilling accumulation is more efficient at warmer temperatures, Nanninga et al., 2017); and (2) potential that the maximum response to warming was already reached by northern populations due to a transfer to warmer climate at the common garden (Fu et al., 2015; Marchin et al., 2015; Salk, 2011, 2020; Wolkovich et al., 2021). An alternative theory is that southern populations may have reached a critical threshold during transfer to the common garden that elicited a more robust phenotypic response (Liang, 2016; Salk, 2020). It is possible that some populations have already reached a maximum level of climate stress, which may continue to limit their responses to warming, and may not be able to keep pace with climate change (Loarie et al., 2009; Pachauri et al., 2014).

Higher phenological sensitivity to spring warming was not strongly linked to increased productivity and survival of the trees at the common garden. In the short term (i.e., during the study period), populations from southern latitudes were more phenologically sensitive to climate variation but did not show increases in productivity. Populations from colder climates with low leaf-out sensitivity generally have higher chilling requirements and tend to leaf out later in the season, which allowed better avoidance of more frequent spring frosts in their source regions (Nanninga et al., 2017; Wang et al., 2014; Zohner et al., 2020). Conversely, populations from warmer climates with high leaf-out sensitivity tended to shift their phenology more rapidly in response to warming conditions, given their lower chilling requirements and earlier dormancy release at the common garden location. But their lack of increased productivity suggests that constraints such as reduced growth rate and/or shifts to a negative carbon balance (using more carbon stores than the amount of carbon being captured) prevented these populations from taking full advantage of an extended growing season (Piao et al., 2019; Polgar & Primack, 2011; Richardson et al., 2010; Zohner et al., 2020). In the long term (i.e., in the ca. 58 years since the establishment of the common garden), survival was highest for populations from more northern latitudes which had lower leaf-out sensitivity.

**FIGURE 2** Population-level phenological sensitivity, growing season length, and survival. Circles indicate observed sensitivity, growing season length, and survival at the common garden but are displayed at their seed source locations. Sensitivity values were derived by modeling shifts in day of year (DOY) of phenological events at the common garden as a function of shifts in preseason temperature for (a) 90% leaf out, (b) autumn >10% leaf coloration, (c) autumn leaf senescence (>50% leaf coloration and >10% leaf fall), and (d) autumn >90% leaf fall. (e, f) Mean growing season length and total live trees by population. Background gradients in (a–d) represent the strongest bioclimatic predictor of sensitivity (green colors indicate higher values): (a) BIOCLIM 3, isothermality; (b) BIOCLIM 15, precipitation seasonality; (c) BIOCLIM 1, annual mean temperature; (d) BIOCLIM 19, precipitation of coldest quarter. Circle size and color indicate the degree and directionality in (a–d) (red = earlier, blue = later event in response to warming) of climate sensitivity; open circles are nonsignificant ($\alpha = 0.05$). Background shading clipped to northern red oak native range. See Appendix S1: Table S1 for phenological sensitivity values.

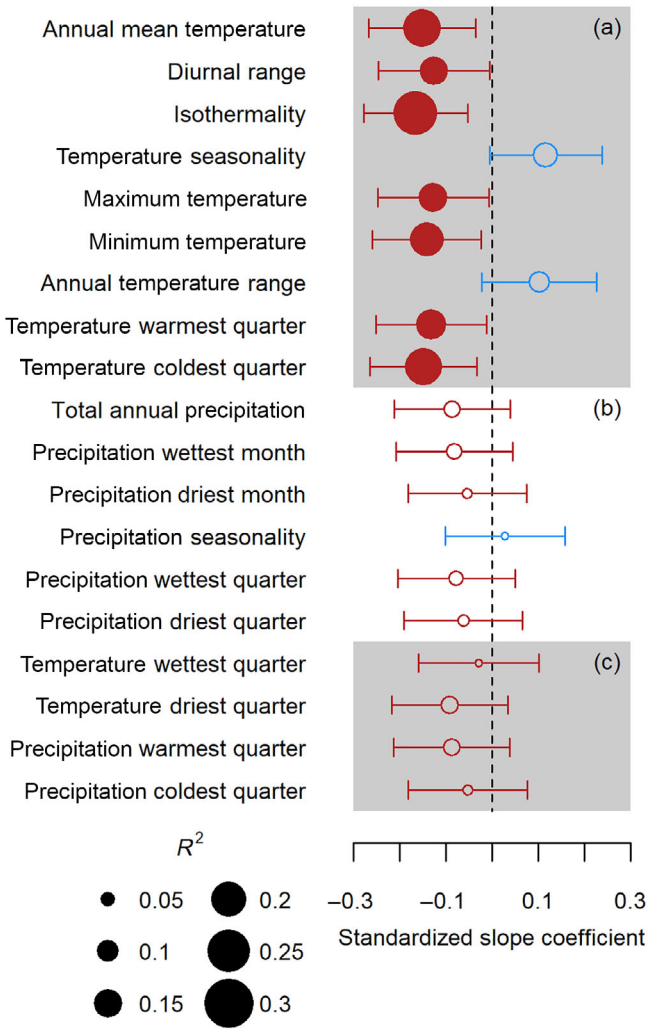


**FIGURE 3** Seed source climate conditions as predictors of leaf-out sensitivity to warming. Variables are grouped by category: (a) temperature, (b) precipitation, and (c) temperature × precipitation interactions. The sensitivity of leaf out to shifts in growing degree days was modeled as a function of seed source climate conditions using Worldclim BIOCLIM variables. BIOCLIM variables were standardized by centering on the value at the common garden and dividing by the standard deviation. Circles indicate standardized coefficient values (relative effect size), and error bars represent 95% confidence intervals. Circle sizes are proportional to $R^2$ values. Color and fill indicate significance of relationship: solid = significant ($\alpha = 0.05$) and open = nonsignificant, red = negative, blue = positive. Negative coefficient values indicate that an increase in the BIOCLIM variable leads to an increase in sensitivity (more negative sensitivity value); conversely, positive coefficient values indicate that an increase in the BIOCLIM variable leads to a decrease in sensitivity (less negative sensitivity value). See Appendix S1: Figure S6 for scatterplots of these relationships and Appendix S1: Table S4 for a description of the BIOCLIM variables.

Differences between the phenological sensitivity and survival of populations from warmer (southern) versus cooler (northern) climates highlights a potential tradeoff. Factors such as overall warmer conditions experienced by northern populations (via seed transfer) that promoted survival and growth during the growing season may be canceled out by the lack of phenological sensitivity to interannual climate variation. Conversely, southern populations with higher phenological sensitivity were able to take advantage of warmer spring conditions, but these populations experienced higher levels of mortality and no significant differences in productivity relative to northern populations. This has implications for species migration (both natural migration and human-mediated management strategies such as assisted migration): Even if populations are relocated within the species' overall native range to more northern latitudes (the expected direction of migration to cooler climate under climate change in North America), they are likely to be poorly adapted to areas with novel conditions, which may lead to reduced survival and/or productivity relative to their historic range or source locations. Yet local populations may experience increased growth in spite of likely delayed onset of the growing season due to a chilling deficit.

A few caveats must be issued in connection with our study. First, the study analyzed only 8 years of measurements from 28 populations in a common garden. Trees experienced abrupt pseudo-climate change via seed transfer during the establishment of the plantation (i.e., warming for northern populations and cooling for southern populations). Although these 8 years included a wide range of environmental conditions and phenological shifts, there could be even more dramatic shifts expected under future climate change (Loarie et al., 2009; Pachauri et al., 2014). Within populations, observed shifts in leaf out were generally linearly related to springtime warming (Appendix S1: Figure S2); however, if chilling requirements were to be no longer met at high levels of future warming, it would be possible for gains in the spring season to be slowed or reversed even for the more highly sensitive warm-adapted southern populations, leading to a nonlinear response (Marchin et al., 2015; Nanninga et al., 2017; Salk, 2011; Wolkovich et al., 2021). Second, the hierarchical method used here does not propagate the uncertainty of the phenological sensitivity models (shifts in phenology as a function of shifts in springtime conditions at the common garden) into the analysis of seed source climate on phenological sensitivity; hierarchical Bayesian approaches for this purpose are an active area of research in ecology and evolution. Therefore, nuances in the spatial patterns and correlations of phenological sensitivity and fitness might become more apparent if there were better methods to propagate error through the entire hierarchical process. Finally, there may be alternatives to phenological sensitivity for

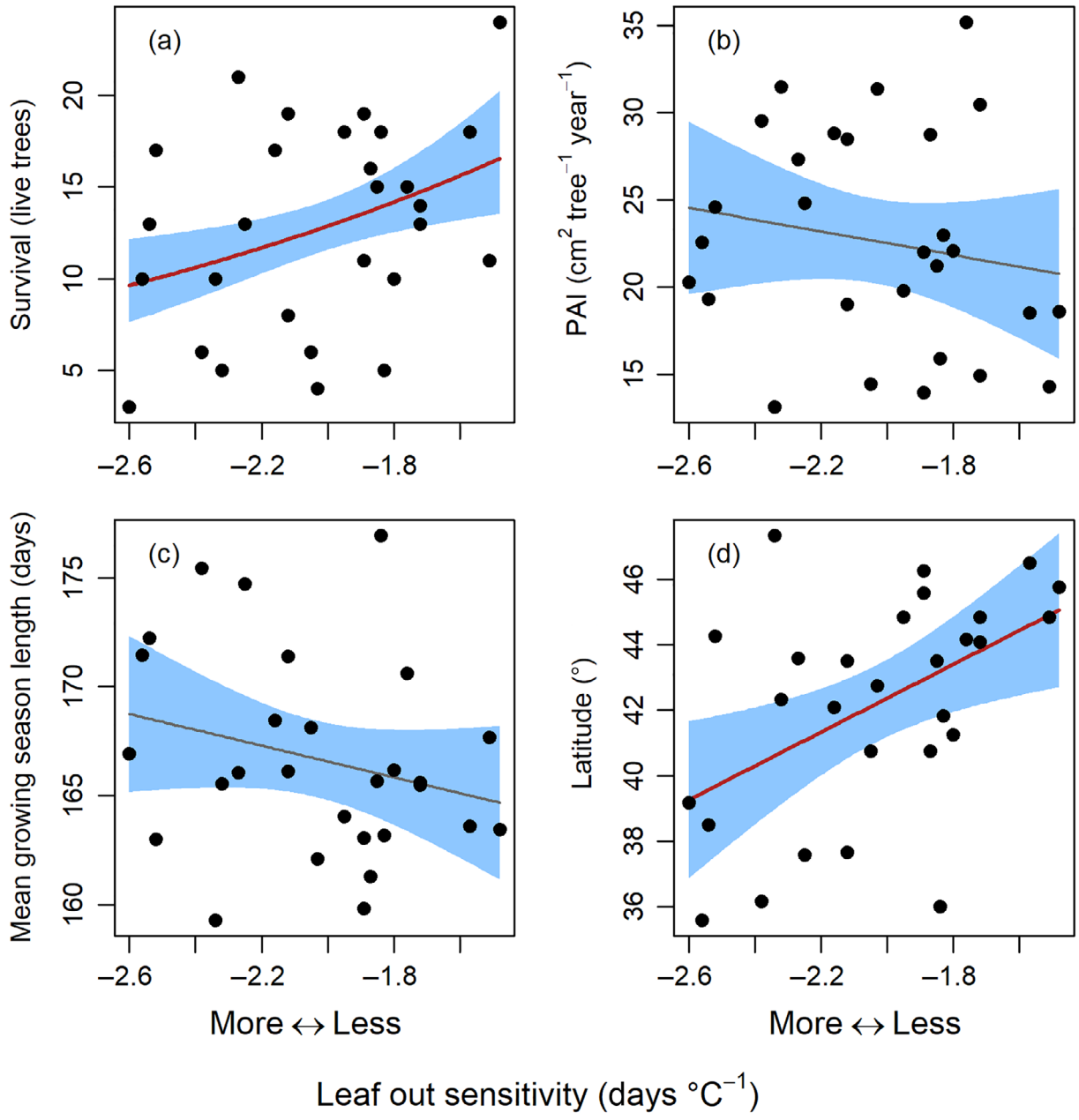


**FIGURE 4** Relationship between spring leaf-out sensitivity and measures of fitness. Leaf-out sensitivity to interannual shifts in preseason temperature was used as a predictor of (a) survival from early 1960s to 2020, (b) average periodic annual increment (PAI) of basal area from 2013 to 2020, and (c) growing season length. (d) Relationship between seed source latitude and leaf-out sensitivity. Red lines in (a) and (d) indicate significant ($\alpha = 0.05$) relationships between leaf-out sensitivity and survival or latitude, respectively, and gray lines in (b) and (c) indicate nonsignificant relationship between leaf-out sensitivity and PAI or growing season length, respectively. Blue areas represent 95% confidence intervals.

quantifying phenotypic plasticity and assessing the fitness of tree species. Our long-term measure of fitness (survival) is the result of events prior to our quantification of phenological sensitivity; this temporal mismatch may explain the lack of strong relationships between phenological sensitivity and fitness. Trees may also have had detectable effects of phenological sensitivity on fitness earlier in their lifespan that became negligible as the plantation aged, or less-fit trees may have died before the beginning of the study period (Steiner et al., 2021). Additional proxies for fitness, such as regeneration, recruitment, and dispersal, also influence the persistence of tree species; however, we observed little to no regeneration of northern red oak in the understory, which is consistent with regional patterns of oak species decline over recent decades due to fire exclusion and canopy closure (Fei et al., 2011; Knott et al., 2019; Zhu et al., 2012).

Taken together, our results provide insight into how climate change may affect the persistence of oak forests. Our study revealed that, although spring phenology of northern red oak responds to both warming and cooling scenarios, autumn phenology does not, and the sensitivity of spring phenology to warmer temperatures was not linked to higher productivity. Over time, other species may come to fulfill similar ecological or economic roles in response to shifts in the distribution and phenology of northern red oak (e.g., biomass, timber, and mast production, regulation of light through canopy closure, and habitat structure; Costanza et al., 2017; Knott et al., 2020) and/or northern red oak may offset shifts in other species, leading to balancing effects of community complexity (Loreau et al., 2001; Symstad et al., 1998). However, many oak species have been declining over recent decades, resulting in significant northward migration of northern red oak (Fei et al., 2011, 2017; Knott et al., 2019). Paired with our results that showed weak relationships between phenological sensitivity and fitness, continued species migration and climate warming may influence the overall productivity and persistence of this economically and ecologically valuable species.

## AUTHOR CONTRIBUTIONS

Jonathan A. Knott and Songlin Fei designed the study. Jonathan A. Knott collected and analyzed data and drafted the manuscript. All authors provided interpretations of results and edited/revised the manuscript.

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## CONFLICT OF INTEREST

The authors have no conflicts of interest to disclose.

## DATA AVAILABILITY STATEMENT

Phenology observational data and seed source climate data are available at the Purdue University Research Repository (Knott et al., 2022; https://doi.org/10.4231/C2WH-Y183). Temperature data from the two closest weather stations used in Appendix S1 are available from the Indiana State Climate Office (https://ag.purdue.edu/indiana-state-climate/) and can be downloaded using the Midwestern Regional Climate Center cli-MATE tool (https://mrcc.purdue.edu/CLIMATE) by searching for hourly temperature data from the KLAF and ACRE weather stations.

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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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