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RESEARCH ARTICLE

Spring ephemeral *Erythronium umbilicatum* may not be vulnerable to phenological mismatch with overstory trees

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Abstract

Premise: The defining life history strategy of spring ephemeral wildflowers is their avoidance of shading by trees during the brief, high-light period before canopy leaf out. Studies suggest that spring ephemerals will experience increased light competition because canopy leaf out is more sensitive to warming than is the phenology of spring ephemerals. However, it remains unclear how longer durations of shade will alter the population dynamics of spring ephemerals and whether all populations are at risk.

Methods: We experimentally shaded *Erythronium umbilicatum* for one to six additional weeks before canopy leaf out to test for immediate and lagged effects of early shading on the timing of senescence and the probability of survival and flowering. To predict the potential for earlier shading, we combined long-term time series of spring air temperature, remotely sensed tree leaf out, and *E. umbilicatum* flowering phenology in North Carolina, United States.

Results: Early shading did not alter *E. umbilicatum* until the following year, when more-shaded plants senesced later. Year-to-year survival did not change, and the probability of flowering was reduced only when plants experienced extremely early shading. Moreover, *E. umbilicatum* phenology was more sensitive than tree leaf out to warming temperatures. We project that, under climate warming, *E. umbilicatum* is unlikely to experience shortened periods of high light.

Conclusions: Our findings show that a plant species' defining life history strategy does not necessarily predict their sensitivity to phenological mismatches. This incongruity complicates, but also underscores the importance of identifying the most vulnerable species and directing our research efforts accordingly.

KEYWORDS

canopy leaf out, climate change, Erythronium, historical data, light competition, Liliaceae, phenology, shade experiment, temperate forest understory, temperature sensitivity

Plants often shift the timing of phenological events earlier in response to warmer spring temperatures, although some plant species respond more strongly to each degree of warming than others (Stuble et al., 2021). Species differences in phenological sensitivity to climate change can disrupt synchronized interactions or create new, historically absent interactions, a phenomenon known as phenological mismatch. Phenological mismatches, whether they exacerbate negative interactions or disrupt positive interactions, can have negative effects on fitness components and population trajectories. Spring ephemerals—perennial, understory herbs found in temperate, deciduous forests—exploit a short period of high light in the early spring when conditions are warm enough for aboveground growth but before the overstory canopy develops (Yancy et al., 2024). This shade avoidance strategy may be vulnerable to climatic changes that advance tree leaf out faster than the onset of the growing season for spring ephemerals, resulting in unprecedented competition for light and a narrower window for growth and reproduction (Alecrim et al., 2022; Miller et al., 2023; reviewed by Lee et al., 2024). Understanding the multiyear effects of increased light competition on spring ephemerals and identifying which species are most likely to experience earlier canopy closure and where is crucial for directing our research and conservation efforts.

Since spring ephemerals exhibit a life history strategy evolved to escape light competition and are only active above ground for a short period of time, any decrease in the duration of their high-light window would reduce their carbon budgets (Heberling et al., 2019) and should have an effect on their phenology, resource allocation, or fitness components. In *Erythronium* species, for example, the effects of shade on the current growing season include reduced fruit and seed set, reduced plant growth above- and belowground, and earlier senescence (Kim et al., 2015; Augspurger and Salk, 2017). Furthermore, reduced carbon budgets can exacerbate the physiological trade-offs between investment in aboveground structures in the same year and in belowground energy storage, which may affect survival and reproduction in the following year. However, no studies have experimentally examined the effects of early canopy shade on the following year fitness components. Because spring ephemerals are long-lived perennials, it is important to examine multiyear effects of shade on fitness components to understand how populations might be affected.

Despite evidence that shorter high-light windows can have negative consequences for some spring ephemeral species, the geographic locations where spring ephemerals face the greatest risk to climate change are still uncertain since different data sets bear conflicting results. In one study that spanned most of the eastern half of the United States, researchers used tree leaf out date and spring ephemeral first flowering date from herbarium specimens to predict that light availability windows will decrease for spring ephemeral communities since tree leaf out is more sensitive to warming spring temperatures than is spring ephemeral flowering (Lee et al., 2022; Miller et al., 2023). In contrast, Alecrim et al. (2022) used community science data from the National Phenology Network repository and found that light windows for spring ephemerals are increasing in duration at higher latitudes in North America, but remain constant at lower latitudes. Despite contradictory evidence from recent studies regarding where in North America spring ephemerals are most susceptible to early tree leaf out (divergent findings were discussed by Lee et al., 2024), both suggest that the phenological response to climate change is species and location specific. For example, while members of the genus *Erythronium* are some of the earliest to emerge and more sensitive to spring temperatures than other ephemerals, they could be found in forests dominated by trees with strong sensitivity to warming (such as *Acer rubrum* and *Fagus grandifolia*), which would still put them at risk of phenological mismatch with the canopy (Miller et al., 2023). Studies using alternative sources of data are needed to corroborate predictions from these models, which will help clarify when and where spring ephemerals may be most at risk.

To shed light on species-specific responses to early shade and location-specific interactions, we use *Erythronium umbilicatum*, a common species found in the southeastern United States and subject of several historical studies in Durham, North Carolina (Motten, 1982, 1986). Members of this genus have been used in previous shade experiments although the lagged effects of shortened light windows have yet to be explored (Kim et al., 2015; Augspurger and Salk, 2017). Here, we aimed to (1) test how early shade affects the current year and following year phenology and fitness components using an artificial shade experiment and (2) to understand the extent of phenological mismatch between *E. umbilicatum* flowering and canopy leaf out using a novel combination of long-term ecological data and satellite imagery.

MATERIALS AND METHODS

Study site and focal species

We conducted this study at two sites in the Duke Forest in Durham, North Carolina, United States – Korstian Division: Gate 24 (35.983790, −79.032756; hereafter G24) and the Oosting Natural Area (35.980770, −79.064930; hereafter ONA). These sites are uniquely suited for this study since researchers previously monitored the flowering phenology of spring ephemerals at the same sites in 1978–1980 and again in 2015–2017 (Motten, 1986; R. M. Dalton, unpublished data). The dominant tree species at these sites include *Acer rubrum*, *Fagus grandifolia*, *Liriodendron tulipifera*, and *Liquidambar styraciflua*.

We characterized the effects of early shade on *Erythronium umbilicatum* subsp. *umbilicatum* Parks and Hardin (Liliaceae), a spring ephemeral species common to the Piedmont region of North Carolina, with a range that extends north to Maryland and West Virginia and south to Florida. *Erythronium umbilicatum* can be found in moist to mesic hardwood forests in floodplains and along gentle slopes (Radford et al., 2010). The life cycle of *E. umbilicatum* comprises two distinct phases—underground root and shoot growth that takes place during the autumn and winter and aboveground growth that begins at the end of winter and continues through early spring (Lapointe, 2001). At our study sites, leaves and shoots typically emerge in late January or early February. During the spring epigeous growth period, plants photosynthesize and direct energy toward storage in the corm (the undifferentiated energy storage organ) or toward sexual reproduction in the form of flowers and fruits. Unlike other yellow *Erythronium* species of the eastern United States, *E. umbilicatum* does not reproduce asexually through rhizomes (Parks and Hardin, 1963).

In any given year, most individuals are vegetative at our sites (e.g., in our 2-year study, about 85% of individuals did not flower in either year). When flowering does occur, it often happens immediately after leaf emergence. Populations in the Piedmont of North Carolina reach peak flowering in March and finish flowering by the beginning of April. Each flower remains open from 5 to 10 days. Common pollinators include a variety of native bees, particularly andrenid bees, and *Apis mellifera* (Motten, 1983).

Aim 1: Assess effects of experimental shade on senescence, survival, and reproductive success

Experimental setup

We applied a gradient of early shade onset to 1-m^2 plots of naturally occurring *E. umbilicatum* in weekly increments from 6 weeks ahead of natural canopy closure to no additional shading, then tested for (1) immediate shading responses in plants and (2) lagged effects in the following year when all plants experienced ambient shading when the canopy leafed out. For the shade treatment, we suspended shade cloth tents made of woven high-density polyethylene (Winemana, Hong Kong, China) over treated plots. The cloths were designed to block >90% of solar radiation, mimicking full canopy leaf out (>95% reduction in light levels; Augspurger et al., 2005). We oriented the open ends of the shade cloth tents to face north and south to maximize the shaded plot area over the course of the day. We also deployed tents as a sham control that were made of loosely woven, light-transmitting nylon to control for potential fabric effects (e.g., on herbivores, pollinators, air flow, or precipitation; Jevrench, Zhongxiang, Hubei, China; Appendix S1). We removed the shade and sham control cloths after canopy leaf out naturally occurred in 2023.

At the outset of the experiment in 2023, we identified all study plots and randomly assigned each to a treatment (Figure 1; 1–6 weeks of shade, 1–6 weeks of sham control, or uncovered true control). Beginning in the second week of February, we deployed a total of five replicate shade cloths and one replicate sham control each week over 6 weeks, until the end of March. Logistical constraints forced our design to be unbalanced, and we alternated which site received two vs. three shade tents and which site received the sham control. In total, we deployed up to five replicate plots for each of the six shade treatment durations, one plot for each sham control duration, and 12 replicate uncovered controls for a total of 45 plots across both sites (Figure 1). Due to time constraints in the middle of the season, we switched to deploying treatments only at site ONA. In addition, we only deployed three shade replicates and no sham control the week of March 20.

We tagged all *E. umbilicatum* individuals present in each plot (from 4 to 30 individuals). In 2023, we visited the plots twice per week between 20 February and 19 April and recorded the date of senescence for each tagged plant. We considered a plant senescent if ≥ 50% of the total leaf area was yellow, if only the bare structural remains of the leaf were found (defined by Muller, 1978), or if the leaf was completely missing after signs of yellowing on prior observation days. In the first year of the study, we only focused on the timing of senescence since some plants had

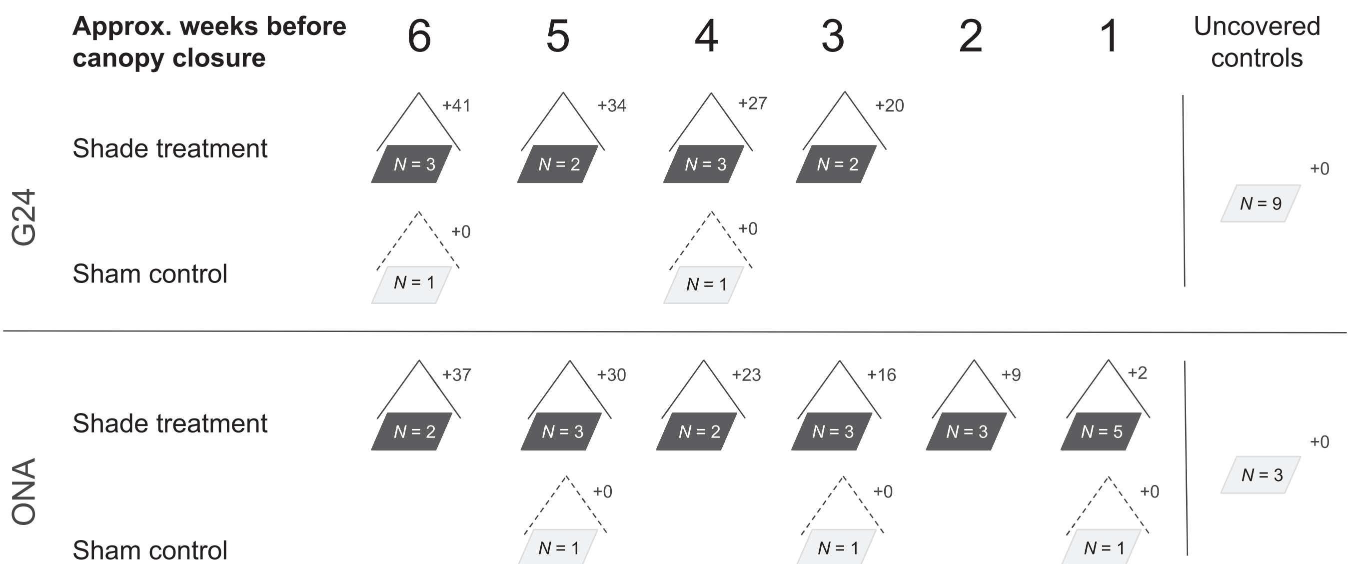

FIGURE 1 Shade and sham control deployment schedule, locations, and replicate quantity in 2023. The actual number of days of extra shade that each plot received relative to canopy leaf out at each site is represented by the +numbers next to each plot. This number is the difference between the DOY of natural canopy leaf out (EVI > 4250) in 2023 and the DOY that the treatment was deployed. This EVI threshold occurred on 2 April 2023 (DOY 92) at site G24 and 29 March 2023 (DOY 88) at site ONA. Sample size of number of plots deployed on each day indicated within each plot.

already started to flower before we set up the plots. In 2024, we revisited the same plots twice per week, from the end of January through the end of April. We recorded if and when the tagged plants emerged, flowered, fruited, and senesced.

To evaluate the intended and unintended abiotic effects of the shade and sham control cloths, we measured the soil moisture as volumetric water content (VWC) in the southwest corner of a subset of plots at ONA on a fair-weather day in early March 2023 (HydroSense II Handheld Soil Moisture Sensor, Campbell Scientific, Logan, UT, USA; $N_{\text{control}} = 24$, $N_{\text{shade}} = 9$, $N_{\text{sham}} = 2$). We monitored light intensity (lux) and soil surface temperature by deploying a pair of HOBO Pendant data loggers (HOBO UA-002-64 Pendant Light and Temperature Data Logger, Onset, Bourne, MA, USA) in four shade plots and one sham plot at ONA. We placed the Pendants on top of the soil and leaf litter, with the light sensors facing upward. Each pair consisted of a Pendant in the middle of the plot and one southwest of the plot, just outside the covered area. The Pendants recorded data every 10 min from 28 March to 4 April 2023.

Analyses

Shade calculations

Our experiment imposed a range of experimental shade durations on plants, and we used two different clocks to measure the treatment magnitude experienced by plants in a given plot. First, we calculated the number of days since the shade cloth was applied as

$$T_{\text{since shade onset}} = \begin{cases} t_{\text{obs}} - t_{\text{shaded}}, & \text{when } t_{\text{obs}} > t_{\text{shaded}} \\ 0, & \text{when } t_{\text{obs}} \le t_{\text{shaded}} \text{ \& uncovered control plots,} \end{cases} \quad (1)$$

where t is the day of year (DOY), subscript obs is the date of observation and and shaded is the date that the shade treatment was applied. We used this metric for phenological events occurring during the shade treatment in 2023 because there is no mechanism for future days of shading to affect the current phenology of the plants. The second measure calculated the total duration of additional shade days applied to the plot as

$$D_{\text{additional shade}} = \begin{cases} t_{\text{canopy leaf out}} - t_{\text{shaded}}, & \text{shaded plots} \\ 0, & \text{uncovered control plots,} \end{cases} \quad (2)$$

where t is the day of year and subscripts indicate the timing of canopy leaf out and date that the shade treatment was applied. We determined the day of year of natural canopy leaf out using an enhanced vegetation index (EVI) threshold of 4250, which occurred on 2 April 2023 at G24 ($t_{\text{canopy leaf out}} = 92$) and 29 March 2023 at ONA ($t_{\text{canopy leaf out}} = 88$). We used this metric to measure the cumulative amount of extra shading experienced by plants, which was appropriate for plant responses to the treatments that occurred after canopy leaf out (i.e., when controls were also shaded) and for lagged responses to shading over the following year. In both years, all true control plots had zero days of extra shade.

Environmental impacts of shade cloth

To quantify the impact of the shade and sham control cloths on light availability and air temperature, we compared daytime light and temperature (10:00–16:45 hours) and nighttime temperature (19:00–04:45 hours) of the paired pendants ($N_{\text{shade}} = 4$, $N_{\text{sham}} = 1$). We analyzed the data using two-way ANOVA with a random intercept of plot and a first-order autoregressive variance structure to account for temporal autocorrelation of the residuals. We compared soil moisture values measured in all plots on 6 March 2023 using a one-way ANOVA.

Phenology, survival, and fitness components

To quantify the effect of shade on the timing of senescence in 2023 and 2024, we fit binomial generalized linear mixed models (GLMMs) with a logit link and binomial error distribution in which the probability that an individual plant had senesced was predicted as a function of observation DOY, days of extra shade in 2023, and the interaction between them. Since each plot was assessed on multiple days, we included a random intercept of plot nested within site. We then performed a Type III Wald χ^2 test to test for a significant interaction effect between observation DOY and number of days of extra shade.

To quantify the effect of shade in 2023 on the probability of survival, flowering, and fruiting given flowering in 2024, we fit binomial GLMMs with a logit link and binomial error distribution in which the probability of an individual emerging, flowering, or fruiting in 2024 was predicted as a function of days of extra shade in 2023. We included a random intercept of plot nested within site in our models.

To assess the impact of the sham control cloth compared to ambient conditions, we ran the same analyses as above on the sham control plot data and used days of extra sham control (rather than days of extra shade) as the predictor.

Estimate the rates at which spring ephemeral flowering and tree leaf out phenology are changing over time

Spring ephemeral response to warming temperatures

We chose peak bloom as our phenological estimator for *E. umbilicatum* because of its robustness to sample size and detection biases that impact other phenological indicators

(Moussus et al., 2010). To model the day of peak bloom of *E. umbilicatum* each year as a function of temperature, we aggregated observations from data sets collected at our study sites between 1978 and 1980 by Motten (1982) and ourselves between 2015 and 2017 and between 2023 and 2024. Motten visited G24 and ONA at 2- to 3-day intervals and recorded qualitatively when the *E. umblicatum* population was in full bloom at each site, defined as the range of dates between when floral abundance at each site began to increase and decrease most rapidly (Motten, 1982). For those years, we estimated the day of peak bloom at G24 and ONA as the median day within Motten's reported full bloom range. In 2015, 2016, and 2017, R. M. Dalton visited 24 plots across sites G24 and ONA at 2- to 3-day intervals and recorded the number of flowering *E. umbilicatum* individuals per plot from January to the end of April. In 2023 and 2024, we similarly monitored flowering phenology in 45 plots across both sites. To estimate the day of year that peak flowering occurred between 2015 and 2024, we fit curves to the raw flowering data using Poisson regressions with a log link function and included the day of year squared as the predictor with a random intercept of plot (Appendix S2). We designated the maximum peak of the curves as the day of year that peak flowering occurred.

We then correlated peak bloom DOY from the three data sets with monthly, 4-km resolution parameter–elevation regressions on independent slopes model (PRISM) temperature data for January through April from each observation year at each site (Daly et al., 1994; PRISM Group, 2024). Our study sites were located ca. 3 km apart in two adjacent grid cells. We associated each site's peak bloom dates with temperatures from that site's specific grid cell in each year. We performed model selection using Akaike's information criterion, corrected (AICc) using the dredge function in the R package MuMIN (v1.48.4; Bartón, 2024) to identify the candidate model containing the mean monthly temperature or mean of consecutive monthly temperatures weighted by the number of days in each month, that best predicted peak flowering date (Appendix S3). We then took the best candidate model and used AICc to determine whether including an interactive or additive effect of site improved the fit. We found that the mean air temperature of February through April, without an effect of site, best predicted peak bloom date of spring ephemerals. We used the fitted linear model (peak bloom $\text{DOY} = \beta_0 + \beta_1 \times \text{temperature}_{\text{Feb-Ap}}$; Figure 2; Appendix S4) to hindcast when peak bloom would occur over time from 1970 to 2024, given a mean February through April temperature obtained from the PRISM Group (2024) (Figure 3).

Tree leaf-out response to warming temperatures

We estimated the timing of tree leaf out from 2000 to 2024 from the remotely sensed MODIS Terra enhanced vegetation index (EVI) timeseries (MOD13Q1.061; Didan, 2021). The earliest available data were from the year 2000. The spatial resolution of the EVI data product is 250 m, and the temporal resolution is 16 days, which allowed us to differentiate our two study sites and extract six to eight EVI observations each year that spanned the leaf-out period (early February through the end of April). The EVI is beneficial compared to other spectral indices because it retains its sensitivity in areas with a high leaf area index which is important for capturing more minute changes in leaf out later in the season. When the tree canopy is fully closed, EVI is at its maximum.

We used an absolute EVI threshold of 4250, which was approximately the mean EVI value across all years at both sites, as a proxy for when the canopy reached 50% green up

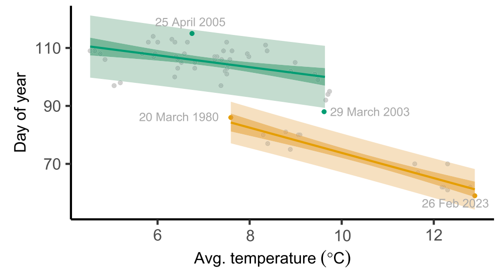

FIGURE 2 Best-fit models to predict the day of year that peak flowering and tree leaf out (EVI > 4250) will occur, given a mean spring temperature. Gold line (lower) represents *E. umbillicatum* peak flowering; green line (upper) represents tree leaf out. The mean of February through April temperatures was the strongest predictor of the timing of peak flowering. The mean of January through March temperatures was the strongest predictor for the timing of tree leaf out. Points represent raw data; lines represent fitted model with 95% confidence (dark ribbon) and prediction intervals (light ribbon). Colored points and text highlight the minimum and maximum observed day of year that the phenological events occurred. All temperature data were collected from the PRISM Group (2024) database.

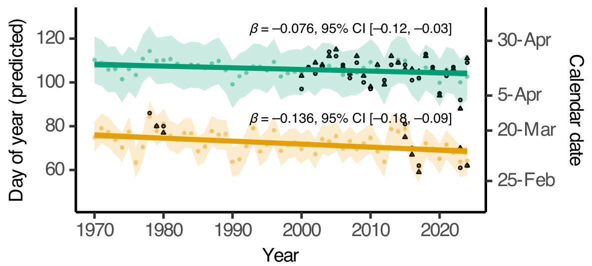

FIGURE 3 The flowering phenology of *E. umbilicatum* (gold) is predicted to shift earlier in the year relative to the timing of tree leaf out (green), although there was no significant interaction between type of phenological event and year ($F_{3,\ 216} = 1391$, $R^2_{\text{adj}} = 0.95$, $P = 0.07$). Linear regressions (shown in Figure 2) were used to hindcast when a phenological event would have occurred in each year, given that year's mean February through April temperature for flowering and mean January through March temperature for tree leaf out. Colored points and jagged ribbons represent those predictions and 95% prediction intervals. For comparison to these predictions, open circles (G24) and triangles (ONA) represent direct observations of phenological events. These observations are the same raw data presented in Figure 2, but were not involved directly in the linear fits shown here. Straight lines with 95% confidence intervals are outputs from the linear model that correlates year with predicted day of year of phenological event.

each year as our phenological estimator for canopy closure. To find the day of year that EVI > 4250 each year at each site, we first normalized the EVI data within each year and site to constrain data within zero and one $EVI_{normalized} = (EVI - EVI_{min})/(EVI_{max} - EVI_{min})$, where EVI_{min} is the minimum EVI value recorded at a site in a given year and EVI_{max} is the maximum EVI value. We used a quasibinomial GLM with a logit link to model normalized EVI as a function of year, site, DOY and their interactions and used the fitted lines from the model to estimate when EVI > 4250 each year (Appendix S5). Canopy leaf out occurred rapidly; the EVI typically increased from <10% to >90% in about 56 days.

To find in which months the mean temperature (or mean of consecutive monthly temperatures weighted by the number of days in each month) was the strongest predictors of the DOY that EVI > 4250 occurred, we obtained monthly mean temperatures from the PRISM Group (2024) database for each site for January through April from 2000 to 2024. We performed model selection with AICc using the dredge function from the R package MuMIN (Bartón, 2024) (Appendix S3). We then took the best candidate model and used the AICc to determine whether including an interactive or additive effect of site improved the fit. We determined that the mean of January, February, and March temperatures, without an effect of site, was the strongest predictor of an EVI > 4250, and used the fitted model (EVI > 4250 DOY = $\beta_0 + \beta_1 \times \text{temperature}_{\text{Jan-Mar}}$; Figure 2; Appendix S4) to hindcast the DOY that EVI > 4250 occurred for each year from 1970 to 2024, given a mean January–March temperature obtained from the PRISM Group (2024) climate data (Figure 3).

Comparing peak bloom and green-up response to warming air temperature

We compared the phenological change of *E. umbilicatum* peak flowering with change in tree canopy green up as a measure of potential mismatch. Although *E. umbilicatum* leaf phenology would better capture the effect of canopy closure on photosynthesis, historical data on leaf phenology were not collected. We expect that the compressed growing season of spring ephemerals would cause their flowering phenology to closely follow—and therefore serve as a good proxy for—leaf expansion. At G24, the period between leaf expansion and peak flowering was 14 days in both 2023 and 2024. At ONA, the period was 23 and 15 days, respectively.

We used the two fitted linear models (peak bloom DOY = $\beta_0 + \beta_1 \times \text{temperature}_{\text{Feb-Ap}}$, EVI > 4250 DOY = $\beta_0 + \beta_1 \times \text{temperature}_{\text{Jan-Mar}}$) to hindcast when the phenological events occurred each year, given a mean spring temperature from 1970 to 2024 (Figure 3). We then fit a linear model through those predicted points to estimate how those phenological events are trending over time (phenological event DOY = $\beta_0 + \beta_1 \times \text{year} \times \text{type}$; Figure 3). A greater sensitivity of *E. umbilicatum* to warming temperatures than that of tree leaf out suggests a longer high light growing season as the climate warms and vice versa.

Previous studies commonly use a single, a priori temperature variable to predict both flowering phenology and tree leaf out (Alecrim et al., 2022; Miller et al., 2023), rather than using the strongest predictors for each phenological event. To investigate whether each method provides different results, we also modeled peak flowering time as a function of the mean of January, February, and March temperatures (peak bloom DOY = $\beta_0 + \beta_1 \times \text{temperature}_{\text{Jan-Mar}}$) and modeled both peak flowering and EVI > 4250 as a function of mean March temperature (peak bloom DOY = $\beta_0 + \beta_1 \times \text{temperature}_{\text{March}}$, EVI > 4250 DOY = $\beta_0 + \beta_1 \times \text{temperature}_{\text{Mar}}$; Appendices S4, S6). We chose to examine these two temperature variables since they were the top two predictors of EVI > 4250, but performed differently when used to predict peak flowering (Appendix S3). We used the fitted linear models to hindcast when the phenological events occurred each year, given a mean spring temperature from 1970 to 2024. We then fit a linear model through those predicted points to estimate how those phenological events are trending over time (phenological event DOY = $\beta_0 + \beta_1 \times \text{year} \times \text{type}$; Appendix S7).

We performed all analyses in R 4.4.2 and RStudio 2024.04.1 + 748 (R Core Team, 2024; Posit team, 2024). We fit all generalized linear mixed models with the R package lme4 (Bates et al., 2015). To analyze the Pendant data using a two-way ANOVA and a first-order autoregressive variance structure, we used the glmmTMB package (Brooks et al., 2017). We then used the R package car to perform Wald χ^2 tests to test for model significance (Fox and Weisburg, 2019). For post hoc comparisons across treatments, we performed Tukey pairwise comparisons using the R package emmeans (Lenth, 2024).

RESULTS

Aim 1: Assess effects of experimental shade on senescence, survival, and reproductive success

Environmental conditions of each treatment

Compared to ambient and sham conditions, the shade cloth significantly reduced visible light intensity by 80.5% ($\chi^2 = 32.9$, df = 1, $P < 0.0001$; Appendix S8) and daytime temperature by 6.6°C ($\chi^2 = 12.6$, df = 1, $P < 0.0001$; Appendix S9). Light levels and daytime temperature inside the sham control plot were not significantly different to ambient conditions in a post hoc Tukey test (Appendices S8, S9). The sham control and shade cloths did not significantly affect nighttime temperatures ($\chi^2 = 0.05$, df = 1, $P = 0.825$) or soil moisture ($F_{2,\ 31} = 0.05$, $P = 0.974$).

Effect of shade on timing of senescence and fitness components

The duration of additional shade did not affect the timing of plant senescence during the same growing season ($\chi^2 = 1.40$, df = 1, $P = 0.237$; Figure 4A; Appendix S10). Shade duration

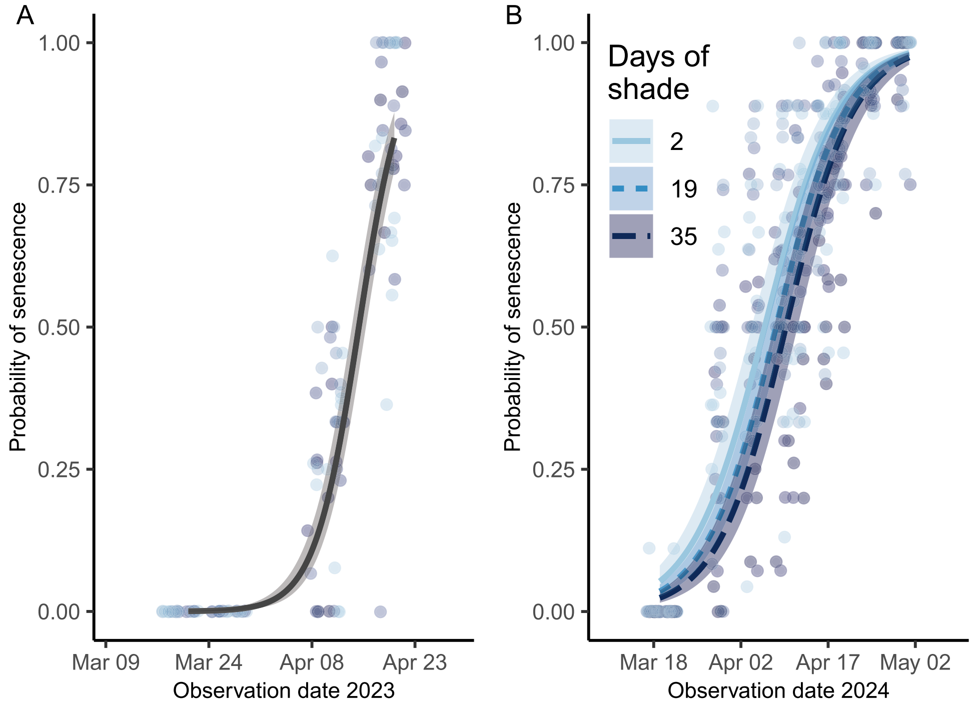

FIGURE 4 Experimental shade in 2023 (A) did not affect the timing of senescence in 2023 ($P = 0.237$) but (B) did affect the timing of senescence in 2024. Plants that received more days of shade in 2023 senesced later in 2024 ($P = 0.025$). The line in A depicts the logistic regression model fit across all shade treatments and the lines in B depict the mean number of days of extra shade (19 days) and ±1 SD number of days of extra shade (2 and 35 days). Points are raw data. Ribbons represent the upper and lower 95% CI.

also did not affect survival in the following year ($\chi^2 = 0.50$, df = 1, $P = 0.481$). The effect of shade only became apparent later in the following growing season. Increasing shade duration in 2023 decreased the probability of flowering in 2024 ($\chi^2 = 8.97$, df = 1, $P = 0.003$; Figure 5; Appendix S11), although it did not affect fruiting given flowering ($\chi^2 = 1.14$, df = 1, $P = 0.286$). Shade in 2023 also delayed senescence in 2024 ($\chi^2 = 5.06$, df = 1, $P = 0.025$; Figure 4B; Appendix S10). Each week of additional shade in 2023 delayed senescence in the following year by approximately 0.6 days.

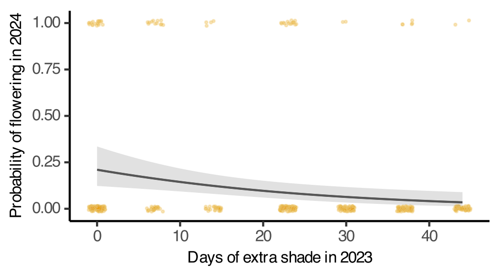

FIGURE 5 Longer experimental shade in 2023 decreased the probability of flowering in 2024 ($P = 0.003$). Points are individual plants (jittered to avoid overplotting), line is fitted model with 95% CI.

Effect of sham control on timing of senescence and fitness components

The duration of sham control cloth did not affect the timing of plant senescence during the same growing season ($\chi^2 = 1.77$, df = 1, $P = 0.183$). In the next growing season, 2023 sham control had no lagged effects on 2024 survival ($\chi^2 = 0.42$, df = 1, $P = 0.516$), flowering ($\chi^2 = 0.01$, df = 1, $P = 0.91$), or senescence ($\chi^2 = 0.80$, df = 1, $P = 0.371$).

Aim 2: Extent of phenological mismatch between *Erythronium umbilicatum* flowering and tree canopy leaf out

The timing of *E. umbilicatum* flowering and tree leaf out was best predicted by different temperature cues. Moreover, *E. umbilicatum* flowering and tree leaf out differed in their phenological sensitivity to their respective temperature cues. For *E. umbilicatum*, the strongest predictor for peak flowering was the mean of February through April temperatures (Appendix S3). For every degree of temperature increase, peak flowering occurred on average 4.35 (± 0.41 SE) days earlier ($R^2 = 0.89$; Figure 2; Appendix S4). The strongest predictor of EVI > 4250, was the mean of January through March temperatures (Appendix S3). For every degree of mean temperature increase during these months, green up occurred on average 2.1 (±0.52) days earlier ($R^2 = 0.23$; Figure 2; Appendix S4). We repeated the model comparisons using summed growing degree days (GDD) with a 5°C base temperature in place of mean temperatures. Here too, the cues and sensitivities differed between *E. umbilicatum* and tree leaf out: The timing of peak flowering was best predicted by February, March, April GDD, and tree leaf out was best predicted by March GDD (Appendix S12).

Using these temperature sensitivities to hindcast recent phenological change, we estimated that *E. umbilicatum* flowering has shifted earlier at a rate of 1.4 (±0.5) days per decade ($F_{1,\ 86} = 13.44$, $P = 0.0004$), but the timing of tree leaf out has only shifted at a rate of 0.7 (±0.4) days per decade ($F_{1,\ 108} = 18.7$, $P = 0.0003$; Figure 3), although there was no significant interaction between type of phenological event and year ($F_{3,\ 216} = 1391$, $P = 0.07$). Taken together, we estimate that the shade-free interval between *E. umbilicatum* peak flowering and tree leaf out has increased by 0.7 days per decade. Likewise, the GDD-based analysis (Appendix S12) revealed a 0.7 days per decade increase in the shade-free interval.

We also modeled the timing of *E. umbilicatum* peak flowering as a function of mean of January through March temperatures and both peak flowering and EVI > 4250 as a function of mean March temperatures to investigate whether using a single temperature variable for both phenological events would result in different outcomes. When we modeled peak flowering as a function of the mean of January through March temperatures, we found the timing of *E. umbilicatum* flowering to be less sensitive to warming temperatures. For every degree of mean January through March temperature increase, peak flowering occurred on average only 3.66 (±0.41) days earlier ($R^2 = 0.85$; Appendix S4). Despite this decrease in sensitivity, using the mean January through March temperature model to hindcast recent change in flowering time did not change the rate of advancing flowering time from our original results. Flowering of *E. umbilicatum* still shifted earlier at a rate of 1.4 (±0.3) days per decade ($F_{1,\ 108} = 18.74$, $P = 0.0003$). However, when we used mean March temperature to predict both peak flowering and EVI > 4250, we found both *E. umbilicatum* flowering and canopy green up to be less sensitive to warming temperatures. For every degree of mean March temperature increase, peak flowering occurred on average only 2.72 (±1.0) days earlier, and green up occurred on average only 1.36 (±0.35) days earlier (Appendices S4, S6). Moreover, using the mean March temperature sensitivity to hindcast recent change in both phenological events reduced the rate of advancing flowering time to only 0.6 (±0.2) days per decade and advancing canopy closure to 0.3 (±0.2) days per decade (Appendix S7). There was also no significant difference between the timing of spring ephemeral flowering and tree leaf out in response to warming temperatures over time ($F_{3,\ 216} = 1269$, $P = 0.35$).

DISCUSSION

Effect of shade on timing of senescence

In contrast to what we would expect from carbon budgets and the results from previous shade experiments (Vezina and Grandtner, 1965; Kim et al., 2015; Augspurger and Salk, 2017), we found that early shade did not alter the timing of senescence in the year that the shade treatment was applied. We can conceive of two mechanisms for this surprising response. First, the shaded plants in our experiment may have acclimated to shade conditions, especially since our shade cloth only reduced light by 80%, when natural full canopy closure can reduce light by more than 90%. Relatedly, experimentally shaded leaves of *Erythronium japonicum* were larger and had a greater specific leaf area, which allowed them to continue to grow and maintain a carbon balance despite reduced light conditions (Kim et al., 2015). Another possible mechanism is that temperature might be more influential than shade as a predictor of *E. umbilicatum* senescence. Lapointe (2001) found that senescence is triggered when carbohydrate reserves have been fulfilled, which occurs faster under warmer temperatures, regardless of the amount of shade.

Our shade treatment significantly delayed the timing of senescence in the following year. One possibility for this lagged effect of shade is that shaded plants did not store as much energy in their corm the year shading occurred (Muller, 1978) and thus extended leaf life span in the following year to compensate for reduced carbon acquisition and storage. The surprising lagged effect of shade on senescence in the following year emphasizes the need for additional multiyear studies to directly assess the mechanisms for delayed response to shade.

Effect of shade on demographic fitness components in the following year

Longer periods of shade did not alter *Erythronium* survival. Relatedly, previous work found that winter cold had a stronger effect on survival than did shade (Augspurger and Salk, 2017). While 1 year of extra shade did not reduce survival, repeated years of early canopy closure and decreased carbon acquisition might reduce individual survival over longer periods of time.

Extra days of experimental shade did reduce the probability of flowering in the following year. A reduction in stored carbon under longer periods of shade could explain this result, since spring ephemerals rely on energy stored in the previous year for growth and flowering in the next (Risser and Cottam, 1968). In control plots, the probability of flowering was 0.22. If light windows were to decrease by 6 days by 2080 (as projected for some spring ephemerals by Heberling et al., 2019), the probability of flowering would decrease by 20.5%. While a 20.5% reduction in the probability of flowering may seem extreme, the negative effects of early canopy shade may not be detrimental to *E. umbilicatum* populations since the intrinsic growth rate of long-lived *Erythronium* species is least sensitive to fluctuations in the number of seedlings and more sensitive to relative growth rate and survival (Takada et al., 1998). To understand how early shade might impact spring ephemeral populations, we should also study the effects of shade on following year demographic fitness components such as survival, growth, and reproduction.

Assessing the risk of phenological mismatch

Although increased shade would likely reduce reproductive success in *E. umbilicatum*, the free-living populations in our area may not actually experience increased shade in the future. We found that *E. umbilicatum* is more sensitive to warming temperatures than are the canopy trees at our sites, thus the duration of the growing season might actually be increasing. On average, *E. umbilicatum* flowering is shifting 1.4 (± 0.5) days earlier per decade, whereas the trees are shifting only 0.7 (± 0.4) days per decade earlier. If this trend holds over time, *E. umbilicatum* in North Carolina could experience longer periods of high light in the spring than it has historically as the climate warms. Our findings are congruent with previous studies that found that *Erythronium* species are especially sensitive to warming temperatures and unlikely to experience decreasing light windows at lower latitudes in the short term as the climate warms (Alecrim et al., 2022).

While the results of our study suggest that *E. umbilicatum* may be resilient to the impacts of early shade, populations may still be vulnerable as the climate warms for several reasons. First, nonlinear phenological responses to climate change can slow or even reverse species responses to warming (Iler et al., 2013; Pope et al., 2013), particularly with species that have a chilling requirement to break dormancy as do *Erythronium* spp. (Risser and Cottam, 1967; Yoshie and Yoshida, 1989). In the future, *Erythronium* species might not receive enough chilling degree days to break dormancy, resulting in delayed emergence and flowering as the climate warms. Second, emerging earlier each year could be dangerous for *E. umbilicatum* as growing season frost events are becoming more common around our study sites despite warmer average spring temperatures (Marino et al., 2011), and an advanced flowering period coincides with times of year that historically have had more frost events (Appendix S13). More studies are needed on the effects of highly variable spring temperatures and late season frost events on the ability for spring ephemerals to shift their phenology. Finally, we investigated how 1 year of early shade affects phenology, survival, and reproduction in the next year. Under future climate conditions, spring ephemerals could experience multiple consecutive years of early canopy cover. More work needs to be done to understand the effects of consecutive years of early shade events.

One unique aspect of our study is that we used different temperature predictors in our models correlating mean spring temperatures with the phenological events, tree leaf out, and spring ephemeral peak flowering. We chose this approach since trees and spring ephemerals are known to be more sensitive to different climatic variables (Basler and Korner, 2014; Zohner et al., 2016; Jánosi et al., 2020). We suggest using the temperature predictors that are most relevant to each interacting group to best represent the mechanism by which phenological mismatch occurs. Phenological mismatch could arise when interacting species respond to the same cue but at different rates or if they respond to different cues. Studies that assume the former mechanism may under or overestimate phenological mismatch if the predictor variable is not a good fit. With the present study, if we used mean March temperatures as the predictor of both phenological events, we would have estimated that the shade-free interval between *E. umbilicatum* peak flowering and tree leaf out has only increased by 0.3 days per decade. Future studies could improve upon our approach by looking at how trees and spring ephemerals respond to different variables (such as accumulated growing degree days, soil temperature, chilling, precipitation, snowpack, photoperiod) and the interactions between them.

In this study, we also used the novel approach of combining long-term ecological data sets and satellite data to shed light on species-specific and location-specific interactions, which can be an effective method when tree and ephemeral data are not available from the same source. Both types of data sets are highly valuable and can be used in future studies to model the potential for phenological mismatch between trees and spring ephemerals globally. There is great potential for community scientists to accumulate similar data for other species and across large temporal and spatial scales (such as data sets from the USA National Phenology Network and Project Budburst). Going forward, it will be important to have standardized ways to collect data and record phenological events.

CONCLUSIONS

It is critical to understand how threats such as climate change impact spring ephemerals, which are important for energy and nutrient cycling in temperate deciduous forests (Muller, 1978). Spring ephemerals are also important resources for many pollinator species, during a season when few floral resources are available (Schemske et al., 1978; Motten, 1986; Dailey and Scott, 2006). However, our understanding of which spring ephemeral species will be most sensitive to changing temperatures and how early shade will affect them is limited, which hinders our ability to protect and manage valuable ecosystems. Our results demonstrate that not all spring ephemerals will be sensitive to phenological mismatch with the canopy and highlight that a species' defining life history traits do not necessarily predict vulnerability. Future studies are still needed to accurately predict the geographic and taxonomic variation in phenological responses to warming and the extent of ecosystem-level effects of changes in the spring-ephemeral community.

AUTHOR CONTRIBUTIONS

M.S., W.P.K., E.M.W., and A.S. conceived the research idea. M.S., R.M.D., E.M.W., and E.R. collected and curated the

data. M.S. analyzed the data with input from E.M.W., E.Y., and W.P.K. M.S. wrote the manuscript with input from all authors. This work is not a product of the U.S. Government or the U.S. Environmental Protection Agency, and R.M.D. is not doing this work in any governmental capacity. The views expressed are those of R.M.D. only and do not necessarily represent those of the U.S. Government or the EPA.

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DATA AVAILABILITY STATEMENT

The data from this study are openly available on Dryad at https://doi.org/10.5061/dryad.0k6djhbc9.

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SUPPORTING INFORMATION

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

Appendix S1. Photograph of a sham control plot (white) and shade treatment plot (black) at site G24 in the Korstian Division of the Duke Forest in Durham, North Carolina, USA.

Appendix S2. Poisson regression fit to counts of number of flowers per plot at each site in the specified years.

Appendix S3. List of months and consecutive combinations of months considered as predictors of each phenological event.

Appendix S4. Output of linear models predicting the DOY that peak flowering and an EVI threshold of 4250 occurs as a function of mean spring temperatures.

Appendix S5. Logistic regression fit to normalized annual enhanced vegetation index (EVI) data, then back-transformed to the original data scale, from 2000 to 2024.

Appendix S6. Linear models to predict the day of year that peak flowering and tree leaf out will occur given a mean March temperature.

Appendix S7. Linear regressions were used to predict when a phenological event would occur given a mean March temperature for flowering and tree leaf out.

Appendix S8. Shade cloth significantly reduced the amount of light in the plots, while the sham control light condition was not significantly different from ambient conditions ($\chi^2 = 32.9$, df = 1, $P < 0.0001$).

Appendix S9. Shade cloth significantly decreased daytime temperature compared to ambient and sham control conditions ($\chi^2 = 12.59$, df = 1, $P < 0.0001$).

Appendix S10. Effects of observation day (center scaled), the number of days of extra shade, and the interaction between them in 2023 on the probability of senescence in 2023 and 2024.

Appendix S11. Effect of the number of days of extra shade in 2023 on the probability of flowering in 2024.

Appendix S12. List of GDD accumulation during each month and consecutive combinations of months considered as predictors of each phenological event.

Appendix S13. Historical occurrence of full days below freezing (Tmax ≤ 0°C) and for which the minimum temperature was below freezing (Tmin ≤ 0°C) at two sites in the Duke Forest, North Carolina.

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