




Extirpated prairie species demonstrate more variable phenological responses to warming than extant congeners

Meredith A. Zettlemoyer^{1,2,3,7} , Katarina Renaldi⁴, Michael D. Muzyka⁵, and Jennifer A. Lau^{1,2,6}

Manuscript received 13 July 2020; revision accepted 20 January 2021.

¹ Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060-9505, USA

² Department of Plant Biology, Michigan State University, East Lansing, MI 48824-6406, USA

³ Department of Plant Biology, University of Georgia, Athens, GA 30602-5004, USA

⁴ Michigan State University, East Lansing, MI 48824-6406, USA

⁵ Independent researcher, Kalamazoo, MI 49004-6683, USA

⁶ Department of Biology, Indiana University, Bloomington, IN 47405-7005, USA

⁷ Author for correspondence (e-mail: meredith.zettlemoyer25@uga.edu)

Citation: Zettlemoyer, M. A., K. Renaldi, M. D. Muzyka, and J. A. Lau. 2021. Extirpated prairie species demonstrate more variable phenological responses to warming than extant congeners. *American Journal of Botany* 108(6): 1–13.

doi:10.1002/ajb2.1684

PREMISE: Shifting phenology in response to climate is one mechanism that can promote population persistence and geographic spread; therefore, species with limited ability to phenologically track changing environmental conditions may be more susceptible to population declines. Alternatively, apparently nonresponding species may demonstrate divergent responses to multiple environmental conditions experienced across seasons.

METHODS: Capitalizing on herbarium records from across the midwestern United States and on detailed botanical surveys documenting local extinctions over the past century, we investigated whether extirpated and extant taxa differ in their phenological responses to temperature and precipitation during winter and spring (during flowering and the growing season before flowering) or in the magnitude of their flowering time shift over the past century.

RESULTS: Although warmer temperatures across seasons advanced flowering, extirpated and extant species differed in the magnitude of their phenological responses to winter and spring warming. Extirpated species demonstrated inconsistent phenological responses to warmer spring temperatures, whereas extant species consistently advanced flowering in response to warmer spring temperatures. In contrast, extirpated species advanced flowering more than extant species in response to warmer winter temperatures. Greater spring precipitation tended to delay flowering for both extirpated and extant taxa. Finally, both extirpated and extant taxa delayed flowering over time.

CONCLUSIONS: This study highlights the importance of understanding phenological responses to seasonal warming and indicates that extirpated species may demonstrate more variable phenological responses to temperature than extant congeners, a finding consistent with the hypothesis that appropriate phenological responses may reduce species' likelihood of extinction.

KEY WORDS climate change; extinction; flowering time; herbaria; historical data; phenology; prairie; temperature; spring warming; winter warming.

Phenology, or the timing of life history events, is critical to fitness and population persistence (Parmesan and Yohe, 2003; Cleland et al., 2007). While some species and populations exhibit little phenological plasticity (i.e., shift their phenology little in response to environmental variation), other species and populations respond strongly to temperature and precipitation (Visser and Both, 2005; Matthews and Mazer, 2016; Thackeray et al., 2016; Cremonese et al., 2017) and other environmental variables such as nutrient availability or competition (Smith et al., 2012; Xia and Wan, 2013; Du et al., 2019; Wang and Tang, 2019). Phenological plasticity may promote population growth (or limit population declines) in the face of climate change and has been associated with invasiveness and range size

(Crawley et al., 1996; DeFalco et al., 2007; Willis et al., 2008, 2010; Cleland et al., 2012; Pearson et al., 2012; Wolkovich et al., 2013; Lustenhouwer et al., 2018; Zettlemoyer et al., 2019b; Reeb et al., 2020), suggesting that species that are less phenologically plastic may be more at risk of population declines and eventual extirpation (Møller et al., 2008; Willis et al., 2008; Forrest and Miller-Rushing, 2010; Miller-Rushing et al., 2010).

If failure to adjust phenology is in fact correlated with population decline and extirpation (or if phenological plasticity correlates with population growth and persistence), species' phenological traits could be key predictors of local extinction risk, particularly under future climates. However, whether a failure to shift phenology is linked to

local extinction events remains uncertain. Traits of locally extinct species may correspond with historical responses of those species to environmental change, thereby informing predictions of extinction risk for these species across their ranges as well as for similar threatened species (Purvis et al., 2000; Collen et al., 2010). Herbarium specimens and other historical data sets such as repeated botanical surveys provide valuable records of local extinction events (Lang et al., 2018; Meineke et al., 2018; Zettlemoyer et al., 2019a). They span decades, include dozens of species replicates, and often contain species that have recently declined due to contemporary changes such as rising temperatures (Primack et al., 2004; Meineke et al., 2018). Individual plants contained in herbaria also provide a valuable record of how phenology shifts over time in response to climate (Willis et al., 2017; Ellwood et al., 2019). The time span and geographic area encompassed by herbarium specimens represent greater climatic variation than traditional observational or manipulative studies, thus providing a more complete picture of phenological shifts (Davis et al., 2015).

The bulk of studies investigating phenological plasticity have focused on phenological responses to temperature in the context of warming. However, a surprising number of species do not appear to advance flowering in response to warming (Rafferty and Ives, 2011; Cook et al., 2012; Parmesan and Hanley, 2015). Rather than being insensitive to rising temperature, species may respond to climate changes beyond spring warming such as changing precipitation patterns or winter warming, and temperate species may respond differently to environmental conditions in different seasons (Cook et al., 2012). Warmer winters and earlier snowfall generally accelerate phenology (Arft et al., 1999; Bjorkman et al., 2016). Drought can accelerate (Cremonese et al., 2017) or delay flowering (Cui et al., 2017), while heavy rainfall can extend the growing season later into the year (Schuster and Dukes, 2017). Finally, species may delay flowering in response to warming during some seasons, but advance flowering in response to warming in other seasons (Parmesan and Hanley, 2015). For example, 81 of 490 studied species from the United States and United Kingdom delayed flowering due to winter warming and advanced flowering due to spring warming, resulting in no observable overall phenological response to temperature (Cook et al., 2012). Phenological shifts in response to winter warming or shifts in precipitation also could prove maladaptive if it makes plants more susceptible to late frost events or other harsh environmental conditions (Elzinga et al., 2007). Failing to consider climatic conditions in seasons other than spring may thus result in underestimating the proportion of species able to shift their phenology in response to climate change.

We used herbarium specimens from across the midwestern United States to examine the flowering phenologies of eight confamilial (often congeneric) pairs of locally extinct (defined here as species that have disappeared from a particular county) (Zettlemoyer et al., 2019a) and extant prairie species. We investigated how locally extinct vs. extant species' phenologies have shifted over the last 155 years (ca. 1860–2015) and in response to temperature and precipitation experienced during spring (during flowering and the growing season before flowering) and winter. By considering the responses of both locally extinct and extant species, we investigated whether the inability to shift phenology in response to temperature or precipitation or over time is associated with local extinction. By considering responses to both spring and winter climatic variables, we addressed the importance of seasonal variation on phenology. We asked the following questions: (1) How does the phenology of locally extinct and extant species respond to temperature and precipitation experienced during the month of flowering, during the

growing season before flowering, and during the winter before flowering? (2) Does the phenology of locally extinct and extant species differ, and do those differences influence phenological responses to climate? (3) Has the phenology of locally extinct and extant species shifted over time? If the hypothesis that failure to adjust phenology contributes to population decline holds, we expect that locally extinct species' phenology will be less sensitive to temperature and precipitation than extant species.

MATERIALS AND METHODS

Study system

Kalamazoo County, covering 1492 km² in southwestern Michigan, United States, boasts a diverse and well-documented flora that was surveyed from ca. 1890–1940 (Hanes and Hanes, 1947) and was resurveyed from ca. 1994–2003 (McKenna, 2004). These historical records describe the presence/absence of native and introduced vascular plants in Kalamazoo County (note that no historical abundance data are available). Rare, prairie specialist species are at high risk of local extinction in the county (Zettlemoyer et al., 2019a). From these species, we selected 17 native prairie species in which one species within a family is locally extinct (“locally extinct”), while the other persists (“extant”) (7 pairs and 1 triplet; Table 1). The species selected represent all available pairs of native, perennial, prairie specialist forbs. Although the locally extinct species are not extinct across their entire range, they are rare species likely susceptible to population declines elsewhere (Daru et al., 2018). We limit our study taxa to prairie specialist species because they are at higher risk of loss than species that can persist in other habitat types (Kuussaari et al., 2009; Zettlemoyer et al., 2019a) and so that differences in habitat use (e.g., the ability to use other grossly different habitat types) would not be confounded with local extinction. However, we acknowledge that many other differences between taxa may be associated with local extinction (e.g., abundance or niche breadth differences beyond broad habitat type preferences). We selected confamilial pairs to control for trait differences due to taxonomic relatedness (van Kleunen et al., 2010), although we also test for and account for phylogenetic relatedness in our analyses (see below). Our approach is akin to comparisons of native vs. non-native species in that it identifies traits and responses associated with shifts in abundance or range size, in this case rarity and eventual extirpation (Murray et al., 2002; van Kleunen and Richardson, 2007). This combination of historical data sets documenting local extinctions and herbarium records for assessing phenology provides us with the capacity to test the hypothesis that phenology influences not only population declines but local extinctions.

Phenological data

We examined 1090 herbarium specimens from locations spanning the midwestern United States. Although this phenological scale (the Midwest) differs from the scale of extinction (Kalamazoo County), we included samples from the states of Michigan, Ohio, Indiana, Illinois, and Wisconsin to increase sample size (Appendix S1). Due to the difference in scale, we performed all analyses on the full data set and on specimens collected in Michigan. Because the results of the full and the spatially

restricted model were qualitatively similar, we present the results from the broader midwestern data set in the main text and report Michigan-only results in Appendix S2.

We visited the Michigan State University and University of Michigan herbaria to examine specimens in person; we found all other specimens online in the Consortium of Midwest Herbaria (<http://midwestherbaria.org/portal/>). We checked for changes in species names over time when we first examined the historical data sets. We excluded specimens that had no reproductive structures present. From each specimen, we recorded the number of buds, flowers, senescing flowers, and fruits. For species with flowering heads, we visually estimated the proportion of each head in bloom, multiplied that by the average number of flowers and buds per head, and calculated approximate numbers of flowers and buds. For each specimen, we also noted date and year collected (ranging from 1860–2015), and location (latitude and longitude).

Herbarium specimens, while useful in phenological studies, pose challenges due to biases (Daru et al., 2018). Specimens may have been more intensively collected in different years; however, we detect little evidence that any bias in collection efforts across time differed for locally extinct and extant species (status \times decade $F_{1,28} = 0.01, P = 0.91$). Because error in phenology estimated from a specimen can be high (Schmidt-Lebuhn et al., 2013), we examined at least 50 specimens per species (Panchen and Gorelick, 2017; Table 1; $N_{\text{locally extinct}} = 532$ and $N_{\text{extant}} = 484$ specimens; $N_{\text{total}} = 937$ specimens). To make the data set more robust than records from a single herbarium, we incorporated records from 27 herbaria across the Midwest.

We conducted all analyses on two response variables currently debated as the most appropriate phenological metrics from herbarium data: discrete phenology vs. a continuous estimate (Pearson, 2019). First, we used collection day of year as a proxy for flowering day of year (Day of Year [DOY]), following Park et al. (2018). However, herbarium specimens represent a discrete life stage and are often biased toward mature flowers (Schmidt-Lebuhn et al., 2013), resulting in later first-flowering estimates than detected in the field (Davis et al., 2015). To compare this discrete flowering date to a phenological estimate spanning budding to fruiting specimens, we also quantified phenology along a continuum (Moussus et al., 2010; Panchen and Gorelick, 2017). We calculated a developmental index (DI) for each specimen based on number of different reproductive structures as:

$$DI = \left(\frac{\text{No. of reproductive structures}}{1 (\text{No. buds}) + 2 (\text{No. flowers}) + 3 (\text{No. senescing flowers}) + 4 (\text{No. fruits})} \right) \cdot \ln(\text{DOY})$$

This DI accounts for variation in phenology by incorporating a continuum of phenological phases from budding to fruiting across specimens collected on varying dates. As a result of the coefficients preceding each floral stage (buds, flowers, senescing flowers, and fruits), species further along in their phenology (i.e., a greater proportion of fruits than buds; flowered earlier) have a lower DI. For example, a specimen with 10 buds collected on Julian day 200 has a lower DI (5.3) than a specimen with 10 buds collected on Julian day 300 (5.7) and a higher DI than a specimen collected on Julian day 200 but with 10 fruits

instead of buds (DI = 1.32). DI and DOY estimates were weakly correlated (Pearson's $r = 0.11, P = 0.0003$; correlations ranged from $r = -0.03$ to $r = 0.42$ across taxa).

Climate data

We used the CLIMOD database (<http://climod2.nrcr.cornell.edu/>) and the Applied Climate Information System (rcc-acis.org) to collect all temperature and precipitation data. Weather data was queried from the ACIS using the tidy, httr, sqldf, jsonlite, and lubridate packages in R v3.5.3 (Grolemund and Wickham, 2011; Ooms, 2014; Grothendieck, 2017; R Core Team, 2019; Wickham, 2019; Wickham and Henry, 2019). We used each specimen's date, year, and county of collection to search all available records from contemporaneously operating weather stations and calculated the mean of each climatic variable across weather stations.

Given that temperature commonly influences flowering time (Fitter and Fitter, 2002) and has been associated with phenological shifts in a wide range of both plant and animal taxa (Thackeray et al., 2016) and that precipitation can also influence flowering phenology (Schuster and Dukes, 2017), we collected temperature and precipitation data for three seasonal time periods: during flowering ($T_{\text{flowering}}$ or $P_{\text{flowering}}$), during the growing season (T_{growing} or P_{growing}), and during the winter before flowering (T_{winter} or P_{winter}). Each species was assigned a set range of dates for each seasonal metric based on its mean flowering date (e.g., the mean flowering date for *Monarda fistulosa* across the entire data set was 22 July, so all *Monarda fistulosa* specimens had a flowering season of 30 days before 22 July, a growing season of 1 April–22 July, and a winter season of November–March). Specifically, $T_{\text{flowering}}$ and $P_{\text{flowering}}$ were calculated as the means of daily temperatures ($^{\circ}\text{C}$) or precipitation (mm) at the specimen's location during the year in which a specimen was collected 30 days before the species' mean flowering date. T_{growing} and P_{growing} were calculated as the mean of daily temperatures ($^{\circ}\text{C}$) or precipitation (mm) experienced between 1 April (which we denote as approximately the beginning of the Midwest growing season based on average last frost dates [Michigan State University College of Agriculture and Natural Resources, 2019]) and the species' mean flowering date. T_{winter} and P_{winter} were calculated as the mean of daily temperatures ($^{\circ}\text{C}$) or precipitation (mm) during the winter season before flowering (November–March, based on when snowfall occurs across the region represented in this study [Appendix S3]).

Data analyses

We first tested for relationships between year, geography, and each individual climatic variable using linear models. We included $T_{\text{flowering}}$, T_{growing} , T_{winter} , $P_{\text{flowering}}$, P_{growing} , and P_{winter} as separate response variables and year, latitude, and longitude as predictor variables (interactions were never significant ($P \geq 0.1$) and removed from analyses) (Appendices S4, S5).

Because flowering time and shifts in abundance can be phylogenetically conserved (Willis et al., 2008), we tested for phylogenetic signal in extinction status, mean flowering time, and phenological sensitivity to each climatic variable ($T_{\text{flowering}}$, T_{growing} , T_{winter} , $P_{\text{flowering}}$, P_{growing} , P_{winter}). Sensitivity is defined here as the slope (days/ $^{\circ}\text{C}$ or cm) of locally extinct vs. extant species' overall phenological response to each climatic

TABLE 1. Species (abbreviation), plant family, mean flowering date, range of years represented by species samples, and sample size for the seven confamilial pairs and one triplet (*Penstemon*) included in this study. Superscript LE indicates a locally extinct species. Mean flowering date, year range, and sample size are provided for each species and for locally extinct vs. extant species overall.

Species	Family	Mean flowering date (Julian day)	Year range	Sample size
<i>Aster (Symphyotrichum) ericoides</i> (L.) G.L.Nesom (AE)	Asteraceae	21 Sept (264.23)	1888–2006	100
<i>Aster (Symphyotrichum) sericeus</i> Vent. (AS) ^{LE}	Asteraceae	16 Sept (259.84)	1860–2008	99
<i>Baptisia tinctoria</i> (L.) Vent. (BT)	Fabaceae	17 July (198.20)	1870–2015	50
<i>Baptisia bracteata</i> Muhl. ex Elliott (BB) ^{LE}	Fabaceae	27 May (147.10)	1981–2010	100
<i>Eryngium yuccifolium</i> Michx. (EY)	Apiaceae	27 July (208.86)	1880–2010	50
<i>Thaspium trifoliatum</i> (L.) A.Gray (TT) ^{LE}	Apiaceae	12 June (163.40)	1876–1998	50
<i>Liatris aspera</i> Michx. (LA)	Asteraceae	3 Sept (246.45)	1902–2011	49
<i>Liatris punctata</i> Hook. (LP) ^{LE}	Asteraceae	26 Aug (238.74)	1980–2014	39
<i>Monarda fistulosa</i> L. (MF)	Lamiaceae	22 July (203.97)	1889–2015	108
<i>Pycnanthemum tenuifolium</i> Schrad. (PT) ^{LE}	Lamiaceae	4 Aug (216.63)	1896–2012	50
<i>Penstemon digitalis</i> Nutt. ex Sims (PD)	Plantaginaceae	25 June (176.03)	1892–2011	48
<i>Penstemon hirsutus</i> (L.) Willd. (PH) ^{LE}	Plantaginaceae	10 June (161.69)	1890–2008	99
<i>Penstemon pallidus</i> Small (PP) ^{LE}	Plantaginaceae	3 June (154.69)	1895–2005	50
<i>Ratibida pinnata</i> (Vent.) Barnhart (RP)	Asteraceae	27 July (208.76)	1887–2011	50
<i>Ratibida columnifera</i> (Nutt.) Woot. & Standl. (RC) ^{LE}	Asteraceae	14 July (195.11)	1896–2011	50
<i>Silphium perfoliatum</i> L. (SP)	Asteraceae	8 Aug (220.09)	1882–2013	50
<i>Silphium terebinthinaceum (compositum)</i> Elliot non. Jacq. (ST) ^{LE}	Asteraceae	16 Aug (228.76)	1891–2011	48
Locally extinct species		18 July (199.47)	1872–2014	532
Extant species		13 Aug (225.56)	1880–2015	484

variable (Park et al., 2018; calculated from the linear mixed models described below). We obtained a phylogenetic tree from Phylomatic (phylodiversity.net/phyloomatic) using the Zanne et al. (2014) tree (Appendix S6). We tested for phylogenetic conservatism using the phylogenetic function in the package picante in R (v1.3-0; Kembel et al., 2010; R Core Team, 2019). The phylogenetic function measures Blomberg's K , a test statistic that compares the observed phylogenetic signal in a trait with the signal under a Brownian motion model of trait evolution. $K = 0$ indicates random evolution; $K = 1$ indicates trait conservatism; $K > 1$ indicates species being more similar than expected (Blomberg et al., 2003). The function also measures PIC.variance.P, which tests for greater phylogenetic signal than expected; traits with PIC.variance.P ≤ 0.05 show non-random phylogenetic signal (Kembel et al., 2010). Since phenological sensitivity to temperature ($T_{\text{flowering}}$, T_{growing} , T_{winter}) was phylogenetically conserved (Appendix S7), we performed phylogenetic generalized least squares (PGLS) analyses for each measure of phenological sensitivity with Brownian motion models of trait evolution (Garland et al., 1993; Martins and Hansen, 1997). We incorporated the constructed phylogeny (Appendix S6) into the covariance structure using the ape package (v. 1.3-4; Paradis, 2012). Each of the six phenological sensitivity measurements was included as a separate response variable, and status was included as the predictor variable. Models were fit using the gls function in the nlme package (v.3.1-119; Pinheiro et al., 2015).

To test for shifts in phenology due to variation in temperature or precipitation and whether extant and locally extinct species differ in phenological responses to climate, we used random slope linear mixed models to determine the effects of $T_{\text{flowering}}$, T_{growing} , T_{winter} , $P_{\text{flowering}}$, P_{growing} , P_{winter} , status (locally extinct vs. extant), and interactions of status with each climatic variable (e.g., status $\times T_{\text{flowering}}$, status $\times T_{\text{growing}}$, etc.) on flowering phenology (response variables: DOY or DI). Models were fit using Type III ANOVA with Satterthwaite's approximation of denominator degrees of freedom using the lmerTest package in R (v3.1-3; Kuznetsova et al., 2017). We included latitude and longitude as covariates to control for spatial variation in phenological responses from cooler, high latitude populations to warmer,

low latitude populations and from wetter eastern populations to drier western populations, respectively. Because of the high number of potential model terms, we did not include all interactions and instead only included interactions between latitude, longitude, climatic variables, and status when there was a biologically reasonable hypothesis for the interaction based on prior studies (Appendix S8). We fit random slopes for each species' response to each climatic variable (i.e., each species varied in its slope to reflect species-specific phenological responses to climate) (Bliese and Ployhart, 2002). We then used backward elimination to simplify the two models (one for DOY and another for DI), sequentially removing predictors with the highest P -value greater than α ($\alpha = 0.1$) until no collinear predictors were included and all P -values were greater than α . Results for full models prior to elimination are provided in Appendix S9. We provide Akaike information criterion values for sequential models for DOY produced via backward elimination in Appendix S10 (procedures for DI models were similar). The final model for DOY included status, latitude, longitude, $T_{\text{flowering}}$, T_{growing} , T_{winter} , $P_{\text{flowering}}$, P_{growing} , status $\times T_{\text{flowering}}$, status $\times T_{\text{winter}}$, latitude $\times T_{\text{growing}}$, latitude $\times T_{\text{winter}}$, latitude $\times P_{\text{growing}}$, and longitude $\times T_{\text{winter}}$ as predictor variables. The final model for DI included status, latitude, longitude, $T_{\text{flowering}}$, T_{growing} , T_{winter} , P_{growing} , status \times longitude, status $\times T_{\text{flowering}}$, status $\times T_{\text{growing}}$, latitude $\times T_{\text{growing}}$, longitude $\times T_{\text{flowering}}$, and longitude $\times T_{\text{winter}}$ as predictor variables.

Earlier-flowering species often respond more strongly to climate change (Park et al., 2018). To determine whether any phenological differences between locally extinct and extant taxa could be attributed to relative flowering time, we re-conducted the analyses described above including each species' mean flowering date (calculated as mean DOY) as a covariate. We again included hypothesized interactions between mean flowering date (MFD), latitude, longitude, status, and climatic variables (Appendix S8). The final model for DOY included status, latitude, longitude, $T_{\text{flowering}}$, T_{growing} , T_{winter} , $P_{\text{flowering}}$, P_{growing} , MFD, status $\times T_{\text{flowering}}$, latitude \times MFD, longitude \times MFD, $T_{\text{flowering}}$ \times MFD, T_{winter} \times MFD, $P_{\text{flowering}}$ \times MFD, latitude \times $P_{\text{flowering}}$, longitude $\times T_{\text{growing}}$, and longitude $\times P_{\text{flowering}}$ as predictor variables.

Since these are complex models with many interactions, we also examined DOY and DI as a function of latitude and longitude then conducted downstream analyses on the residuals, thereby removing variation associated with geography. Using this method, individuals with a negative residual value flower earlier than expected after controlling for geography and vice versa. Models included the six climatic variables, status, MFD, and their interactions as predictor variables and the random slopes described above. Results are quantitatively similar, so we present residual models in Appendix S11. We chose to present DOY and DI models in the main text because they explicitly test for differences in phenological responses across space, which we expect based on spatial variation in responses to climate change (Bradshaw and Holzapfel, 2006).

To test for phenological changes over time independently from responses to climate (Panchen and Gorelick, 2017), we used general linear models with DOY or DI included as separate response variables and year, status, and their interactions as predictor variables and latitude and longitude as covariates. As above, we fit random slopes for each species' phenological response over time.

To further investigate how locally extinct vs. extant taxa differ in phenological responses to climate, we examined differences in phenological responses to year and climatic variables within each confamilial pair of locally extinct and extant species by fitting separate models for each species pair. We included DOY and DI as two separate response variables, and status, $T_{flowering}$, $T_{growing}$, T_{winter} , $P_{flowering}$, $P_{growing}$, P_{winter} latitude, longitude, the interactions of status with each climatic variable status \times latitude, and status \times longitude as predictor variables. Mean flowering date was not included as a covariate due to its collinearity with status. To investigate how locally extinct vs. extant taxa differ in phenological responses over time, we again fit separate models for each species pair; we included DOY and DI as separate response variables, status, year, and the interaction of status \times year as predictor variables, and latitude and longitude as covariates. We applied a Bonferroni correction for multiple comparisons.

RESULTS

Phylogenetic conservatism of local extinction and flowering time

Mean flowering time and phenological sensitivity to each temperature variable ($T_{flowering}$, $T_{growing}$, and T_{winter}) are phylogenetically conserved (Appendix S7, all $P \leq 0.06$), while sensitivity to precipitation is not phylogenetically conserved (Appendix S7; all $P \geq 0.1$). Not surprisingly, given how species were selected for this study (congeneric or confamilial pairs of locally extinct and extant species), local extinction is randomly distributed across phylogeny in this data set ($K = 0.008$, $P = 0.99$), similarly to

extinction events across Kalamazoo County (Zettlemoyer et al., 2019a).

Locally extinct vs. extant species' responses to temperature and precipitation

Locally extinct and extant species differed in the consistency of their phenological responses to warming (Fig. 1). Under warmer temperatures during the month of flowering ($T_{flowering}$), both locally extinct and extant species accelerated flowering on average. However, locally extinct species demonstrated more variable responses to warmer temperatures during flowering. Overall, this variability resulted in locally extinct species appearing to accelerate their phenologies less in response to $T_{flowering}$, on average, than extant species (DOY: status $\times T_{flowering}$ $\chi^2_{1,255.43} = 29.85$, $P \leq 0.0001$; extant response = -4.98 ± 0.51 days/ $^{\circ}$ C; locally extinct response = -1.41 ± 0.62 days/ $^{\circ}$ C; Appendix S12; Fig. 2A, B; full model $\chi^2_{1,184.32} = 0.04$, $P = 0.83$; Appendix S9). Using DI as the response variable, extant species advanced flowering while locally extinct species, on average, did not shift flowering under warmer temperatures during flowering (DI: status $\times T_{flowering}$ $\chi^2_{1,457.08} = 32.03$, $P \leq 0.0001$; extant response = -0.04 ± 0.01 days/ $^{\circ}$ C; locally extinct response = -0.004 ± 0.006 days/ $^{\circ}$ C; Appendices S12–14; full model $\chi^2_{1,481.81} = 4.63$, $P = 0.03$; Appendix S9). This difference in the mean responses of locally extinct and extant taxa was largely due to more consistent advances in flowering time

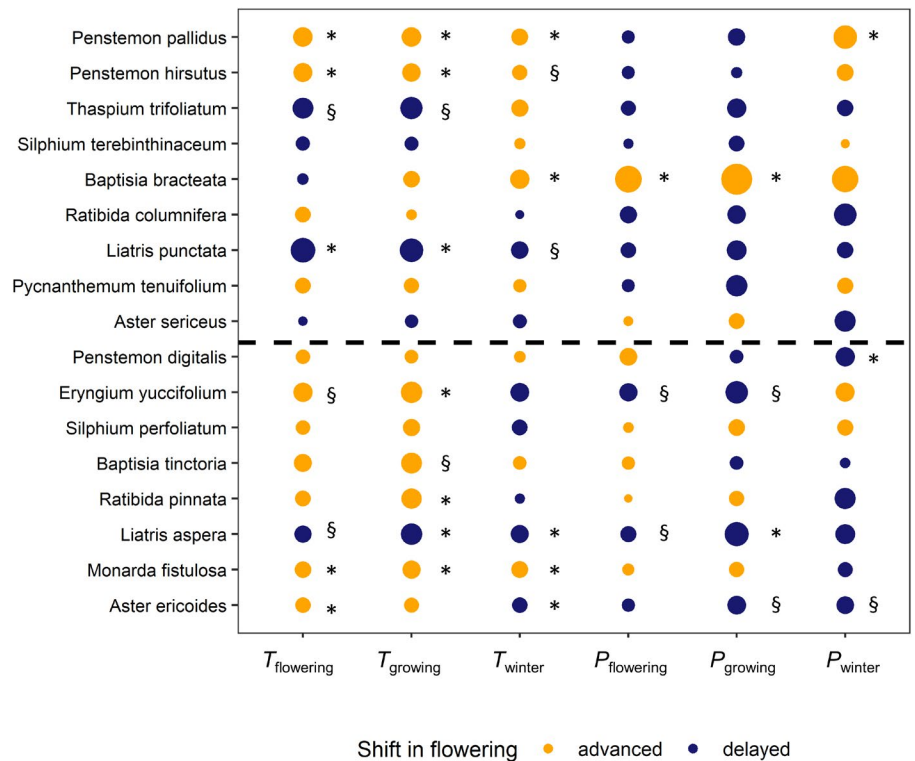


FIGURE 1. Locally extinct and extant species vary in the direction and magnitude of their phenological responses to climate. Effect of climatic variables ($T_{flowering}$, $T_{growing}$, T_{winter} , $P_{flowering}$, $P_{growing}$, P_{winter}) on flowering phenology (day of year) of locally extinct and extant species. Dot size represents the number of days shifted per 1°C or per 1 mm precipitation. Blue circles indicate delayed flowering; orange circles indicate advanced flowering. Species above the black dashed line are locally extinct; species below the line are extant. * $P \leq 0.05$, § $P \leq 0.1$.

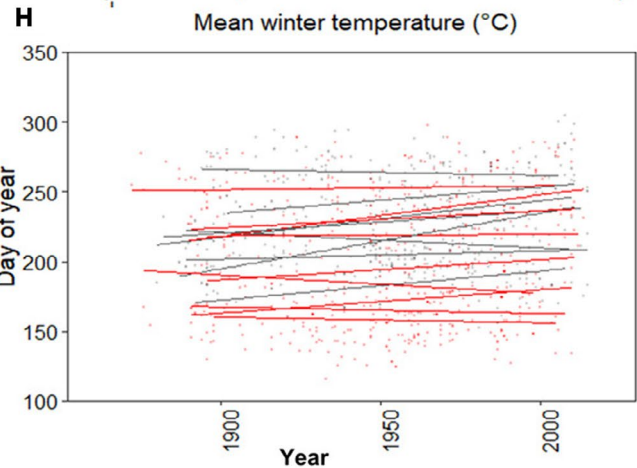
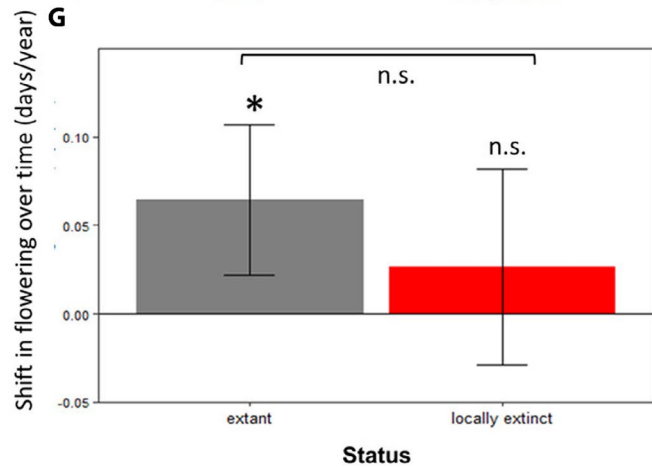
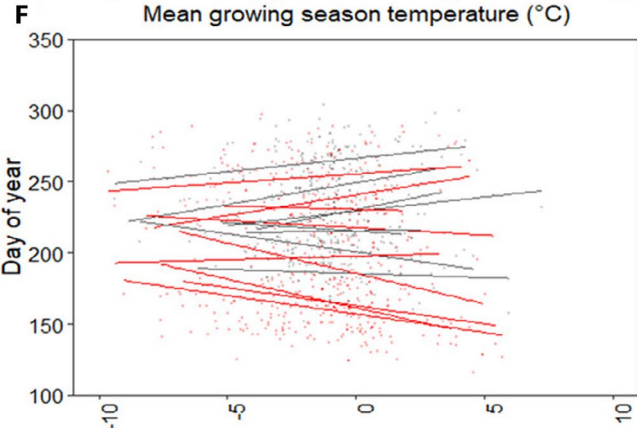
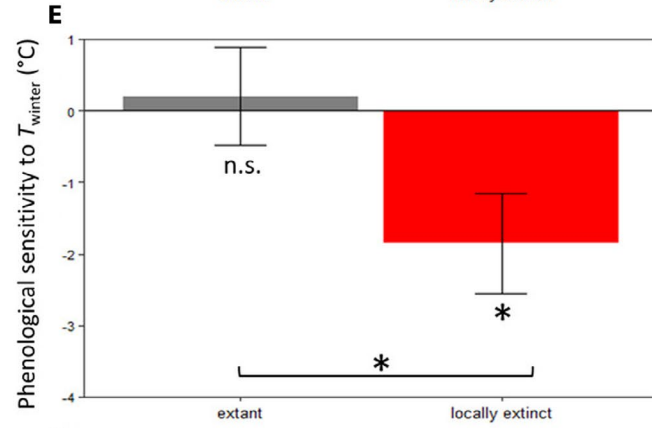
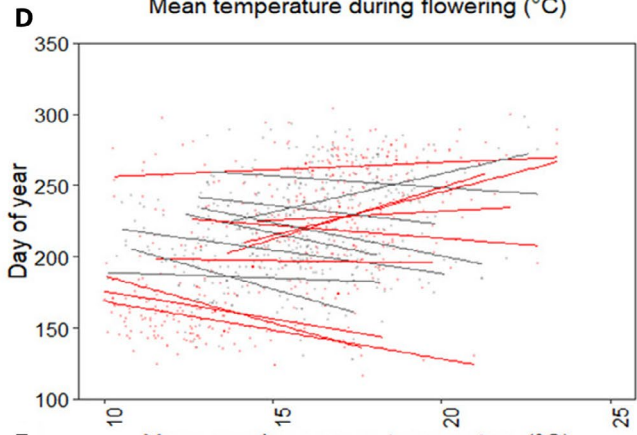
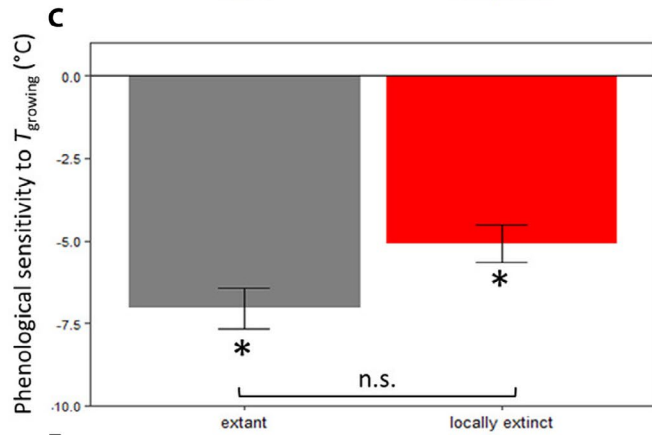
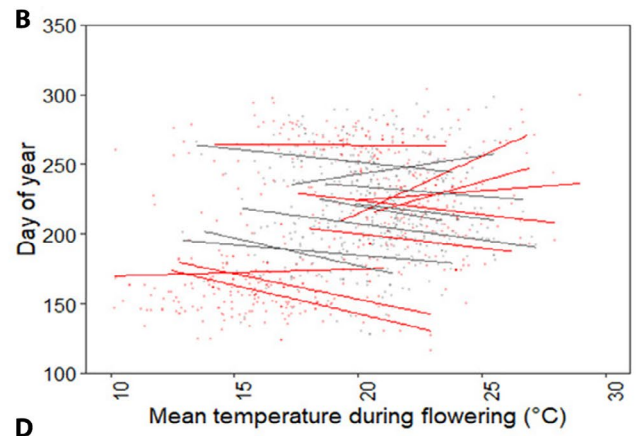
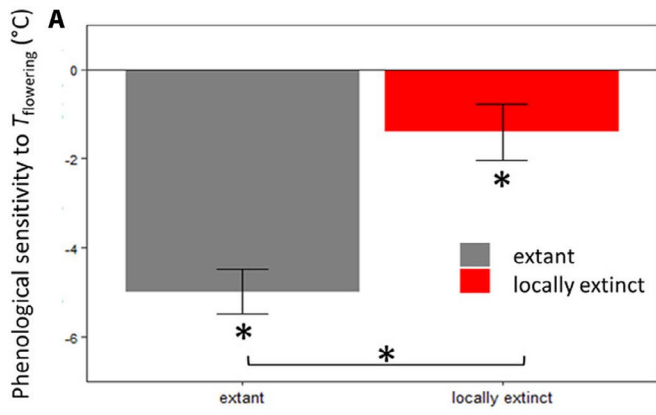


FIGURE 2. Locally extinct and extant species differ in the magnitude of their phenological responses to temperature and over time. Left: Phenological sensitivity to (A) $T_{\text{flowering}}$, (C) T_{growing} , and (E) T_{winter} ($^{\circ}\text{C}$), and (G) year in locally extinct (red) vs. extant (grey) species. Sensitivity is defined here as the slope (days/ $^{\circ}\text{C}$ or year) of locally extinct vs. extant species' overall phenological response to temperature and over time (Park et al., 2018). Positive values indicate delayed flowering; negative values indicate advanced flowering. Asterisks over a bar indicate a significant response to temperature; asterisks over a bracket indicate a significant difference between locally extinct and extant species; "n.s." indicates a nonsignificant response. Note that mean responses can be influenced by both variation in phenological sensitivity (the magnitude of response) and variation in the direction of phenological response. Right: Effect of (B) $T_{\text{flowering}}$, (D) T_{growing} , (F) T_{winter} , and (H) year on flowering phenology (day of year) of all species included in this study. Red and gray lines show locally extinct and extant species, respectively. We fit random slopes for each species' response to $T_{\text{flowering}}$, T_{growing} , and T_{winter} .

for extant taxa. Seven of eight extant species advanced flowering under warmer temperatures during the month of flowering (two significantly advanced; $P \leq 0.05$), while for locally extinct species, only four of nine advanced flowering (two significantly) and another five tended to delay flowering under warmer temperatures (Figs. 1, 3A; Appendix S15). When controlling for phylogeny, locally extinct and extant species did not differ in their phenological sensitivity to $T_{\text{flowering}}$, although extant species still tended to advance their flowering earlier in response to $T_{\text{flowering}}$ more so than locally extinct species (Appendix S16).

Under warmer growing season temperatures, both locally extinct and extant species advanced flowering by an average of 3.14 ± 0.99 days/ $^{\circ}\text{C}$ (DOY: T_{growing} $\chi^2_{1, 749.88} = 21.69$, $P \leq 0.0001$; Appendix S12; Fig. 2C, D; full model $\chi^2_{1, 926.15} = 1.40$, $P = 0.24$; Appendix S9). Twelve of 17 (5 of 9 locally extinct and 7 of 8 extant) species tended to advance flowering under warmer growing season temperatures (five significantly advanced) (Appendix S15; Figs. 1, 3B). Using DI, on average, extant species advanced flowering, while locally extinct species did not shift flowering under warmer growing season temperatures (status $\times T_{\text{growing}}$ $\chi^2_{1, 709.41} = 32.57$, $P \leq 0.0001$; extant response = -0.05 ± 0.01 days/ $^{\circ}\text{C}$; locally extinct response = -0.005 ± 0.007 days/ $^{\circ}\text{C}$; Appendices S12–S14; full model $\chi^2_{1, 647.27} = 4.17$, $P = 0.04$; Appendix S9). This difference in the mean responses of locally extinct and extant taxa is again likely due to inconsistent advances in flowering time for locally extinct taxa (Appendix S14B). After accounting for phylogeny, locally extinct and extant species tended to differ in their phenological responses to T_{growing} (status $t = 1.87$, $P = 0.08$; Appendix S16).

Under warmer winter temperatures, locally extinct species generally advanced flowering, while extant species did not consistently respond to warmer winter temperatures (DOY: status $\times T_{\text{winter}}$ $\chi^2_{1, 980.83} = 12.38$, $P = 0.0005$; extant response = 0.20 ± 0.68 days/ $^{\circ}\text{C}$; locally extinct response = -1.86 ± 0.69 days/ $^{\circ}\text{C}$; Appendix S12; Fig. 2E, F; full model $\chi^2_{1, 905.75} = 0.84$, $P = 0.35$; Appendix S9). Six of nine locally extinct species tended to advance flowering under warmer winter temperatures (two significantly advanced), while for extant species, two species significantly delayed and another three tended to delay flowering under warmer winter temperatures (Appendices S14, S15; Figs. 1, 3C). Even after accounting for phylogeny, locally extinct and extant species differed in their responses to winter temperatures, with locally extinct species advancing flowering more so than their extant congeners under warmer winter temperatures (status $t = -2.15$, $P = 0.04$; Appendix S16). However, using DI, both locally extinct and extant species accelerated flowering under warmer winter temperatures by an average of 0.34 ± 0.15 days/ $^{\circ}\text{C}$ (DI: T_{winter} $\chi^2_{1, 9715.50} = 6.46$, $P = 0.03$; Appendices S12, S13; full model $\chi^2_{1, 939.17} = 4.89$, $P = 0.03$; Appendix S9).

Locally extinct species flowered earlier than extant species (status: DOY $\chi^2_{1, 85.10} = 38.99$, $P \leq 0.0001$; DI $\chi^2_{1, 869.03} = 4.84$, $P = 0.03$; Appendix S12; full model $\chi^2_{1, 936.41} = 0.54$, $P = 0.46$; Appendix S9). Early-flowering species tended to advance flowering more than

late-flowering species under warmer temperatures during flowering and winter (DOY: MFD $\times T_{\text{flowering}}$ $\chi^2_{1, 470.47} = 2.84$, $P = 0.09$; MFD $\times T_{\text{winter}}$ $\chi^2_{1, 56.83} = 2.61$, $P = 0.1$; Appendix S12; full model: MFD $\times T_{\text{flowering}}$ $\chi^2_{1, 574.66} = 2.33$, $P = 0.12$; MFD $\times T_{\text{winter}}$ $\chi^2_{1, 924.27} = 1.61$, $P = 0.20$; Appendix S9; Fig. 2B). When including MFD as a covariate, locally extinct species, on average, still advanced flowering less in response to warmer temperatures during flowering than extant species (status $\times T_{\text{flowering}}$: DOY $\chi^2_{1, 142.66} = 4.27$, $P = 0.04$; DI $\chi^2_{1, 142.66} = 15.89$, $P < 0.0001$; locally extinct DOY response = -3.34 ± 4.03 days/ $^{\circ}\text{C}$ (DI response = -0.08 ± 0.04); extant DOY response = -5.52 ± 2.45 days/ $^{\circ}\text{C}$ (DI response = -0.14 ± 0.10); Appendix S12; full model $\chi^2_{1, 407.18} = 1.46$, $P = 0.23$; Appendix S9). However, including MFD as a covariate eliminated the previously observed differences between extant and locally extinct species' responses to winter warming (status $\times T_{\text{winter}}$ removed from models including MFD; full model $\chi^2_{1, 920.60} = 0.01$, $P = 0.90$). Instead, both locally extinct and extant species tended to advance flowering under warmer winter temperatures by 4.97 ± 3.12 days/ $^{\circ}\text{C}$ (T_{winter} : DOY $\chi^2_{1, 63.07} = 2.54$, $P = 0.1$; DI $\chi^2_{1, 931.40} = 4.42$, $P = 0.04$; overall DI response = -0.32 ± 0.15 days/ $^{\circ}\text{C}$). This result suggests that differences in mean flowering time between locally extinct and extant species explain differences between locally extinct and extant taxa in phenological responses to winter warming but not warming during flowering.

Greater precipitation during flowering and the growing season delayed flowering by 0.16 ± 0.70 and 1.44 ± 1.17 days/mm, respectively (DOY: $P_{\text{flowering}}$ $\chi^2_{1, 772.63} = 3.77$, $P = 0.05$; P_{growing} $\chi^2_{1, 782.80} = 2.94$, $P = 0.08$; Appendix S12; full model: $P_{\text{flowering}}$ $\chi^2_{1, 78.27} = 2.51$, $P = 0.12$; P_{growing} $\chi^2_{1, 785.82} = 0.27$, $P = 0.60$; Appendix S9; Fig. 4; Appendices S17, S18). We also detected a pattern for early-flowering species to advance flowering under increased precipitation during flowering (DOY: MFD $\times P_{\text{flowering}}$ $\chi^2_{1, 133.96} = 8.52$, $P = 0.004$; full model $\chi^2_{1, 925.33} = 5.09$, $P = 0.02$), but this effect was driven by one early-flowering species, *Baptisia bracteata*. Locally extinct and extant taxa did not differ in their responses to precipitation (status \times precipitation variables were never included in simplified models; full model status \times precipitation variables all $P > 0.6$). However, when phylogenetic relationships are accounted for, locally extinct and extant species differed in their phenological sensitivity to precipitation during flowering and during the growing season (status: $P_{\text{flowering}}$ $t = 5.01$, $P = 0.0002$; P_{growing} $t = 3.04$, $P = 0.008$). Specifically, locally extinct delayed flowering, while extant species advanced flowering under increased precipitation during flowering and during the growing season (Appendix S16).

Phenological shifts over time and variation across space

Locally extinct and extant species both delayed flowering over time (year: DOY $\chi^2_{1, 1006.01} = 10.32$, $P = 0.001$; Appendix S12; Fig. 2G, H; but DI $\chi^2_{1, 1006.01} = 0.08$, $P = 0.78$). Over space, specimens from southern latitudes advanced flowering under

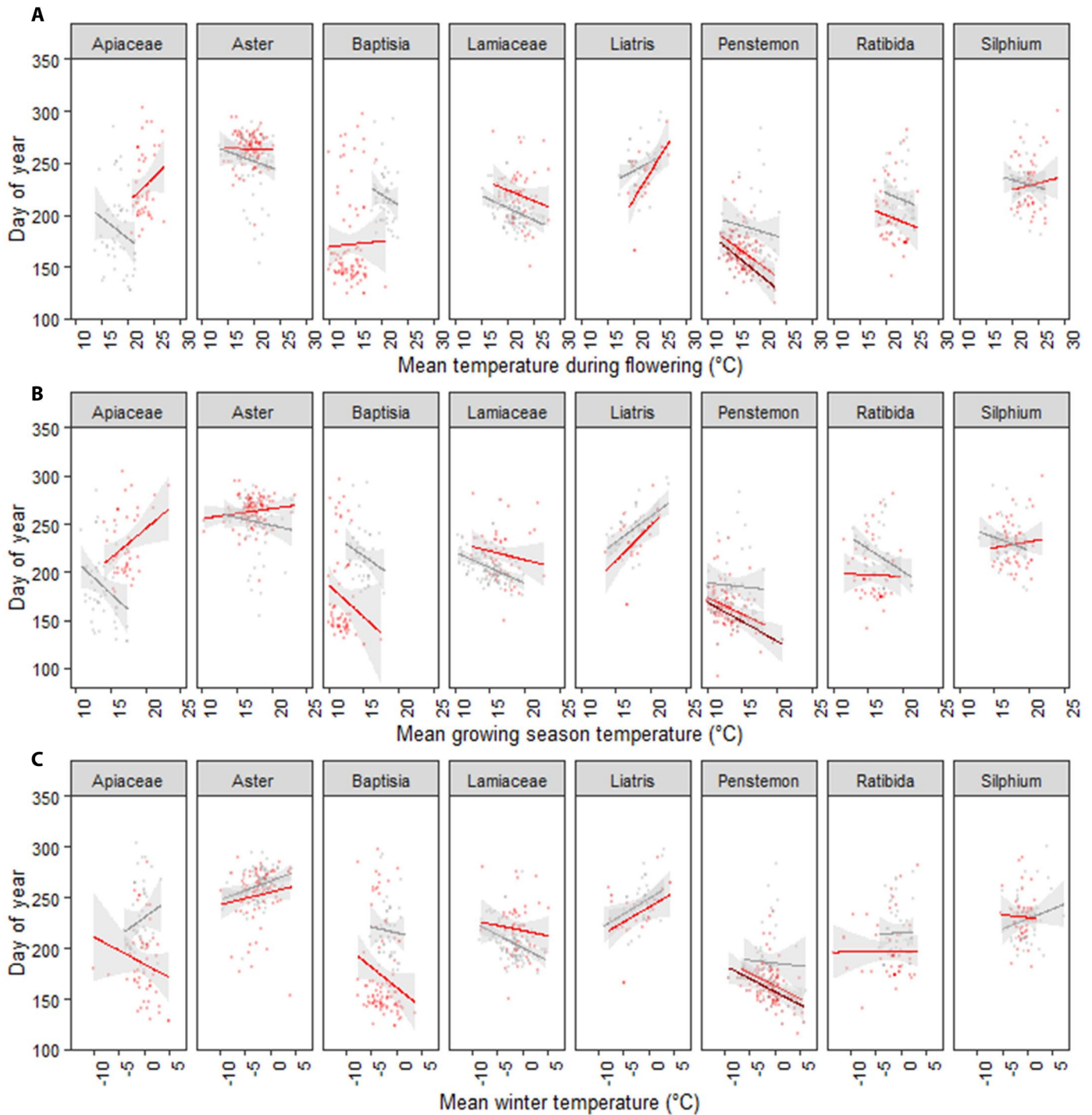


FIGURE 3. Effect of (A) $T_{\text{flowering}}$ (B) T_{growing} and (C) T_{winter} (°C) on flowering phenology (day of year) of all species pairs (and 1 triplet; *Penstemon*) included in this study. Each panel represents one congeneric (or confamilial) pair. Red and gray lines show locally extinct and extant species within a pair, respectively. Gray areas represent 95% confidence intervals.

warmer growing season temperatures more so than those from northern latitudes (DOY: latitude $\times T_{\text{growing}}$ $\chi^2_{1, 771.50} = 13.17$, $P = 0.0003$; DI: $\chi^2_{1, 949.16} = 6.88$, $P = 0.009$; Appendix S12; full model $\chi^2_{1, 903.43} = 3.85$, $P = 0.05$; Appendix S9). This was true for six of the 17 species studied, while for another six species, southern populations delayed flowering more so than northern populations (Appendix S19). Early-flowering species flowered later,

while late-flowering species flowered earlier in more northern and western populations (MFD \times latitude: DOY $\chi^2_{1, 734.47} = 5.19$, $P = 0.02$; DI $\chi^2_{1, 775.78} = 8.92$, $P = 0.003$; MFD \times longitude: DOY $\chi^2_{1, 907.62} = 11.86$, $P = 0.0005$; Appendix S12; full model: MFD \times latitude $\chi^2_{1, 898.24} = 3.64$, $P = 0.05$; MFD \times longitude $\chi^2_{1, 779.85} = 4.51$, $P = 0.03$; Appendix S9). Other interactions with geography were species- and model-specific (Appendix S12).

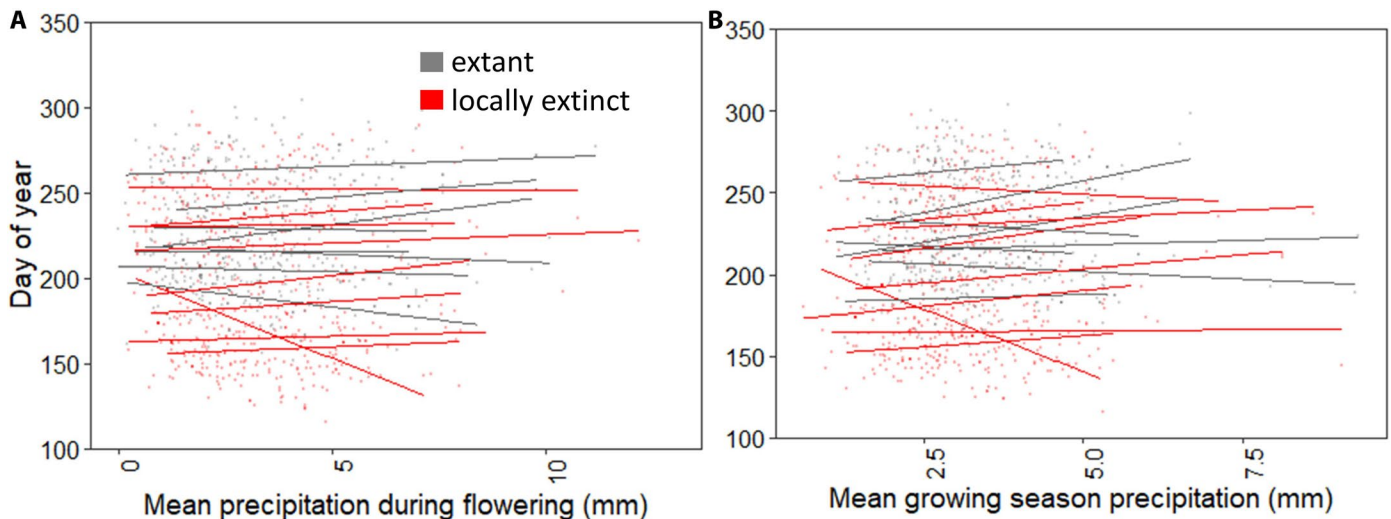


FIGURE 4. Effect of (A) $P_{\text{flowering}}$ and (B) P_{growing} (mm) on flowering phenology (day of year) of all species included in this study. Red and gray lines show locally extinct and extant species, respectively. We fit random slopes for each species' response to $P_{\text{flowering}}$ and P_{growing} . The species advancing flowering in both panels is locally extinct *Baptisia bracteata*.

DISCUSSION

Consistent with previous findings of advancing phenology under climate warming, the 17 native prairie species studied here advanced flowering under warmer spring and winter temperatures. However, locally extinct species advanced flowering less consistently in response to warmer spring temperatures during flowering than extant species. In other words, locally extinct species' responses to warmer spring temperatures are more variable than those of extant species. These results support previous work positing that species that do not respond appropriately to rising spring temperatures may experience population declines (Willis et al., 2008, 2010; Miller-Rushing et al., 2010; Thackeray et al., 2016) and further suggest that understanding idiosyncrasies in species' responses to climate change could be important for conservation efforts. In contrast, locally extinct species advanced flowering more than extant species as winter temperatures warmed. This result illustrates the increasing need to examine warming across seasons when examining phenological shifts. This study, by highlighting differences in the consistency of phenological responses between locally extinct and extant taxa, implicates phenology as a potential response to global change underlying local extinction events.

In our study, species advanced flowering under spring temperatures (during flowering and the growing season), but locally extinct species on average advanced flowering less than extant species. Two things could explain the reduced average response of locally extinct species to spring warming. First, locally extinct species' responses appear more idiosyncratic. While extant species demonstrated consistent responses to spring warming, locally extinct species were just as likely to delay as to advance flowering in response to spring warming. Second, locally extinct species might be less phenologically plastic to spring temperature. Lack of phenological responses have been detected in species ranging from North American grasslands and mountains to the United Kingdom to the Mongolian steppe (Bradley et al., 1999; Dunnell and Travers, 2011; Cook et al., 2012, Liancourt et al., 2012), and there are several hypotheses for why temperate species might not shift their phenology under rising temperatures. First, other abiotic factors such as soil moisture

or precipitation may regulate flowering more than temperature (Körner and Basler, 2010; Caffarra et al., 2011; Crimmins et al., 2011). In our study, increasing amounts of spring precipitation generally delayed flowering, similar to phenological patterns detected in other forbs such as *Trillium obtusum* (Matthews and Mazer, 2016). Alternatively, some species might be more sensitive to static cues such as photoperiod. For instance, early-flowering species (here, locally extinct) might respond to photoperiod to prevent growth in the winter or early spring (Pau et al., 2011). Second, warming might affect early- and late-flowering species differently (Sherry et al., 2007; Cornelius et al., 2013; CaraDonna et al., 2014; Park and Schwartz, 2015) and locally extinct species typically flowered earlier than extant species in our data set. In our case, we find that earlier-flowering species advanced flowering under warmer temperatures during flowering more than later-flowering species, so earlier flowering is unlikely to explain the observed reduced phenological responses among locally extinct taxa. Third, species may delay flowering if they do not experience sufficient winter chilling requirements (vernalization): if winter warming delays vernalization, species may flower later in the spring (Schwartz and Hanes, 2010; Yu et al., 2010; Cook et al., 2012; Hart et al., 2014). Finally, variable temperatures, altered snowmelt timing, and frost events may select for delayed phenology if accelerated flowering leads to increased risk of reproductive consequences under novel environmental conditions (Elzinga et al., 2007; Cooper et al., 2011; Rafferty et al., 2013; Iler et al., 2019). However, in separate analyses testing whether the absolute value of phenological sensitivity to each temperature metric ($T_{\text{flowering}}$, T_{growing} , and T_{winter}) differed between locally extinct and extant species, locally extinct and extant species did not differ in the magnitude of their phenological responses to temperature (Appendix S20). This finding suggests that the locally extinct and extant species studied here are similarly plastic to temperature in terms of their flowering phenology, but the direction of locally extinct species' phenological responses are more variable.

While locally extinct species were more variable in their phenological responses to spring temperatures than their extant

congeners, they advanced flowering in response to winter warming more consistently than extant species. As described above, flowering earlier under warmer winter temperatures can expose plants to disproportionately harsh abiotic conditions from earlier snowmelt as plants are exposed to cold air and soil temperatures, resulting in negative consequences for growth, survival, and reproduction (Rosa et al., 2015; CaraDonna and Bain, 2016). Since the early-flowering, locally extinct species studied here accelerated flowering in response to warmer winters, they may have experienced such losses and subsequent population declines. This finding illustrates the need to examine species' responses to seasonal temperatures, as failures to identify phenological responses across seasons may incorrectly identify some species' phenology as insensitive to climate. For example, Cook et al. (2012) reanalyzed species responses to spring vs. winter warming in species previously found to exhibit non-responding phenology in the United Kingdom and United States. They found that 17% of species advanced flowering under spring warming and delayed flowering under winter warming, but these patterns were obscured by previous use of a single environmental variable. Similarly, winter warming decreased the effects of spring warming on phenological advancement in the Alps (Vitasse et al., 2018) and Switzerland (Güsewell et al., 2017). However, none of these studies addressed whether species' responses to warm spring vs. winter temperatures had consequences for population persistence. Here, locally extinct species are more consistent in their responses to winter rather than spring warming. This result suggests that rare or locally extinct species' phenology might respond to different seasonal temperatures than more common species. We might have misidentified one set of taxa as unresponsive to climate had we examined either winter or spring temperature independently. Ultimately, variable responses to different environmental conditions could lead to the conclusion that species do not respond to warming temperatures when in fact they respond to diverse temperatures cues across seasons.

Earlier flowering is often associated with species success (Willis et al., 2010; Cleland et al., 2012), particularly in invasive species (Willis et al., 2010; Wolkovich et al., 2013; Zettlemoyer et al., 2019b). In contrast, our study reveals that locally extinct species flower earlier than extant species. Early-flowering species advanced flowering under warmer spring temperatures more so than later-flowering species, similar to other studies in the Great Plains (Sherry et al., 2007) and the Rocky Mountains (CaraDonna et al., 2014) (although other studies find that early-flowering species delay flowering relative to late-flowering species [Cornelius et al., 2013; Park and Schwartz, 2015; Park et al., 2018]). Our finding suggests that changes in phenology (and subsequent effects on population dynamics) might be affected by historical flowering times. Our data set is skewed toward the Asteraceae, which generally flower later in the season. We reran analyses including only one pair of Asteraceae at a time: in two of four models, the interaction of status $\times T_{\text{winter}}$ became nonsignificant, and in all four models, effects of monthly and growing season precipitation became nonsignificant (data not shown). It is possible that these late-flowering species respond more strongly to precipitation across the growing season, although this result could also be due to low power.

Comparing two phenological metrics

We used two phenological response variables to compare discrete (day of year) vs. continuous (developmental index, DI) estimates of

phenology. These two metrics yielded qualitatively similar results in terms of the direction but not magnitude of phenological response. Specifically, using DI as a metric of phenology, we found that while extant species advance flowering in response to both spring temperatures ($T_{\text{flowering}}$ and T_{growing}), the variability in locally extinct species' responses resulted in the appearance of no average phenological shift in response to spring warming. Day of year represents a "binary method" wherein all specimens with at least buds are included. However, this method can have higher variance because it does not account for phenological events spanning longer periods of time (Panchen and Gorelick, 2017). It also skews results toward mature flowers (Schmidt-Lebuhn et al., 2013), which can result in later estimates of phenology. In contrast, DI is likely more conservative because it accounts for phenology along a continuum. Indeed, our DI results resulted in smaller estimates of phenological sensitivity with lower standard error (e.g., flowering advanced by almost 5 days per °C, ± 0.5 days, for extant species using DOY, but by only 0.04 ± 0.01 days using DI). DI estimates were also clustered toward the earlier end of the continuum (Appendix S13), suggesting that DI might have better accounted for specimens that were still early in their flowering phenology (i.e., had fewer developed flowers).

CONCLUSIONS

On average, we find that native prairie species advanced their flowering phenologies in response to both spring and winter warming, a combination of environmental cues that is rarely examined together (Cook et al., 2012). However, locally extinct species accelerated phenology less consistently than extant species in response to warmer springs but advanced flowering more than extant species in response to warmer winters. This result highlights a need to examine phenological responses to multiple environmental cues to accurately predict phenological shifts under climate change. Our results also indicate that locally extinct species' responses to temperature are more idiosyncratic than those of extant species.

Locally extinct species flowered earlier than extant species, suggesting that historical flowering time might contribute to subsequent population declines. By examining historical responses to changing climates in recently extinct species, this study not only supports the hypothesis that ineffective phenological responses correlate with population declines but suggests that phenology plays a role in contemporary extinction events. Our use of locally extinct vs. extant species provides a novel framework for examining mechanisms that might influence species declines and extirpations across a species' range. However, further work is needed to determine whether delayed or nonresponsive phenology is associated with lower fitness or population growth rates (Miller-Rushing et al., 2010; Iler et al., 2019). We note that many other traits likely influence population declines and local extinction and that climate change is only one possible cause of extinction. This caveat is highlighted by the fact many locally extinct species responded similarly to extant taxa, advancing flowering greatly under spring warming and minimally responding or even delaying flowering in response to winter warming. Ongoing experimental work is investigating the role of climate warming, nitrogen enrichment, and herbivory on population demography in reintroduced populations of these same locally extinct vs. extant prairie species. As these species are rare prairie specialists, likely at-risk throughout their range, understanding their phenological trends where they will persist may prove a useful tool in their conservation.

ACKNOWLEDGMENTS

The authors thank S.E. Johnson for help collecting temperature data and A. Fryday and R. Rabaler for collections access. L. Brudvig, E. Zipkin, the Lau and Haddad labs, and several anonymous reviewers provided valuable feedback on this manuscript. Support for this work was provided by the National Science Foundation Research Experience for Undergraduates program (K.R.) (Award #1757530). This is Kellogg Biological Station publication #2147.

AUTHOR CONTRIBUTIONS

M.A.Z. and K.R. designed the study, K.R. collected the data, J.A.L. provided input on phenological metrics, and M.D.M. wrote code to access weather databases. M.A.Z. wrote the manuscript, and all authors contributed to revisions.

DATA AVAILABILITY

All data generated for this study are available in the Dryad Digital Repository: <https://doi.org/10.5061/dryad.x0k6djhhn> (Zettlemoyer et al., 2021).

SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1. Herbaria information.

Appendix S2. Effects of climate and year on phenology (Michigan specimens).

Appendix S3. Snowfall.

Appendix S4. Correlations between climate, year, and geography.

Appendix S5. Effects of time and geography on climate.

Appendix S6. Phylogeny of study species.

Appendix S7. Phylogenetic signal of extinction status and phenology.

Appendix S8. Model hypotheses.

Appendix S9. Effects of climate and year on phenology (full models).

Appendix S10. Backward elimination.

Appendix S11. Effects of climate and year on phenology (residuals).

Appendix S12. Effects of climate and year on phenology (DOY and DI).

Appendix S13. Effects of climate and year on developmental index.

Appendix S14. Species-specific effects of temperature on developmental index.

Appendix S15. Species-specific phenological responses to climate and over time.

Appendix S16. Phylogenetic analyses of the effect of status on phenological sensitivity to climate.

Appendix S17. Species-specific effects of precipitation on phenology (DOY).

Appendix S18. Species-specific effects of precipitation on phenology (DI).

Appendix S19. Effects of latitude and growing season temperature on phenology.

Appendix S20. Absolute values of phenological plasticity in locally extinct and extant species.

LITERATURE CITED

- Arft, A. M., M. D. Walker, J. Gurevitch, J. M. Alatalo, M. S. Bret-Harte, M. Dale, M. Diemer, et al. 1999. Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs* 69: 4991–5110.
- Bjorkman, A. D., S. C. Elmendorf, A. L. Beamish, M. Vellend, and G. H. R. Henry. 2016. Contrasting effects of warming and increased snowfall on Arctic tundra plant phenology over the past two decades. *Global Change Biology* 21: 4651–4661.
- Bliese, P. D., and R. E. Ployhart. 2002. Growing modeling using random coefficient models: model building, testing, and illustrations. *Organizational Research Methods* 5: 362–387.
- Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. *Evolution* 57: 717–745.
- Bradley, N. L., A. C. Leopold, J. Ross, and W. Huffaker. 1999. Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences, USA* 96: 9701–9704.
- Bradshaw, W. E., and C. Holzapfel. 2006. Climate change. Evolutionary response to rapid climate change. *Science* 9: 1477–1478.
- Caffarra, A., A. Donnelly, I. Chuine, and M. B. Jones. 2011. Modelling the timing of *Betula pubescens* budburst. I. Temperature and photoperiod: a conceptual model. *Climate Research* 46: 147–157.
- CaraDonna, P. J., A. M. Iler, and D. Inouye. 2014. Shifts in flowering phenology reshape a subalpine plant community. *Proceedings of the National Academy of Sciences, USA* 111: 4916–4921.
- CaraDonna, P. J., and J. A. Bain. 2016. Frost sensitivity of leaves and flowers of subalpine plants is related to tissue type and phenology. *Journal of Ecology* 104: 55–64.
- Cleland, E. E., I. Chuine, A. Menzel, H. A. Mooney, and M. D. Schwartz. 2007. Shifting plant phenology in response to global change. *Trends in Ecology and Evolution* 22: 357–365.
- Cleland, E. E., J. M. Allen, T. M. Crimmins, J. A. Dunne, S. Pau, S. E. Travers, E. S. Zavaleta, and E. M. Wolkovich. 2012. Phenological tracking enables positive species responses to climate change. *Ecology* 93: 1765–1771.
- Collen, B., A. Purvis, and G. M. Mace. 2010. When is a species really extinct? Testing extinction inference from a sighting record to inform conservation assessment. *Diversity and Distributions* 16: 755–764.
- Cook, B. I., E. M. Wolkovich, and C. Parmesan. 2012. Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences, USA* 109: 9000–9005.
- Cooper, E. J., S. Dullinger, and P. Semenchuk. 2011. Late snowmelt delays plant development and results in lower reproductive success in the High Arctic. *Plant Science* 180: 157–167.
- Cornelius, C., A. Leingärtner, B. Hoiss, J. Krauss, I. Steffan-Dewenter, and A. Menzel. 2013. Phenological response of grassland species to manipulative snowmelt and drought along an altitudinal gradient. *Journal of Experimental Botany* 64: 241–251.

- Crawley, M. J., P. H. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 351: 1251–1259.
- Cremonese, E., G. Filippa, M. Galvagno, C. Sinisacalco, L. Oddi, U. M. di Cella, and M. Migliavacca. 2017. Heat wave hinders green wave: The impact of climate extreme on the phenology of a mountain grassland. *Agricultural and Forest Meteorology* 247: 320–330.
- Crimmins, T. M., M. A. Crimmins, and C. D. Bertelsen. 2011. Onset of summer flowering in a 'Sky Island' is driven by monsoon moisture. *New Phytologist* 191: 468–479.
- Cui, T., L. Martz, and X. Guo. 2017. Grassland phenology response to drought in the Canadian prairies. *Remote Sensing* 9: 1258–1279.
- Daru, B. H., D. W. Park, R. B. Primack, C. G. Willis, D. S. Barrington, T. J. S. Whitfield, T. J. Seidler, et al. 2018. Widespread sampling biases in herbaria revealed from large-scale digitalization. *New Phytologist* 217: 939–955.
- Davis, C. C., C. G. Willis, B. Connolly, C. Kelly, and A. M. Ellison. 2015. Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany* 102: 1599–1609.
- DeFalco, L. A., G. C. J. Fernandez, and R. S. Novak. 2007. Variation in the establishment of a non-native annual grass influences competitive interactions with Mojave Desert perennials. *Biological Invasions* 9: 293–307.
- Du, Y., B. Yang, S. C. Chen, and K. Ma. 2019. Diverging shifts in spring phenology in response to biodiversity loss in a subtropical forest. *Journal of Vegetation Science* 30: 1175–1183.
- Dunnell, K. L., and S. E. Travers. 2011. Shifts in the flowering phenology of the northern Great Plains: Patterns over 100 years. *American Journal of Botany* 98: 935–945.
- Ellwood, E. R., K. D. Pearson, and G. Nelson. 2019. Emerging frontiers in phenological research. *Applications in Plant Science* 7: e1234.
- Elzinga, J. A., A. Atlan, A. Biere, L. Gigord, A. E. Weis, and G. Bernasconi. 2007. Time after time: flowering phenology and biotic interactions. *Trends in Ecology and Evolution* 22: 432–439.
- Fitter, A. H., and R. S. R. Fitter. 2002. Rapid changes in flowering time in British plants. *Science* 296: 1689–1691.
- Forrest, J., and A. J. Miller-Rushing. 2010. Toward a synthetic understanding of the role of phenology in ecology and evolution. *Philosophical Transactions of the Royal Society B, Biological Sciences* 365: 3101–3112.
- Garland, T., W. S. Dickerman, C. M. Janis, and J. A. Jones. 1993. Phylogenetic analysis of covariance by computer simulation. *Systematic Biology* 42: 265–292.
- Grolemund, G., and H. Wickham. 2011. Dates and times made easy with lubridate. *Journal of Statistical Software* 40: 1–25.
- Grothendieck, G. 2017. sqldf: manipulate R data frames using SQL. R package version 0.4.11. Website: <https://cran.r-project.org/web/packages/sqldf/sqldf.pdf>.
- Güsewell, S., R. Furrer, R. Gehrig, and B. Pierratgalla. 2017. Changes in temperature sensitivity of spring phenology with recent climate warming in Switzerland are related to shifts of the preseason. *Global Change Biology* 23: 5189–5202.
- Hanes, C. R., and F. N. Hanes. 1947. Flora of Kalamazoo County, Michigan: vascular plants. Anthoensen Press, Portland, ME, USA.
- Hart, R., J. Salick, S. Ranjitkar, and J. Xu. 2014. Herbarium specimens show contrasting phenological responses to Himalayan climate. *Proceedings of the National Academy of Sciences, USA* 111: 10615–10619.
- Iler, A. M., A. Compagnoni, D. W. Inouye, J. L. Williams, P. J. CaraDonna, A. Anderson, and T. E. X. Miller. 2019. Reproductive losses due to climate change-induced earlier flowering are not the primary threat to plant population viability in a perennial herb. *Journal of Ecology* 107: 1931–1943.
- Kembel, S. W., P. D. Cowan, M. R. Helmus, W. K. Cornell, H. Morlon, D. D. Ackerly, S. P. Blomberg, and C. O. Webb. 2010. Picante: R tools for integrating phylogenies and ecology. *Bioinformatics* 26: 1463–1464.
- Körner, C., and D. Basler. 2010. Phenology under global warming. *Science* 327: 1461–1462.
- Kuusaaari, M., R. Bommarco, R. K. Heikkinen, A. Helm, J. Krauss, R. Lindborg, E. Öckinger, et al. 2009. Extinction debt: a challenge for biodiversity conservation. *Trends in Ecology and Evolution* 24: 564–571.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest package: tests in linear mixed effects models. *Journal of Statistical Software* 82: 1–26.
- Lang, P. L. M., F. M. Willems, J. F. Scheepens, H. A. Burbano, and O. Bossdorf. 2018. Using herbaria to study global environmental change. *New Phytologist* 221: 110–122.
- Liancourt, P., L. Spence, B. Boldgiv, A. Lkhagva, B. R. Helliker, B. B. Casper, and P. S. Petraitis. 2012. Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology. *Ecology* 93: 815–824.
- Lustenhouwer, N., R. A. Wilschut, J. L. Williams, W. H. van der Putten, and J. M. Levine. 2018. Rapid evolution of phenology during range expansion with recent climate change. *Global Change Biology* 24: 534–544.
- Martins, E. P., and T. F. Hansen. 1997. Phylogenies and the comparative method: a general approach to incorporating phylogenetic information into the analysis of interspecific data. *American Naturalist* 98: 778–789.
- Matthews, E. R., and S. J. Mazer. 2016. Historical changes in flowering phenology are governed by temperature × precipitation interactions in a widespread herb in western North America. *New Phytologist* 210: 157–167.
- McKenna, D. D. 2004. Flora and vegetation of Kalamazoo County, Michigan. *Michigan Botanist* 43: 137–359.
- Meineke, E. K., C. C. Davis, and T. J. Davies. 2018. The unrealized potential of herbaria for global change biology. *Ecological Monographs* 88: 505–525.
- Michigan State University College of Agriculture and Nature Resources. 2019. Frost free date table. Website: <https://tinyurl.com/yy9efkn3> [accessed 1 June 2019].
- Miller-Rushing, A. J., T. T. Høye, D. W. Inouye, and E. Post. 2010. The effects of phenological mismatches on demography. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 365: 3177–3186.
- Møller, A. P., D. Rubolini, and E. Lehikoinen. 2008. Populations of migratory bird species that did not show a phenological response to climate change are declining. *Proceedings of the National Academy of Sciences, USA* 105: 16195–16200.
- Moussis, J., R. Julliard, and F. Jiguet. 2010. Featuring 10 phenological estimators using simulated data. *Methods in Ecology and Evolution* 1: 140–150.
- Murray, B. R., P. H. Thrall, A. M. Gill, and A. B. Nicotra. 2002. How plant life-history and ecological traits relate to species rarity and commonness at varying spatial scales. *Austral Ecology* 27: 291–310.
- Ooms, J. 2014. The jsonlite package: a practical a consistent mapping between JSON data and R objects. arXiv:1403.2805 [Preprint].
- Panchen, Z. A., and R. Gorelick. 2017. Prediction of Arctic plant phenological sensitivity to climate change from historical records. *Ecology and Evolution* 7: 1325–1338.
- Paradis, E. 2012. Analysis of phylogenetics and evolution with R, 2nd ed. Springer, NY, NY, USA.
- Park, D. S., I. Breckheimer, A. C. Williams, E. Law, A. M. Ellison, and C. C. Davis. 2018. Herbarium specimens reveal substantial and unexpected variation in phenological sensitivity across the eastern United States. *Philosophical Transactions of the Royal Society, B, Biological Sciences* 374: 20170394.
- Park, I. W., and M. D. Schwartz. 2015. Long-term herbarium records reveal temperature-dependent changes in flowering phenology in the southeastern USA. *International Journal of Biometeorology* 59: 347–355.
- Parmesan, C., and M. E. Hanley. 2015. Plants and climate change: complexities and surprises. *Annals of Botany* 116: 849–864.
- Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 421: 37–42.
- Pau, S., E. M. Wolkovich, B. I. Cook, T. J. Davies, N. J. B. Kraft, K. Bolmgren, J. L. Betancourt, and E. E. Cleland. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* 17: 3633–3643.
- Pearson, D. R., Y. K. Ortega, and S. J. Sears. 2012. Darwin's naturalization hypothesis up-close: Intermountain grassland invaders differ morphologically and phenologically from native community dominants. *Biological Invasions* 14: 901–913.
- Pearson, K. D. 2019. Spring- and fall-flowering species show diverging phenological responses to climate in the Southeast USA. *International Journal of Biometeorology* 63: 481–492.
- Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R Core Team. 2015. nlme: linear and nonlinear mixed effects models. R package version 3.1-119.

- Primack, D., C. Imbres, R. B. Primack, A. J. Miller-Rushing, and P. del Tredici. 2004. Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany* 91: 1260–1274.
- Purvis, A., J. L. Gittleman, G. Cowlshaw, and G. M. Mace. 2000. Predicting extinction risk in declining species. *Proceedings of the Royal Society, B, Biological Sciences* 26: 1947–1952.
- Rafferty, N. E., P. J. CaraDonna, L. A. Burkle, A. M. Iler, and J. L. Bronstein. 2013. Phenological overlap of interacting species in a changing climate: an assessment of available approaches. *Ecology and Evolution* 3: 3183–3193.
- Rafferty, N. E., and A. R. Ives. 2011. Effects of experimental shifts in flowering phenology on plant-pollinator interactions. *Ecology Letters* 14: 69–74.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Website: <http://www.R-project.org/>.
- Reeb, R. A., I. Acevedo, J. M. Heberling, B. Isaac, and S. E. Kuebbing. 2020. Nonnative old-field species inhabit early season phenological niches and exhibit unique sensitivity to climate. *Ecosphere* 11: e03217.
- Rosa, R. K., S. F. Oberbauer, G. Starr, I. P. La Puma, E. Pop, L. Ahlquist, and T. Baldwin. 2015. Plant phenological responses to a long-term experimental extension of growing season and soil warming in the tussock tundra of Alaska. *Global Change Biology* 21: 4520–4532.
- Schmidt-Lebuhn, A. N., N. J. Knerr, and M. Kessler. 2013. Non-geographic collecting biases in herbarium specimens of Australian daisies (Asteraceae). *Biodiversity and Conservation* 22: 905–919.
- Schuster, M. J., and J. S. Dukes. 2017. Rainfall variability counteracts N addition by promoting invasive *Lonicera maackii* and extending phenology in prairie. *Ecological Applications* 27: 1555–1563.
- Schwartz, M. D., and J. M. Hanes. 2010. Continental-scale phenology: warming and chilling. *International Journal of Climatology* 30: 1595–1598.
- Sherry, R. A., X. Zhou, S. Gu, J. A. Arnone, D. S. Schimel, P. S. Verburg, L. L. Wallace, and Y. Luo. 2007. Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences, USA* 104: 198–202.
- Smith, J. G., W. Sconiers, M. J. Spasojevic, I. W. Ashton, and K. N. Suding. 2012. Phenological changes in alpine plants in response to increased snowpack, temperature, and nitrogen. *Arctic, Antarctic, and Alpine Research* 44: 135–142.
- Thackeray, S. J., P. A. Henrys, D. Hemming, J. R. Bell, M. S. Botham, S. Burthe, P. Helauoet, et al. 2016. Phenological sensitivity to climate across taxa and trophic levels. *Nature* 535: 241–245.
- van Kleunen, M., and D. M. Richardson. 2007. Invasion biology and conservation biology: time to join forces to explore the link between species traits and extinction risk and invasiveness. *Progress in Physical Geography* 31: 447–450.
- van Kleunen, M., E. Weber, and M. Fischer. 2010. A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecology Letters* 13: 235–245.
- Visser, M., and C. Both. 2005. Shifts in phenology due to global climate change: the need for a yardstick. *Proceedings of the Royal Society, B, Biological Sciences* 272: 2561–2569.
- Vitasse, Y., C. Signarbieux, and Y. H. Fu. 2018. Global warming leads to more uniform spring phenology across elevations. *Proceedings of the National Academy of Sciences, USA* 115: 1004–1008.
- Wang, C., and Y. Tang. 2019. Responses of plant phenology to nitrogen addition: a meta-analysis. *Oikos* 128: 1243–1253.
- Wickham, H. 2019. httr: tools for working with URLs and HTTP. R package version 1.4.1. Website: <https://cran.r-project.org/web/packages/httr/index.html/>.
- Wickham, H., and L. Henry. 2019. tidyr: easily tidy data with ‘spread’ and ‘gather’ functions. R package version 0.8.3. Website: <https://cran.rproject.org/web/packages/tidyr/index.html>.
- Willis, C. G., E. R. Ellwood, R. B. Primack, C. C. Davis, J. D. Pearson, A. S. Gallinat, J. M. Yost, et al. 2017. Old plants, new tricks: phenological research using herbarium specimens. *Trends in Ecology and Evolution* 32: 531–546.
- Willis, C. G., R. B. Primack, A. J. Miller-Rushing, and C. C. Davis. 2008. Phylogenetic patterns of species loss in Thoreau’s woods are driven by climate change. *Proceedings of the National Academy of Sciences, USA* 105: 17029–17033.
- Willis, C. G., B. Ruhfel, R. B. Primack, A. J. Miller-Rushing, J. B. Losos, and C. C. Davis. 2010. Favorable climate change response explains non-native species’ success in Thoreau’s woods. *PLoS One* 5: e8878.
- Wolkovich, E. M., T. J. Davies, H. Schaffer, E. E. Cleland, B. I. Cook, S. E. Travers, C. G. Willis, and C. C. Davis. 2013. Temperature-dependent shifts in phenology contribute to the success of exotic species with climate change. *American Journal of Botany* 100: 1407–1421.
- Xia, J., and S. Wan. 2013. Independent effects of warming and nitrogen addition on plant phenology in the Inner Mongolian steppe. *Annals of Botany* 111: 1207–1217.
- Yu, H., E. Luedeling, and J. Xu. 2010. Winter and spring warming result in delayed spring phenology on the Tibetan plateau. *Proceedings of the National Academy of Sciences, USA* 107: 22151–22156.
- Zanne, A. E., D. C. Tank, W. K. Cornwell, J. M. Eastman, S. A. Smith, R. G. FitzJohn, D. J. McGlenn, B. C. O’Meara, et al. 2014. Three keys to the radiation of angiosperms into freezing environments. *Nature* 506: 89–92.
- Zettlemoyer, M. A., D. D. McKenna, and J. A. Lau. 2019a. Species characteristics affect local extinctions. *American Journal of Botany* 106: 547–559.
- Zettlemoyer, M. A., E. H. Schultheis, and J. A. Lau. 2019b. Phenology in a warming world: differences between native and non-native plant species. *Ecology Letters* 22: 1253–1263.
- Zettlemoyer, M. A., K. Renaldi, M. D. Muzyka, and J. A. Lau. 2021. Data from Extirpated prairie species demonstrate more variable phenological responses to warming than extant congeners. *Dryad Digital Repository* <https://doi.org/10.5061/dryad.x0k6djhhn>.