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Nonnative old-field species inhabit early season phenological niches and exhibit unique sensitivity to climate

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Abstract. Native and nonnative plant species can exhibit differences in the timing of their reproductive phenology and their phenological sensitivity to climate. These contrasts may influence species' interactions and the invasion potential of nonnative species; however, a limited number of phenology studies expressly consider phenological mismatches among native and nonnative species over broad spatial or temporal scales. To fill this knowledge gap, we used two complementary approaches: First, we quantified the flowering phenology of native and nonnative plants at five old-field sites across a spatially extensive range of eastern North America. Second, we used herbarium records to compare the sensitivity of flowering and fruiting phenology to climate across a 114-yr time period in a subset of common old-field species in southwestern Pennsylvania. Across the study region, nonnatives reproduced substantially earlier in the growing season than natives, suggesting that nonnatives occupy a unique phenological niche (0.55 months earlier flowering across the North American study sites; 50.1 d earlier flowering and 17.5 d earlier fruiting in southwestern Pennsylvania). Both natives and nonnatives advanced their reproductive phenology between 1900 and 2014 but exhibited contrasting phenological sensitivity to climate factors. During the flowering stage of phenology, nonnatives were more sensitive to changes in precipitation than natives and generally delayed flowering in wetter years. Nonnative plants had greater sensitivity and advanced fruiting when the month preceding fruiting was warmer, while native plants had greater sensitivity and advanced fruiting when the three-month period preceding fruiting was warmer. Our findings suggest that nonnative old-field species occupy an earlier phenological niche relative to native species, which may facilitate their invasion into old-field communities. However, given the different sensitivities of native and nonnative plants to climate factors, present-day patterns of phenology are likely to shift with future climate changes, potentially leading to novel species interactions that may influence the outcomes of invasion.

Key words: climate change; flowering; fruiting; herbarium; invasion; North America; old-field; phenology.

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INTRODUCTION

Phenology, or the timing of life cycle events, is a tightly regulated process that influences species' interactions and community composition (Schwartz 2003, Yang and Rudolf 2010, Burghardt et al. 2015, Chmura et al. 2019). The strength of competition between plant species increases or decreases at different times in the growing season, based on the relative timing of phenology (Carothers and Jaksić 1984, Chesson 2000, Schofield et al. 2018). When two plant species with similar resource requirements have overlapping phenology, spatially explicit mechanisms determine the outcomes of competition, as predicted by traditional models of competition (Tilman 1994). However, when species have nonoverlapping phenology, temporally explicit mechanisms, including priority effects of vacant niche effects, may also influence the outcomes of competition (Wolkovich and Cleland 2011).

Within invaded plant communities, the phenology of competitors may impact native and nonnative plants during the reproductive phases of their life cycle (Wolf et al. 2017). The fitness of plant species hinges on their ability to acquire sufficient resources to ensure the viability of pollen and seed embryos. Resource competition leading up to and during reproduction influences these outcomes. The timing of reproductive phenology can thus shape direct competition between species, via nutrient and light resources, and indirect competition for pollination services (Waser 1978, Weiner 1988, Stone et al. 1998). Thus, more research on the timing of phenology among co-occurring native and nonnative species across broad spatial or temporal scales is needed to further our understanding of how phenological niches shape competition and invasion success.

Plant communities that contain both native and nonnative species likely exhibit unique phenological patterns. Because native and nonnative species evolved in different regions, they may have unique phenological timing and climate sensitivity that is adapted to their environment of origin (Godoy et al. 2009, Tang et al. 2016). Resulting phenological differences between native and nonnative species in-turn affect competitive outcomes (Godoy and Levine 2014, Gioria et al. 2018). For example, nonnatives can fill an early phenological niche and exert seasonal priority effects on co-occurring natives. In this scenario, nonnatives may initiate growth, access soil and light resources, and reproduce earlier than native species, which could potentially reduce resource availability and competitively exclude natives with later phenologies (Dickson et al. 2012, Alexander and Levine 2019). Conversely, nonnatives that exploit vacant temporal niches throughout the growing season may have no competitive impact on native species. Instead, native and nonnative species may coexist if the resources consumed by nonnatives do not ultimately affect resource availability for natives. This can occur if nonnative species are active early or late in the growing season, relative to native species, and have neutral effects on the resource environment (Wolkovich and Cleland 2011, Fridley 2012, Godoy and Levine 2014).

Nonnative species are predicted to have greater phenological sensitivity to climate than native species for two reasons (Willis et al. 2010, Wolkovich and Cleland 2011, Wolkovich et al. 2013, Zettlemoyer et al. 2019). First, greater environmental sensitivity may allow nonnative species to maintain their fitness across a range of environments, which favors expansion within the introduced range (Richards et al. 2006). Second, greater environmental sensitivity may allow nonnatives to rapidly take advantage of favorable conditions in their introduced environment (Richards et al. 2006). If nonnative species currently occupy different phenological niches and exhibit greater phenological sensitivity to changing climates, we may find increases or decreases in the phenological overlap between native and nonnative species as future climate conditions shift. In order to make accurate predictions about native and nonnative phenology under future climate conditions, it may be useful to explore how historic annual variation in the phenology of native and nonnative species is driven by their sensitivity to climate.

We conducted a study comparing the phenology of native and nonnative plant species in old-field ecosystems. Old-field ecosystems, characterized as formerly cultivated land that has been abandoned, are an ideal study system in which to compare native and nonnative species phenology for a variety of reasons: (1) There are a large number of co-occurring native and nonnative species present (Chytrý et al. 2008, Kuebbing et al. 2014), (2) old fields are subjected to frequent anthropogenic disturbance and are often vulnerable to invasion by nonnative plants (Cramer et al. 2008), (3) old-field species, given their close proximity to human settlement, are well-represented in the herbarium record, and (4) native and nonnative species present in old fields have a wide geographic distribution, making this study applicable to much of eastern North America. Additionally, old-field species exhibit reproductive phenology that collectively span the entire growing season, thus enabling the conclusions drawn from this study to be broadly generalizable toward native and nonnative forbs in old-field ecosystems.

Here, we present two datasets describing the reproductive phenology of old-field plant species. We combine flowering phenology data on a comprehensive list of 250 old-field species throughout eastern North America with 924 herbarium specimens of 11 old-field species collected over a 114-yr period in southwestern Pennsylvania. Using these datasets, we address the following questions: (1) Does the timing of reproduction (flowering and fruiting) in native and nonnative species show signs of phenological niche separation across a broad spatial scale? And (2) how sensitive is the reproductive phenology of native and nonnative species to historic climate variation?

METHODS

Flowering phenology of eastern North American old-field plants

We conducted a survey of the flowering phenology of old-field species found throughout eastern North America. To compile a list of old-field species, we searched for published literature that included species lists from research sites in old-field ecosystems. We selected the following research sites and affiliated publications with comprehensive species' lists: Oak Ridge National Lab, Oak Ridge, Tennessee, USA (Souza et al. 2011), Hutcheson Memorial Forest Center at Rutgers, East Millstone, New Jersey, USA (Bard 1952, Allen and Forman 1976, Armesto and Pickett 1985, Leck and Leck 1998), Kellogg Biological Station at Michigan State University (Golberg 1987, Huberty et al. 1998, Emery and Gross 2006), Cedar Creek Ecosystem Science Reserve at University of Minnesota, East Bethel, Minnesota, USA (T*ilman and* K*nops* LTER dataset e054), and the Long-Term Mycorrhizal Research Site at University of Guelph, Guelph, Ontario, Canada (Klironomos 2002, Stanescu and Maherali 2017*a*, *b*). From these publications, we extracted a total of 385 unique plant species reported to occur in old fields. For each site, we recorded the species that were present and the following information from the USDA Plants Database: taxonomic family, functional group (grass, forb, shrub, vine), life history (annual, biennial, perennial), and origin (native or nonnative) (USDA, NRCS 2019). In this dataset, 18.7% of species were recorded at two sites, and 10.1% of species were recorded at more than two sites.

To record flowering phenology for this list of species, we extracted monthly flowering data from the Minnesota Wildflowers Information Organization (MW; Chayka and Dziuk 2018). Minnesota Wildflowers is a nonprofit organization with a mission focused on educating the broader public about native and nonnative plants. The group operates an open-access web database curated by experts who utilize existing field guides, floras, and their observations of flowers in Minnesota. Although focused on a specific region, this is one of the most comprehensive data sources we could find for flowering bloom time information. Thus, while specific bloom times vary for species with larger distributions in more southern or northern areas, we use this comprehensive Minnesota-based dataset as a standard measure for the bloom period for these species. For many species, flowering times are likely earlier in southern, warmer sites compared to northern, cooler sites, but we assume the relative bloom times between species remain similar across regions. In other words, the order and relative timing of species' mean flowering times should be similar across sites. We found support for this assumption by comparing bloom time data of a subset of common species ($n = 144$) with flowering data in the two most species-rich data sources, MW and Flora of North America (FNA; Flora of North America 1993). We found that flower start time was 0.63 months earlier (paired t test, $t = -7.8$, $P < 0.00001$), and bloom duration was 0.63 months longer (paired t test, $t = 5.3$, $P < 0.00001$) in the FNA dataset relative to the MW dataset. However, we found that flower start months between the two datasets were tightly correlated (Pearson's correlation test, $P < 0.001$, $r = 0.724$), which supported our assumption that the order and relative timing of species' mean flowering times is similar.

For all species represented in each flora, we coded the start bloom month and the end bloom month as an integer with month 1 representing January and month 12 representing December. We also calculated the total bloom period in months. For some species, bloom time was reported as seasons rather than months (e.g., mid-spring or early summer). To maintain consistency, we associated the following seasons with specific months for all species records: early spring (March), mid-spring (April), late-spring (May), early summer (June), mid-summer (July), late-summer (August), early fall (September), mid-fall (October), and late-fall (November). The MW database included flowering phenology data for 250 or 65% of species, (n = 66 nonnative and n = 184 native species) in our species list.

Herbarium records

While the flowering phenology survey represents a comprehensive list of old-field species across a broad spatial scale, it does not allow us to examine phenological changes of native and nonnative species through time. Thus, we performed an additional analysis that compared the timing of reproductive phenology in herbarium specimens to historic regional climate conditions. We selected 11 plant species based on their abundance in the Carnegie Museum of Natural History's herbarium (CM) in Pittsburgh, Pennsylvania. All species are common to old-field ecosystems in southwestern Pennsylvania and are comprised of six native and five nonnative forbs across four plant families (Asteraceae, Clusiaceae, Polygonaceae, and Ranunculaceae; Table 1). All species are of European or Eurasian origin, which is consistent with the origin of most old-field nonnatives (Fridley 2008). We scored all specimens of each species that were collected within southwestern Pennsylvania. This nine-county region comprises the western Allegheny plateau and central Appalachian ecoregions in the state (Woods et al. 1996). All specimens were collected between 1900 and 2014. We scored 1262 specimens for the phenological phase at the time of collection. We chose a four-stage phenology scheme (vegetative, budding, fruiting, or flowering) that provides similar results to a finer-scale eight-stage classification scheme (Ellwood et al. 2019). Because many specimens contained both flowering and fruiting reproductive structures, we recorded the phenological phases similar to Panchen et al. (2012). For a given specimen, we visually estimated the proportion of the specimen that was either flowering or fruiting. We classified a specimen as fruiting if >50% of the reproductive parts were in fruit or flowering if >50% of the reproductive parts were in flower, and we never classified a specimen as both fruiting and flowering. A specimen was considered budding if all of the reproductive structures were unopened. If reproductive structures were absent altogether, the specimen was classified as vegetative. For duplicate records (where more than one species was collected with the same phenology, in the same location, on the same day), we randomly selected one specimen to include in analysis. Duplicates represented 24% (n = 304) of the dataset. For our final analysis, we only used specimens in the flowering (n = 460) and fruiting (n = 464) phenophases. We recorded the date of collection for each specimen as the year and Julian day of year (DOY).

Climate data

We obtained historic monthly temperature and precipitation records between the years of 1900–2014 from weather stations within the study region of southwestern Pennsylvania, sourced from NOAA Climate Data Online (Lawrimore et al. 2016). Because complete climate records across the 114-yr period were not available for some counties, we calculated the mean monthly temperature (°C) and precipitation (inches) values from weather stations across the entire study area (Park and Schwartz 2015). This approach provided a detailed climate record for the full study period and location. We calculated spring temperature and precipitation averages for February through May of each year, which is one of the most common climate metrics used in other phenology studies of northeastern United States flora (Primack et al. 2004, Davis et al. 2015).

Because our herbarium study included late-summer and fall-blooming species that may be less responsive to average spring temperatures (Park and Schwartz 2015, Pearson 2019), we also calculated standardized temperature indices (STI) and standardized precipitation indices (SPI) for each herbarium record. The SPI was first developed in order to describe differences in climate across broad spatial and temporal scales (McKee et al. 1993). These indices compare the mean temperature or precipitation value of a given time period within a given year to that

Table 1. List of 11 native and nonnative old-field species.

Species	Family	Origin	No. specimens: Flowering	No. specimens: Fruiting
Hypericum punctatum	Clusiaceae	Native	44	42
Hypericum prolificum	Clusiaceae	Native	31	46
Rudbeckia hirta	Asteraceae	Native	50	21
Solidago canadensis	Asteraceae	Native	81	84
Solidago rugosa	Asteraceae	Native	75	94
Vernonia gigantea	Asteraceae	Native	38	47
Arctium minus	Asteraceae	Nonnative	35	19
Cirsium arvense	Asteraceae	Nonnative	23	27
Hypericum perforatum	Clusiaceae	Nonnative	31	43
Ranunculus acris	Ranunculaceae	Nonnative	23	16
Rumex crispus	Polygonaceae	Nonnative	29	25

Notes: Eleven native and nonnative species that are common to southwestern Pennsylvania old-field ecosystems and well-represented in the Carnegie Museum of Natural History herbarium were used for an analysis on how plant flowering and fruiting was affected by historical changes in climate. We include a species' Latin name, common name, taxonomic family, place of origin (native or nonnative to eastern North America), and number of herbarium species that were scored as either flowering or fruiting.

same time period across the entire study period based on a fitted normal density probability function (Hayes et al. 1999, Fasel 2015). STI and SPI values are reported in units of standard deviation from the median of the climate distribution for the time series. They are useful in comparing climates across large temporal or spatial scales because they represent the probability of occurrence of a certain climate value relative to climate values over a longer period. The exact climate values are standardized to be comparable across hot/cold and wet/dry periods of the growing season. Positive and negative STI or SPI values indicate climate values above and below the median temperature of the long-term time period, respectively. An STI of 1 would indicate a moderately hot period within the time series, while an STI of 2 would represent an extremely hot period within the time series (Fasel 2015). Standardized indices can be computed for any period of months and thus provide more flexibility for comparing the influence of climate on species whose flowering periods span a long growing season (e.g., to compare early spring flowering and late-summer flowering species).

For this study, we calculate STI and SPI values for the 1-, 3-, and 6-month time period prior to the collection date of each specimen. In our study, a one-month STI or SPI (STI-1 and SPI-1, respectively) for April 2000 would be standardized based on median April temperatures or rainfall observed every year from 1900 to 2014. The three-month STI of April 2000 (or, STI-3) would be the standardized mean February, March, and April 2000 temperature relative to that same 3-month period in other years. We used the package STI in R to calculate STI and SPI values, and these were assigned to herbarium specimens based on the month of collection (Fasel 2015).

Statistical analysis

Flowering phenology of eastern North American old-field plants.—To analyze floristic data from old-field species lists, we used linear mixed effect models to test whether the origin of species (native or nonnative), the site where a species was recorded as occurring (Tennessee, New Jersey, Michigan, and Minnesota, USA and Ontario, Canada), and the interaction of origin and site explained variation in three flowering phenology variables (start month of flowering, end-month of flowering, and flowering duration). We added taxonomic family, plant functional group (tree, shrub, vine, grass or forb), and plant life history (annual, biennial, or perennial) as random effects in all models to account for species' traits that might also affect phenology.

We also analyzed a smaller dataset (n = 195 species) of bloom time information collected from the Flora of North America (1993). The FNA dataset estimates bloom timing for a

Table 2. Model output: flowering phenology of eastern North American old-field plants.

Predictors	Estimate	SE	Stat.	*P*
MW bloom start				
(Intercept)	5.54	0.21	26.64	**<0.001**
Origin (Native)	0.55	0.18	3.14	**0.002**
Site (NJ)	0.1	0.19	0.53	0.599
Site (MI)	−0.15	0.30	−0.50	0.614
Site (ON)	0.07	0.21	0.35	0.728
Site (TN)	0.15	0.23	0.65	0.516
Origin:Site (NJ)	0.01	0.22	0.04	0.969
Origin:Site (MI)	0.23	0.36	0.64	0.523
Origin:Site (ON)	0.04	0.29	0.13	0.896
Origin:Site (TN)	−0.14	0.27	−0.51	0.614
Random effects				
σ^2	0.54			
τ_{00}				
Family	0.33			
Growth form	0.00			
Life history	0.02			
N observations	386			
MW bloom duration				
(Intercept)	4.05	0.28	14.45	**<0.001**
Origin (Native)	−0.92	0.20	−4.58	**<0.001**
Site (NJ)	−0.35	0.22	−1.58	0.115
Site (MI)	−0.07	0.34	−0.22	0.828
Site (ON)	−0.09	0.24	−0.39	0.696
Site (TN)	−0.24	0.27	−0.90	0.370
Origin:Site (NJ)	0.43	0.26	1.67	0.095
Origin:Site (MI)	0.06	0.41	0.14	0.892
Origin:Site (ON)	0.12	0.33	0.38	0.706
Origin:Site (TN)	0.20	0.31	0.63	0.532
Random effects				
σ^2	0.72			
τ_{00}				
Family	0.25			
Growth form	0.07			
Life history	0.03			
N observations		386		
MW bloom end				
(Intercept)	8.70	0.31	27.72	**<0.001**
Origin (Native)	−0.38	0.22	−1.75	0.082
Site (NJ)	−0.23	0.24	−0.98	0.330
Site (MI)	−0.21	0.37	−0.57	0.567
Site (ON)	−0.02	0.26	−0.06	0.951
Site (TN)	−0.10	0.29	−0.36	0.719
Origin:Site (NJ)	0.45	0.28	1.61	0.108
Origin:Site (MI)	0.30	0.45	0.67	0.502
Origin:Site (ON)	0.19	0.36	0.53	0.594
Origin:Site (TN)	0.07	0.34	0.22	0.826
Random effects				
σ^2	0.83			
τ_{00}				
Family	0.81			
Growth form	0.02			
Life history	0.08			
N observations	386			

(Table 2. Continued.)

Notes: SE, standard error. Nonnative old-field species flowered, on average, earlier and had longer flower bloom durations than native species across five sites across eastern North America. Lists of old-field plant species found in were compiled from the published literature, and bloom start month and duration were sourced from the Minnesota Wildflowers Information Organization (MW; Chayka and Dziuk 2018). Table results come from a mixed effect model with species origin (native or nonnative) and old-field site (Tennessee [TN], New Jersey [NJ], Michigan [MI], and Minnesota [MN], USA, and Ontario [ON], Canada) as fixed effects and species' taxonomic family, growth form (tree, shrub, vine, herb, or grass), and life history (annual, biennial, perennial) as random effects. Bolded *P* values indicate significant effects at $\alpha = 0.05$. Sigma (σ^2) and tau (τ_{00}) statistics represent the variance of the random effects.

species across its entire geographic range, making it less precise than a more regional flora. We found that model results were qualitatively identical between MW and FNA dataset (Table 2; Appendix S1: Table S1), which further increased our confidence that the MW dataset accurately represents flowering differences between species and is consistent with other floras. We present the MW analysis in the main text because this dataset includes more species, and thus is more comprehensive, than the FNA dataset. All analyses were performed using the lme4 and car packages in R (R Core Team 2012, Bates et al. 2015, Fox and Weisberg 2011).

*Herbarium records and climate data.—*We quantified the phenological sensitivity of native and nonnative species to changing climate conditions using herbarium specimens. We created a full model for each phenophase (flowering or fruiting) and used backward elimination to select a final reduced model. For each full model, we included Julian DOY as our response variable and species' origin (native or nonnative), collection year, standardized temperature indices for the one, three- and six-month period prior to a specimen's collection date (hereafter referred to as STI-1, STI-3, and STI-6, respectively), standardized precipitation indices for the one-, three-, and six-month period prior to a specimen's collection date (hereafter referred to as SPI-1, SPI-3, SPI-6, respectively), average spring temperature, and average spring precipitation as fixed effect. To determine whether native and nonnative plants differed in their sensitivities to particular climate variables, we also included interaction terms between species' origin and each climate fixed effect. For the purpose of this manuscript, we define "sensitivity" as the slope of the phenological response to a particular predictor variable. Species with phenologies that change by a greater number of days (steeper slopes) are considered to be more sensitive to a given climate variable. Finally, we included the county where a species was collected and species nested by their origin as random effects in all models. The original full model structure is as follows: DOY ~ origin + year + STI-1 + STI-3 + STI-6 + average spring temperature + SPI-1 + SPI-3 + SPI-6 + average spring precipitation + origin*STI-1 + origin*STI-3 + origin*STI-6 + origin*SPI-1 + origin*SPI-3 + origin*SPI-6 + origin*average spring temperature + origin*average spring precipitation + origin*year + (1|origin:species) + (1|county).

Because these models were large and many interaction terms were not significant, we used backward stepwise selection to identify the combination of predictor variables and interactions that produced the best statistical model (Appendix S1: Tables S2, S3). We used *F* tests to sequentially remove nonsignificant predictor variables from the full model (Zuur et al. 2009). We subsequently tested for collinearity among the main predictor variables using variance inflation factors (VIF). The VIF for main predictors were all below 5, indicating sufficient independence of the predictor variables (Zuur et al. 2010). We created figures of the fitted model contrasts using the visreg package in R (Breheny and Burchett 2017), which displays the estimated marginal slopes of interaction effects that account for main and random effects in the reduced final models.

RESULTS

Native and nonnative species show signs of distinct phenological niche separation in flowering and fruiting across a broad spatial scale

Nonnative species flowered 0.55 (±0.18 standard error [SE]) months (approximately 17 d) earlier in the growing season than native species among old-field species found across five study sites (Table 2, Figs. 1, 2). Interestingly, we did not find a significant difference in the end-flowering month between natives and nonnatives at any site (Table 2). Because nonnatives started flowering earlier than natives but did not differ in the end-flowering month, we found that nonnative plants also had significantly longer flowering durations than natives by 0.92 (±0.20 SE) months (approximately 29 d; Fig. 3, Table 2). We did not find any significant site-level effects in the model, suggesting that phenological differences between native and nonnative species were consistent across sites (Fig. 1).

Additionally, we found the same significant phenological niche separation between native and nonnative species in our herbarium specimens collected from western Pennsylvania. Model coefficient estimates accounting for all random and fixed effects show that nonnatives flowered 50.1 d (±11.4 SE) and fruited 17.46 d (±4.96 SE) earlier than natives (Fig. 4, Table 3).

Flowering and fruiting phenology are sensitive to historic climate variation

Overall, the timing of flowering and fruiting in native and nonnative plants has significantly advanced throughout the 114-yr study period (Table 3, Figs. 5D, 6C). Flowering has advanced approximately 0.09 (±0.03 SE) days per year and fruiting by 0.12 (±0.03 SE) days per year, according to model estimates that account for variation between species, climate, and collection location. This totals to an advancement of approximately 10 d for flowering and 13 d for fruiting since 1900 (Table 3, Figs. 5D, 6C).

While both native and nonnative plants advanced their reproductive phenology through time, native and nonnative phenology responded differently to many climate variables. Nonnative species significantly delayed their day of flowering when average spring precipitation (February–May) or the month preceding the flowering date was extremely wet (as indicated by an SPI value >2; Fig. 5A, C, Table 3, significant origin by SPI-1 interaction). Conversely, native species flowering time had minimal response to annual variation in precipitation (Fig. 5A, C, Table 3). Interestingly, native and nonnative species both advanced their flowering phenology when the six-month period preceding the flowering date was wetter than average, but nonnative species were more

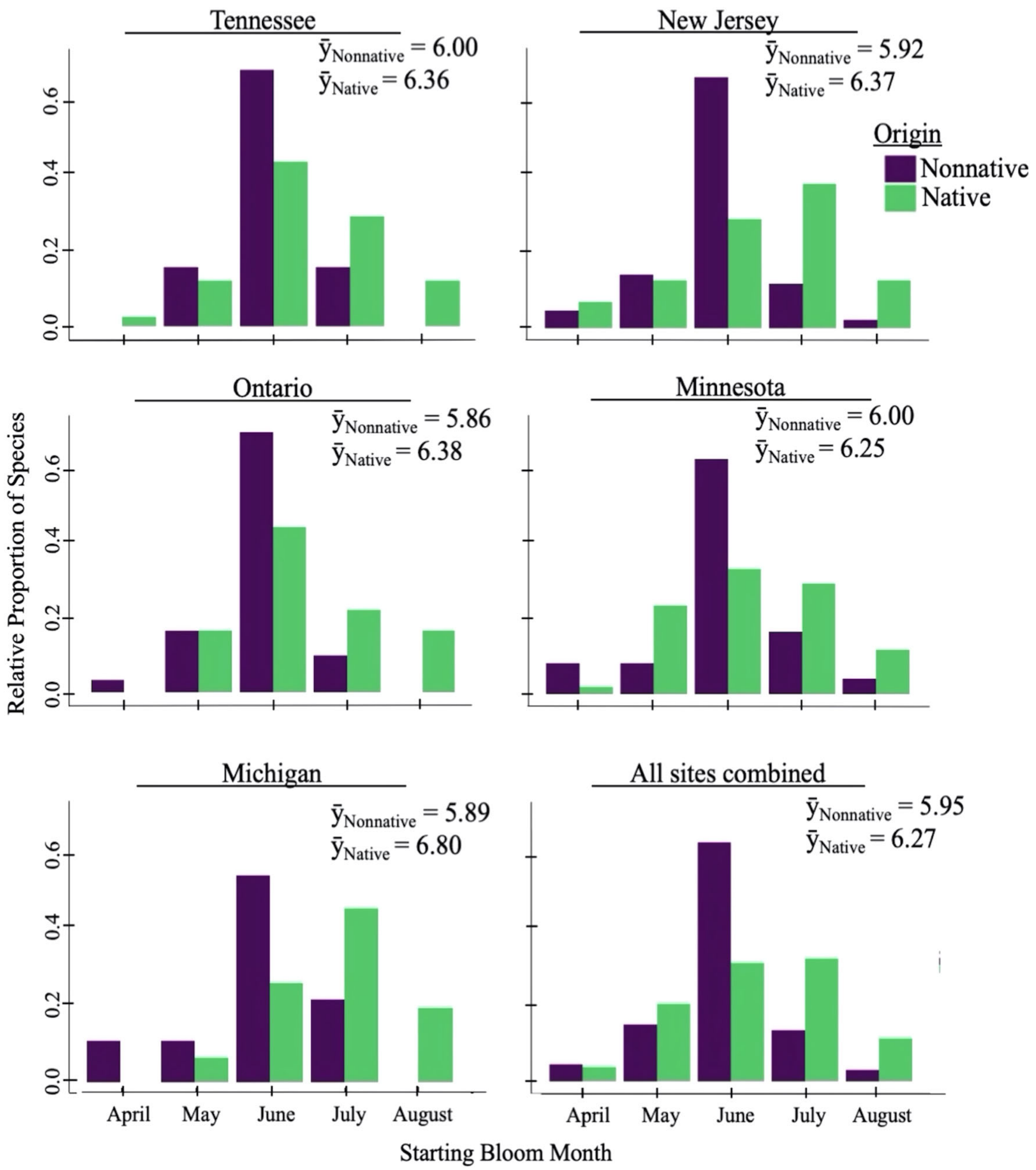

Fig. 1. The month a species starts blooming is on average earlier for nonnative species (dark purple bars) relative to native species (light green bars) in old-field ecosystems. Histograms display the proportion of native and nonnative species that start blooming for each month of the growing season. Lists of plant species were obtained from the Oak Ridge National Lab, Tennessee, USA (native, n = 41 and nonnative, n = 19), Hutcheson Memorial Forest Center, New Jersey, USA (native, n = 86 and nonnative, n = 42), Kellogg Biological Station, Michigan, USA (native, n = 15 and nonnative, n = 9), Long-Term Mycorrhizal Research Site, Ontario, Canada (native, n = 18 and nonnative, n = 30), and Cedar Creek Ecosystem Science Reserve, Minnesota, USA (native, n = 102 and nonnative, n = 24). The final all sites combined histogram represents combined species across all sites (native, n = 184 and nonnative, n = 66). The unadjusted mean flowering month, $\bar{y}$, is represented in numeric months (1–12). Phenology data were sourced from Minnesota Wildflowers Information Organization (Chayka and Dziuk 2018).

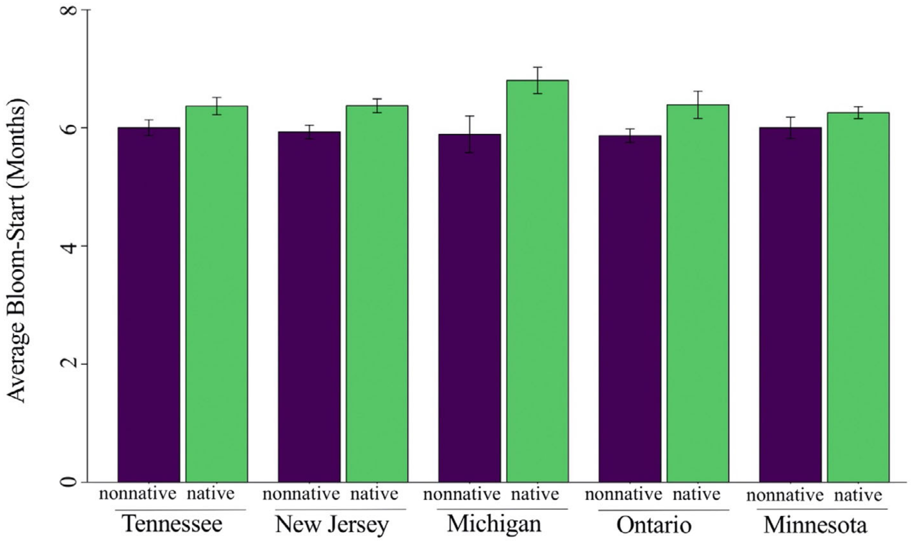

Fig. 2. Across five old-field research sites, the average flowering time of nonnative species (dark purple bars) was earlier than native species (light green bars). Months are represented numerically (1 = January to 12 = December). Species' lists were gathered from published papers from old-field study sites, and average flowering duration for each species was sourced from Minnesota Wildflowers Information Organization (Chayka and Dziuk 2018). See Fig. 1 legend for detailed site location information and sample size of native and nonnative species at each site.

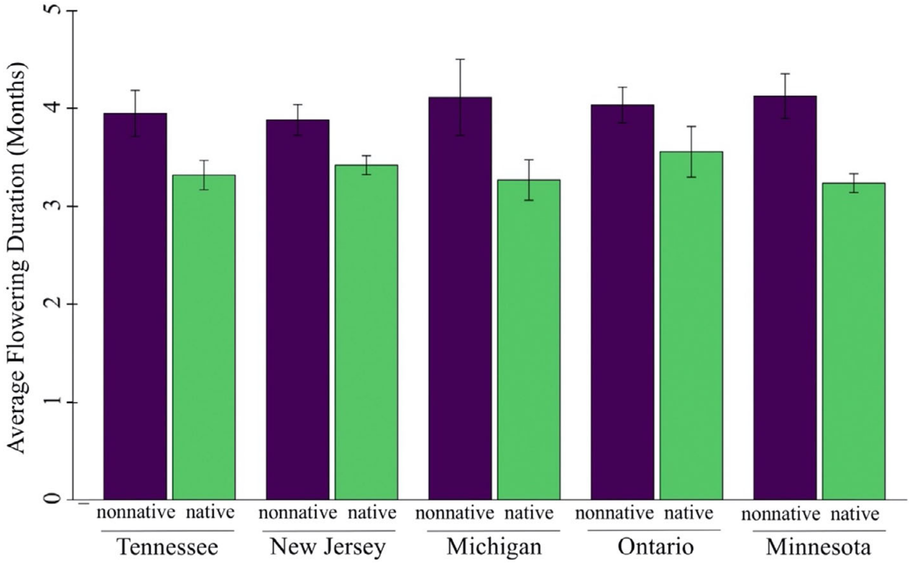

Fig. 3. On average, nonnative old-field plant species had longer flowering durations than native old-field plant across five sites in eastern North America. Species' lists were gathered from published papers from old-field study sites, and average flowering duration for each species was sourced from Minnesota Wildflowers Information Organization (Chayka and Dziuk 2018). See Fig. 1 legend for detailed site location information and sample size of native and nonnative species at each site.

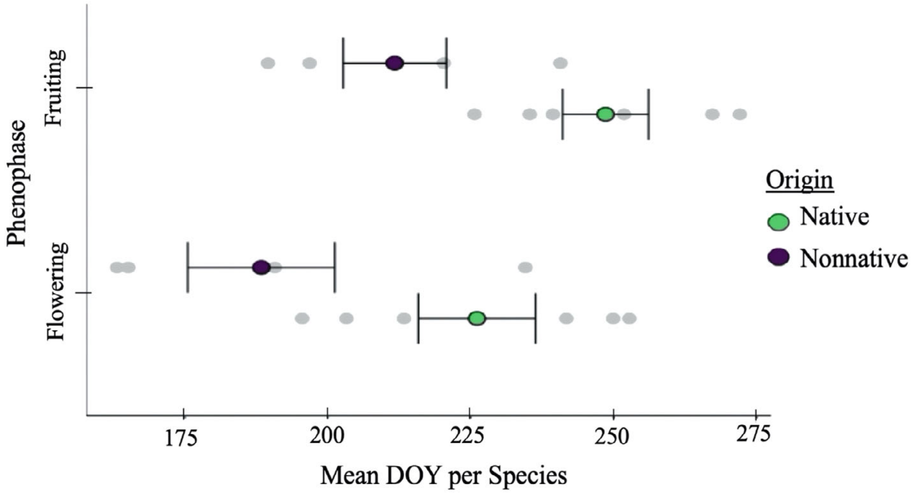

Fig. 4. On average, nonnative old-field plants (dark purple) flowered and fruited earlier in the year than native plants (light green) for herbarium specimens of six native and five nonnative species collected in southwestern Pennsylvania from 1900 to 2014. Day of year (DOY) values represent days of the calendar year (1–365) on which the specimen was collected and scored as either fruiting or flowering. Gray points represent the mean DOY of flowering or fruiting DOY for each individual species across the entire collection period. Error bars represent the standard error of the mean species flowering/fruiting times. See Table 1 for sample sizes for each species and phenophase.

sensitive to increased precipitation (as indicated by a greater slope for nonnatives, estimate = 5.08 ± 1.75 SE; Fig. 5B, Table 3). For both native and nonnative species, flowering phenology advanced when the preceding three-month period before flowering was warmer than average (Table 3, significant STI-3 main effect).

In contrast to flowering, the fruiting phenology of native and nonnative species differed in their sensitivity to historic temperature variation. We found that native plants delayed fruiting, while nonnative species advanced fruiting when the one-month period preceding the fruiting date was warmer than average (Table 3, Fig. 6A). Conversely, native plants advanced their fruiting, while nonnative delayed fruiting when the three-month period preceding the fruiting date was warmer (Fig. 6B, Table 3). As with flowering, both native and nonnatives had advanced fruiting phenology when the six-month period preceding the fruiting date was wetter than average (Table 3). For both native and nonnative species, fruiting phenology was delayed when the three-month period preceding fruiting date was wetter or the average spring precipitation was higher (Table 3).

DISCUSSION

In this study, we surveyed flowering phenology of 250 old-field species found across eastern North America and examined the reproductive phenology of herbarium specimens of 11 common old-field species collected across a 114-yr timespan. We found a strong signal that nonnative plants exhibit early phenological timing in both datasets. The starting flowering time of nonnatives was 17 d earlier than natives for old-field species found across five locations spanning eastern North America, while flowering and fruiting was 50 and 17 d earlier, respectively, across herbarium specimens collected in southwestern Pennsylvania (Tables 2, 3). Thus, phenological differences between native and nonnative old-field species seem to be generalizable within this habitat. Additionally, we found that native and nonnative species have both shifted toward earlier reproductive phenology from 1900 to 2014 but appear to be responding differently to temperature and precipitation cues (Table 3).

We propose two possible explanations for the observed differences in phenological sensitivity between native and nonnative species. First,

Table 3. Model output: herbarium records and climate analysis.

Predictors	Estimate	SE	Stat.	*P*
Flowering DOY				
(Intercept)	343.82	58.19	5.91	**<0.001**
Origin (Native)	50.13	11.36	4.41	**<0.001**
Year	−0.09	0.03	−3.04	**0.003**
STI-3	−2.53	0.93	−2.73	**0.007**
SPI-1	3.60	1.17	3.08	**0.002**
SPI-6	−7.18	1.78	−4.03	**<0.001**
Spring precipitation average	10.58	2.54	4.16	**<0.001**
Origin:SPI-1	−2.53	1.18	−2.15	**0.032**
Origin:SPI-6	5.08	1.75	2.90	**0.004**
Origin:Spring precipitation average	−8.96	2.54	−3.53	**<0.001**
Random effects				
σ^2	307.89			
τ_{00}				
Origin:species	523.53			
County	0.44			
N observations	460			
Fruiting DOY				
(Intercept)	434.54	67.06	6.48	**<0.001**
Origin (Native)	17.46	4.96	3.52	**0.005**
Year	−0.12	0.03	−3.44	**0.001**
STI-1	−1.92	1.45	−1.32	0.188
STI-3	−3.68	1.83	−2.01	**0.045**
STI-6	3.12	1.47	2.12	**0.035**
SPI-3	7.54	1.84	4.10	**<0.001**
SPI-6	−10.18	2.00	−5.09	**<0.001**
Spring precipitation average	7.12	2.05	3.46	**0.001**
Origin:STI-1	4.33	1.45	2.99	**0.003**
Origin:STI-3	−5.62	1.45	−3.88	**<0.001**
Random effects				
σ^2	445.61			
τ_{00}				
Origin:species	252.33			
County	0.00			
N observations	464			

Notes: SE, standard error. Native and nonnative phenology responded to different climate variables in an observational study of 964 herbarium specimens of 11 common old-field species collected between 1900 and 2014 in southwestern Pennsylvania. Table results report the relationship between the day of year (DOY, as Julian calendar day) a herbarium specimen was collected, and scored as either flowering or fruiting, the year the specimen was collected, and a suite of climate variables as fixed effects. We used a standardized temperature Index (STI) and a standardized precipitation index (SPI) for one-, three-, and six-month intervals prior to the collection date of a given specimen. Briefly, STI and SPI are in units of standard deviation and represent the deviation of a given time period from median climate values across the entire dataset (see *Methods* for more details). We also included the species and the county, and a specimen was collected in as random effects. This table reports best fit models for the fruiting and flowering DOY selected from backward selection of a full model (see *Methods* for more detail). Blank spaces in the table are effects removed via backward selection. Sigma (σ^2) and tau (τ_{00}) statistics represent variance of the random effects. Bolded *P* values indicate significant effects at $\alpha = 0.05$.

nonnative species may face a different set of constraints associated with their occupation of an early phenological niche. Unlike late-season natives, they may be forced to balance a fitness trade-off between tracking climate variation and avoiding early season physiological restraints such as frost damage or pollinator limitation (Wilsey et al. 2011, Kudo and Ida 2013, Vitasse and Basler 2013). Eastern North America is characterized by a high degree of spring temperature variation and unpredictability (Zohner et al. 2017). There is evidence that the risk of spring frost damage to plants has increased over time, as spring warming has advanced but late-season

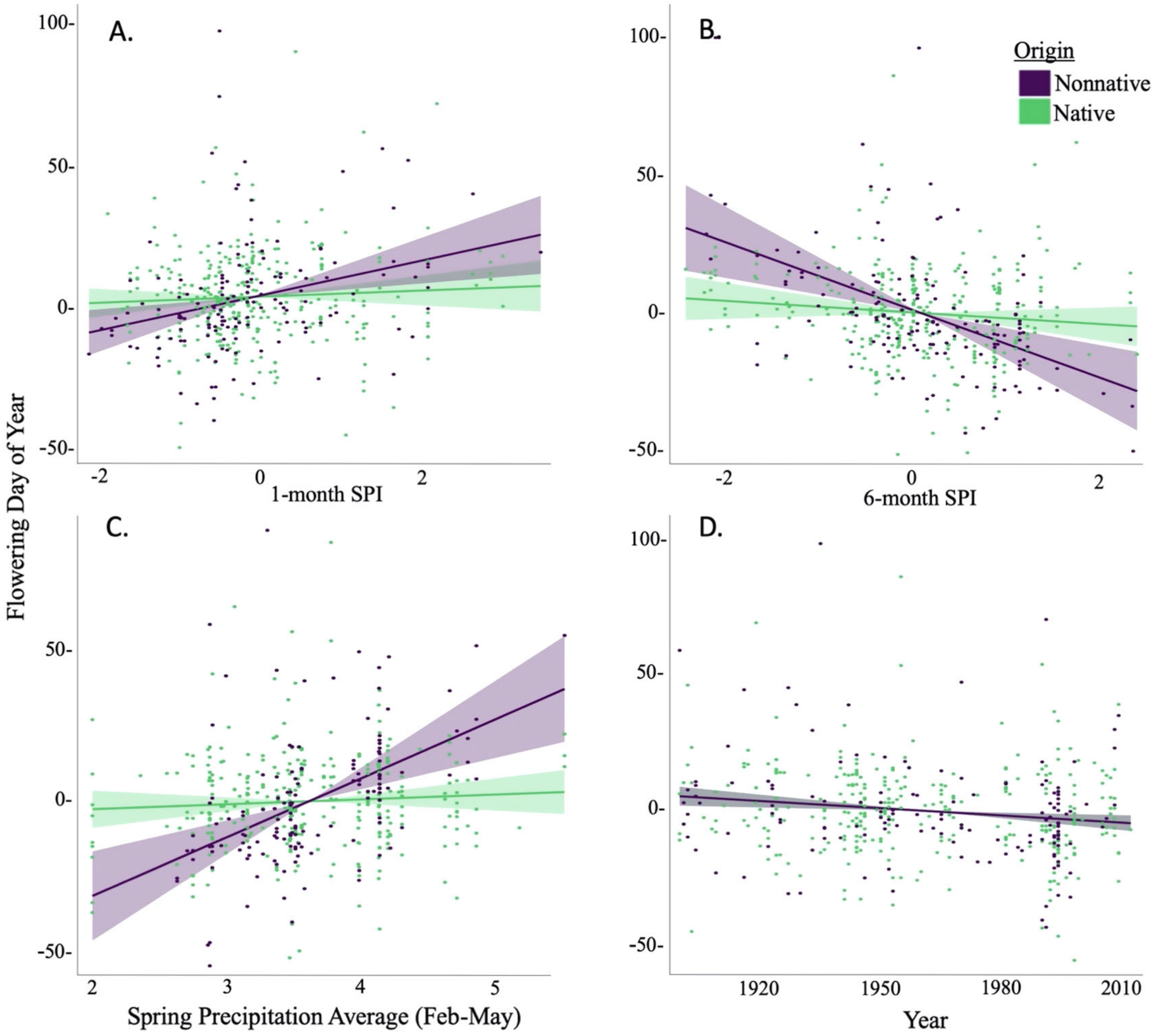

Fig. 5. The flowering phenology of native (dark purple) and nonnative (light green) old-field plant species responded to different degrees to historic precipitation variables including the standardized precipitation indices for a (A) one-month interval and (B) six-month interval prior to the collection date of a given specimen, as well as (C) average spring precipitation (February–May). Briefly, standardized precipitation indices (SPI) are in units of standard deviation and represent the deviation of a given time period from median precipitation values of that same time period across the entire dataset (see *Methods* for more details). (D) The timing of flowering for both native and nonnative species also advanced through time. Data points represent a total of 964 herbarium specimens of 11 common old-field species collected between 1900 and 2014 in southwestern Pennsylvania. Slopes of all figures represent the estimated marginal slopes extracted from linear mixed effect models (see Table 2 for model results).

frost events have not diminished (Inouye 2008, Augspurger 2013). As a result, the altered sensitivity of nonnative species to spring temperatures and precipitation could be an adaptive strategy, promoting their survival in the early growing season.

Second, the unique sensitivity of nonnatives to warming temperatures may also be attributed to differences in the climate in their native range. The climate of Europe—where the majority of nonnative old-field plants were introduced from —is milder and more predictable than in eastern

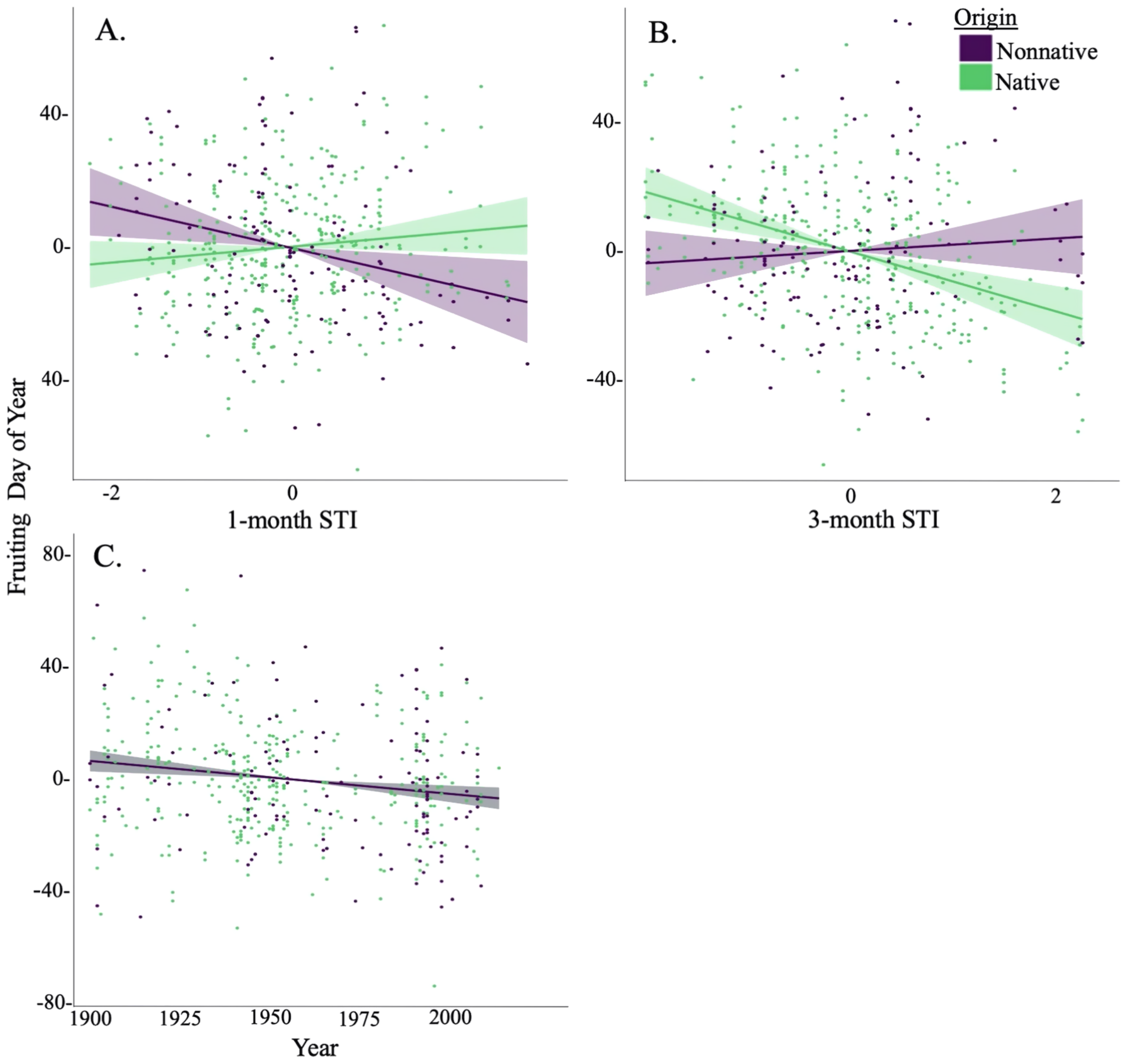

Fig. 6. The fruiting phenology of native (dark purple) and nonnative (light green) old-field plant species responded to different degrees to historic temperature variables including the standardized temperature indicies (STI) for a (A) one-month interval and (B) three-month interval prior to the collection date of a given specimen. Briefly, STI are in units of standard deviation and represent the deviation of a given time period from median temperature values of that same time period across the entire dataset (see *Methods* for more details). (C) The timing of fruiting for both native and nonnative species also advanced through time. Data points represent a total of 964 herbarium specimens of 11 common old-field species collected between 1900 and 2014 in southwestern Pennsylvania. Slopes of all figures represent the estimated marginal slopes extracted from linear mixed effect models (see Table 2 for model results).

North America. Woody plant species that evolved in Europe have lower winter chilling requirements and longer leaf-out periods than those that evolved in North America. This less-conservative leaf-out strategy of European plants relative to North American plants may lead to earlier leaf-out of European plants relative to North American plants in North America

(Zohner and Renner 2017, Zohner et al. 2017), as well as differences in climate sensitivity between European and North American species. We found that nonnatives were more sensitive to warming temperatures in the month preceding their fruiting, while natives were more sensitive to warming temperatures across a three-month period preceding their fruiting. This could support the hypothesis that native North American species are more conservative in their phenological responses, relying on longer warm periods to cue reproduction and growth.

Native and nonnative species differed most in their precipitation sensitivity during the flowering phase of phenology and differed most in their temperature sensitivity during the fruiting phase of phenology (Table 3). Interestingly, the direction of the interactions (whether nonnative plants had earlier or delayed phenology relative to native plants) was contingent on the length of the time period (one to six months preceding the specimen's collection date) being assessed. For example, nonnative plants delayed flowering in response to precipitation increases over the shorter one-month (SPI) and four-month (February–May spring precipitation average) time periods but flowered earlier in response to precipitation increases over a longer six-month (SPI) time period (Fig. 5A–C). Native species' flowering, by contrast, was largely insensitive to precipitation regardless of time period (Fig. 5A–-C). The reason for these differences in precipitation sensitivity is unclear. Plant precipitation cues are well-studied in arid habitats, where infrequent rainfall causes local species to be highly sensitive to changes in precipitation (Fay et al. 2003, Munson and Long 2017). Within mesic habitats like temperate old-field ecosystems, however, rainfall is rarely limiting, and it is generally assumed that precipitation has a smaller effect on plant phenology than temperature (Körner and Basler 2010, Wolkovich et al. 2013). We hope that our results, which have found differences in the precipitation sensitivity of native and nonnative species, will stimulate further research to explore the drivers of phenological sensitivity to precipitation in mesic temperate ecosystems.

We acknowledge the possibility that six-month SPI and STI could be confounded by climate across multiple seasons. This could interfere with our ability to compare sensitivity in species that flower at different times in the year. Because nonnative species reproduce earlier in the growing season, what we may be observing at the six-month time scale is a combined sensitivity to winter and spring cues. For native species with late reproduction, six-month SPI and STI are more likely to encompass spring and summer cues. More research is needed to disentangle the effect of time scale on variation in phenological sensitivity.

Previous experimental studies of herbaceous plants have found evidence that the germination and flowering phenology of nonnative species exhibits greater phenological sensitivity to warming temperature than native species (Wainwright and Cleland 2013, Zettlemoyer et al. 2019). However, responses under experimental conditions have the potential to differ significantly from the experienced responses of species in the field due to the complex, interactive nature of environmental cues (Wolkovich et al. 2012). Plants in natural conditions are known to respond to a combination of abiotic cues, of which warming temperatures and precipitation are not the only drivers (Pau et al. 2011). In our analysis of herbarium specimens, growing season temperature and precipitation factors explained a relatively small amount of variation in flowering and fruiting time in our models (flowering model: marginal $R^2 = 0.27$; fruiting model = 0.34 for fruiting). This suggests that other important environmental variables also affect phenological sensitivity of plant species, which are not accounted for in this study. Winter chilling temperatures and snowfall, for example, can affect the timing of germination and leaf-out and may account for important differences between native and nonnative species (Körner and Basler 2010, Zohner et al. 2017, Park and Mazer 2018). Understanding the interplay between a wider variety of abiotic cues, including warming temperatures, precipitation, photoperiod, snowfall, and winter chilling, will lead to more accurate predictions about phenological changes under future climate conditions.

In our analysis of phenological change of southwestern Pennsylvania old-field plants through time, we found that native and nonnative species are flowering 10 and fruiting 13 d earlier in the growing season than they did a century ago (Figs. 5D, 6D). Considering that climate change has led to a temperature increase of over 1°C and increased precipitation in Pennsylvania since 1900 (Shortle et al. 2015), this evidence suggests that native and nonnative species are both capable of tracking changes in climate in old-field ecosystems. However, we have also found evidence that nonnative species exhibit unique phenological sensitivity to climate. This suggests that the phenologies of native and nonnative species are not truly parallel, and future rates of phenological change may not mirror the historic changes we have observed. Nonnative and native species currently experience distinct patterns of temporal separation. In the future, phenological overlap between early season nonnative species and late-season native species could increase or decrease depending on dynamic shifts in the climate (Wilsey et al. 2018). This could lead to novel species interactions which alter plant fitness and lead to new dynamics of coexistence and competition within invaded plant communities.

Earlier flowering and fruiting of nonnative plants relative to native plants lends support to the hypothesis that nonnative species are invading into an open phenological niche within plant communities. Early phenology of nonnative species may facilitate their invasion into plant communities via two potential mechanisms: seasonal priority effects or the occupation of a vacant temporal niche (Wolkovich and Cleland 2011). To truly differentiate between these two mechanisms, it will be necessary to measure the fitness of co-occurring plant species in the presence and absence of early phenology nonnative species (Godoy and Levine 2014). Priority effects facilitate the establishment of early occurring plants by pre-empting resources early in the growing season, such that late-occurring plants face competitive exclusion or niche modification (Fukami 2015, Wilsey et al. 2015). By contrast, a vacant temporal niche facilitates the establishment of early occurring plants via the availability of unused resources, such that stabilizing niche differences promote coexistence among early and late-occurring species (Godoy and Levine 2014). Few studies have examined how phenological timing impacts species interactions between native and nonnative plants (with the exception of Godoy and Levine 2014 and Alexander and Levine 2019). Phenological traits may have an important influence on the invasibility of nonnative species as well as competitive interactions between native and nonnative species. The pattern uncovered here lays a foundation for future studies to address how phenology shapes the structure and composition of old-field plant communities under present and future climate conditions.

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DATA AVAILABILITY

Data are available from Dryad: http://dx.doi.org/10.5061/dryad.mkkwh70wm

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3217/full