

TEMPERATURE-DEPENDENT SHIFTS IN PHENOLOGY CONTRIBUTE TO THE SUCCESS OF EXOTIC SPECIES WITH CLIMATE CHANGE¹

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- *Premise of the study:* The study of how phenology may contribute to the assembly of plant communities has a long history in ecology. Climate change has brought renewed interest in this area, with many studies examining how phenology may contribute to the success of exotic species. In particular, there is increasing evidence that exotic species occupy unique phenological niches and track climate change more closely than native species.
- *Methods:* Here, we use long-term records of species' first flowering dates from five northern hemisphere temperate sites (Chinor, UK and in the United States, Concord, Massachusetts; Fargo, North Dakota; Konza Prairie, Kansas; and Washington, D.C.) to examine whether invaders have distinct phenologies. Using a broad phylogenetic framework, we tested for differences between exotic and native species in mean annual flowering time, phenological changes in response to temperature and precipitation, and longer-term shifts in first flowering dates during recent pronounced climate change ("flowering time shifts").
- *Key results:* Across North American sites, exotic species have shifted flowering with climate change while native species, on average, have not. In the three mesic systems, exotic species exhibited higher tracking of interannual variation in temperature, such that flowering advances more with warming, than native species. Across the two grassland systems, however, exotic species differed from native species primarily in responses to precipitation and soil moisture, not temperature.
- *Conclusions:* Our findings provide cross-site support for the role of phenology and climate change in explaining species' invasions. Further, they support recent evidence that exotic species may be important drivers of extended growing seasons observed with climate change in North America.

Key words: non-native species; flowering time; introduced species; invasion biology; plant phenology; temperate grasslands; North American prairies.

The search for universal traits that explain how species invade communities outside their native ranges and what attributes of those communities make them invulnerable underlies the field of invasion biology (Elton, 1958; Davis, 2009) and is a fundamental area of community ecology (Tilman, 1985). In recent years, the role of phenology has received increasing attention in this context, with numerous studies documenting novel timing of invaders' green-up, flowering, or senescence (DeFalco

et al., 2007; Resasco et al., 2007; Xu et al., 2007; Godoy et al., 2009; Willis et al., 2010; Hulme, 2011; Fridley, 2012).

Two dominant conceptual models of invasion biology—the vacant niche (Elton, 1958) and invader plasticity (Richards et al., 2006) models—may explain links between phenology and plant invasions. In the vacant phenological niche model, exotic species may establish in introduced communities if there is open temporal niche space. Such open niche space may occur at any point during the growing season, but with climate change introduced species may be especially successful early or late in the season because warming has extended the viable period for plant growth beyond that typically occupied by native species (Wolkovich and Cleland, 2011). The phenological plasticity model suggests that species with the most flexible phenologies may be more successful invaders outside their native ranges (Matesanz et al., 2010). Furthermore, climate change may select for more phenologically flexible species because they can rapidly respond to exploit climatic shifts (Franks et al., 2007; Willis et al., 2010; Anderson et al., 2012), especially in those systems that have shifted away from their long-term means (Trenberth and Josey, 2007). Many plant species have highly plastic flowering times (Vitasse et al., 2010)—a single individual

¹Manuscript received 13 September 2012; revision accepted 14 February 2013.

The authors thank all data collectors and contributors for sharing their data and R. Abbott, R. FitzJohn, N. Salamin, and W. Wen for data collection and analysis help. Comments from J. Craine, H. Kharouba, R. Primack, S. Weller, and two anonymous reviewers improved the manuscript. This work was conducted while E.M.W. was a National Science Foundation Postdoctoral Research Fellow in Biology (DBI-0905806) and also while she was supported by the NSERC CREATE training program in biodiversity research.

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may vary its flowering time over a month from year-to-year (Schwartz, 1994). Flowering times, however, are often also locally adapted across climatic gradients (Wilczek et al., 2010), and rapid evolution may occur in plant species following invasions (Sakai et al., 2001; Colautti et al., 2010). Thus, observed variation in phenology may arise from phenotypic plasticity or genetically based local adaptation of invaders in their new ranges, or a mix of the two processes (e.g., Anderson et al., 2012). For these reasons, we henceforth refer to a model of “invader flexibility” in phenology.

Climate change may lead to an important interplay between invader flexibility in phenology and vacant temporal niches. As growing seasons lengthen with climate change in many systems, novel vacant niches may become available—especially at the start and end of growing seasons; thus, species that can quickly adjust to occupy these open niches may be the most successful. Taken together, the vacant niche and invader flexibility models suggest that the most successful invaders are predicted to be phenologically flexible species that occupy temporal niche space near the start or end of the growing season.

Recent research has found support for these two conceptual models, and their interplay, in helping to explain plant invasions. Several studies have supported the vacant phenological niche model—especially at the start and end of the growing season. In North American grassland systems, for example, invaders often flower and bolt later than native species (Gerlach and Rice, 2003; Pearson et al., 2012). Similarly, in eastern North American forests exotic species drop leaves later in the fall than native species, allowing for additional carbon uptake (Fridley, 2012). Other research has identified that invaders start vegetative growth earlier than native species in some systems (Shustack et al., 2009; Wolkovich and Cleland, 2011; Wainwright et al., 2012). Evidence supporting the invader flexibility model comes from a few community-level studies (Willis et al., 2010; Hulme, 2011), which have found that exotic species have shifted their flowering dates more over time and also tend to track climate change more closely than native species. Willis et al. (2010) highlights how phenological flexibility and vacant niches may together contribute to the success of exotic species: many of the exotic species with the most flexible phenologies also flowered very early in the season. All these studies, however, have been focused on single communities or on a small (generally <100) subset of species, leaving it unclear to what extent phenology facilitates plant invasions at broader spatial and taxonomic scales.

Here we evaluate the role of phenology in explaining the establishment of exotic plant species at five northern hemisphere, temperate sites (Fig. 1, Table 1): three from mesic habitats and two from grassland systems. Using long-term data on plant first flowering dates (spanning a range of 161 yr at Concord, Massachusetts, USA to 9 years at the Konza Prairie Long-Term Ecological Research site [LTER], Kansas, USA) and two alternate reconstructions of their phylogenetic relationships, we test for differences between native and exotic species in three phenological variables: mean annual flowering time (the mean of all first flowering dates for each species at a site), variability (sensitivity) in first flowering dates with interannual temperature and precipitation variation, and the change over time of each species' first flowering dates with increased global temperatures (“flowering time shift” sensu Willis et al., 2010). Expectations from the two models of interest (vacant phenological niche and phenological flexibility) predict that exotic species will tend to (1) flower earlier or later than native species (vacant niche model), and (2) show greater interannual climate sensitivities

and/or greater flowering time shifts when compared with native species (phenological flexibility model). Because these two models are not exclusive, and phenological variables are often correlated (Menzel et al., 2006; Willis et al., 2010; Cook et al., 2012), we also investigate relationships between our phenological variables (e.g., earlier flowering times are often associated with increased temperature sensitivity) and whether they are consistent for both native and exotic species.

MATERIALS AND METHODS

Phenological data—We selected data from sites with long-term phenological records from the Network of Ecological and Climatological Timings Across Regions (NECTAR) database (Wolkovich et al., 2012b). We restricted the data to sites that met the following criteria: (1) included a sampling of exotic species (minimum of five), (2) included a minimum of 5 years of phenology data, (3) could be matched with mean annual climate data, and (4) included observations during the period of dramatically increased global temperatures that are at least partly associated with anthropogenic climate change (noted increases began globally in the 1970s, Trenberth and Josey, 2007), and (5) included a species-rich sampling (minimum of 100 species) of the flora throughout the spring and summer months. This yielded five data sets that included a mix of climates, years of observation, and differing numbers and percentage of exotic species (total species *n*, see Table 1). The Chinnor and Concord data sets have been previously analyzed by Hulme (2011) and by Willis et al. (2010), respectively, for variation in the phenologies of native vs. exotic species. We present a short synopsis of each site here—the shortened names we use for each site are in boldface. For all sites, each species was recorded only once each year for the entire study site.

Chinnor: First-flowering dates (FFD) of common species recorded in and around (generally within several km, all <80 km) Chinnor, Oxfordshire, UK by R.S.R. Fitter (Fitter and Fitter, 2002; Fitter et al., 2005).

Concord: First flowering dates recorded in Concord, Massachusetts, USA by H. D. Thoreau (first period of observation), A. Hosmer (second period of observation), and finally, A. Miller-Rushing and R. Primack across forest, roadside, meadow and wetland habitats. Full details can be found in Miller-Rushing and Primack (2008).

Fargo: First flowering dates of prairie and woodland species recorded in the Red River Valley (mostly tallgrass prairie habitat) of the Great Plains (these data cover North Dakota and Minnesota, USA) collected by O. A. Stevens from 1910–1961 (Travers and Dunnell, 2009) and by S. E. Travers and colleagues from 2007–2010 (Dunnell and Travers, 2011).

Konza: First flowering dates recorded at Konza Prairie LTER site (Flint Hills region of northeastern Kansas, USA) station by volunteers (<http://keep.konza.ksu.edu>). Konza represents a North American tallgrass prairie habitat, where each watershed is managed by different treatments of prescribed fire and native herbivores (bison).

Washington, D.C.: First-flowering dates recorded by over 100 volunteers in the Washington, D.C. area (USA) from 1985–2007 across a mix of habitats (Abu-Asab et al., 2001). A. Goldberg and J. Wurdack were the primary contributors and guided data collection. The data include a mix of cultivated and noncultivated species (indicated by the data collectors), we excluded all observations noted as cultivated for this analysis. The data are publicly available through the Smithsonian National Museum of Natural History (<http://botany.si.edu/dcfiora/springflowers>).

We assigned native vs. exotic status for the four United States sites using the USDA Plants Database (<http://plants.usda.gov/>), excluding a small number of species for which native/exotic status was not confirmed. Nonnative species status for Chinnor was obtained from the Botanical Society of the British Isles online database (<http://www.bsbi.org.uk/>). These two databases provide some consistency in assigning native/exotic status across sites, but also impose limitations on how well we can define species as invaders. In particular, we note that we have not been able to test whether all the exotic species in the study sites are invaders with self-sustaining, spreading populations. Mean annual flowering time (day of year) was calculated as the mean of all first flowering dates for each species at each site.

Flowering time shift calculations—Flowering time shift measures the change over time of each species' flowering date concurrent with increased

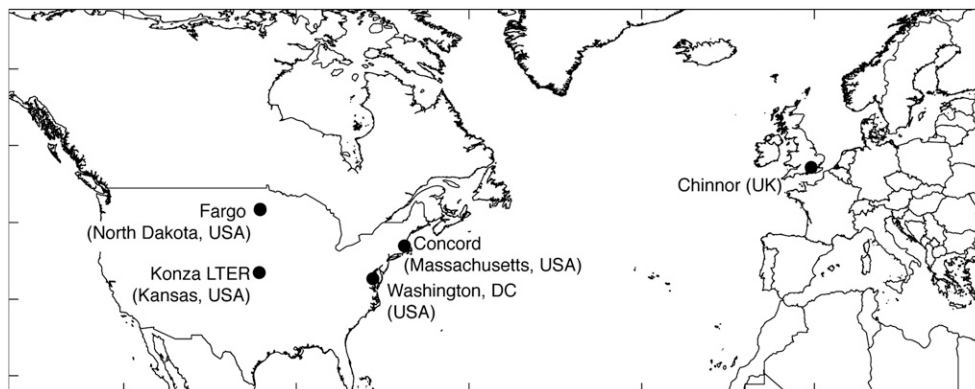


Fig. 1. Location of five sites used in analysis. For details on factors that controlled which sites were included, see *Phenological data* section of Materials and Methods.

global temperatures (Trenberth and Josey, 2007). For Concord and Fargo, we split each data set and determined the mean annual flowering time for each period of observation before and after 1970, which captures the most recent noted rise in global temperatures (Trenberth and Josey, 2007). For Concord, the difference in mean annual flowering times was compared from 1858 to 1904 vs. those from 2003 to 2006; for Fargo, the same difference was compared between the years 1910 and 1961 and 2007 and 2010. For Chinnor (yearly phenological data from 1954 to 2000) and Washington D.C. (yearly phenological data from 1985 to 2007), we regressed first flowering dates against year and took the slope. For the regression approach, we required a minimum of 5 years of data for each species; results presented here, however, are similar when using more than 5 years as a minimum requirement for calculating flowering time shift. We could not calculate flowering time shift for all species (e.g., species that were not observed post-1970 compared to pre-1970 observation periods at Concord or Fargo); thus, the total n for analyses including flowering time shift is lower here than for other analyses (Table 1). The period of data collection from Konza was too short (2001–2009) to calculate flowering time shift.

Climate data and climate sensitivities—For calculating how species' first flowering dates respond to temperature, we used the best-available, local, standardized climate data for each site. Thus, we used climate data from the standardized Global Historical Climatology Network (GHCN, Peterson and Vose, 1997) for all sites, except Concord, for which we used data from the Blue Hills meteorological station (which included temperature data for the entirety of the record). For comparison of mean minimum temperatures between sites (Table 1), we used version 2.1 of the climate grids from the Climate Research Unit (CRU, Mitchell and Jones, 2005), selecting the closest half-degree gridcell to each site and using a standard period of years (1961–1990) for all sites.

We calculated sensitivity in several different ways (described later). For all sensitivities we required a minimum of 5 years of data for a species to be included in sensitivity calculations. We review each sensitivity method here in brief, additional details for these methods can be found in Cook et al. (2012); Mazer et al. (2013, in this issue) and Wolkovich et al. (2012a). We focus our temperature sensitivity results on one method, due to its ease of interpretation and repeatability. For this method we took temperature sensitivity for each species i as the β coefficient from a simple linear regression of:

$$\text{first flowering day of year}_i = \beta_i(\text{MAT}) + \epsilon_i$$

where MAT is mean annual temperature for each site and ϵ is model error.

In Appendix S1 (see Supplemental Data included with the online version of this article), we present complete results from four additional methods to calculate climate sensitivities that used finer-scale climate data. The first additional method used a model based on monthly temperatures that best predicts flowering time, which is similar to several studies, including some studies of the data sets we have reanalyzed here (Fitter et al., 1995; Miller-Rushing and Primack, 2008). For each species at each site, we selected its best fit to mean monthly temperatures from overlapping 3-mo periods (e.g., January–March, February–April) based on R^2 and repeated our regression approach, using this annual 3-mo mean temperature in place of MAT. Second, we also used a growing-degree day (GDD, using 0°C as the threshold) model for the sites with comparable climate data (for all sites except Concord, for which there were no daily data). We summed GDD over overlapping 3-mo periods, standardized to zero mean and unit standard deviation. This standardization controlled for the fact that variability in climate is itself variable across the year—in temperate systems spring and fall months include large variation in temperature while summer months do not—by removing this variation through standardization, we could make direct comparisons of species' responses to GDD across the growing season. We next selected the best-fitting period for GDD based on R^2 .

Our third method included the GDD model but added a precipitation term. For this method, we first fit the GDD and, separately, the precipitation term (a summation of precipitation over each 3-mo period) based on R^2 to select the best 3-mo periods. We then fit the full model including the best-fit GDD and precipitation term and the interaction between the two. At no sites was there a significant interaction of GDD and precipitation between native and exotic species (Appendix S1, see online Supplemental Data). The fourth additional sensitivity model was based on soil moisture and fit only for Konza, as soil moisture data were not available over the period of observation for any other site. We averaged data sampled from six depths at semimonthly intervals into monthly means for the two watersheds sampled: 1D (annually burned) and 20B (no prescribed burning). In both watersheds, soil moisture values peaked annually in March–April and were lowest in August. We then (again) standardized data to zero mean and unit standard deviation and used model-selection based on R^2 .

TABLE 1. Information on the five sites used in our analysis, including species numbers based on models using Phylomatic trees (number of internal nodes of each tree were: *exotic* + *native species* $n - 1$). Because calculations of flowering time shifts required additional data cut-offs (see Materials and Methods) the total species n is smaller.

Site	Min temp ($^\circ\text{C}$)	Years	Exotic spp. n	Native spp. n	Exotic spp. n : flowering time shift models	Native spp. n : flowering time shift models
Chinnor, UK	4.01	1954–2000	53	322	52	319
Concord, MA, USA	5.43	1851–1858, 1878–1903, 2003–2006	98	379	82	280
Fargo, ND, USA	−1.65	1910–1961, 2007–2010	79	226	13	93
Konza LTER, KS, USA	5.93	2001–2009	10	188		
Washington, D.C., USA	8.04	1985–2007	182	266	183	267

values for each species to select 1 mo to regress against flowering date for each species. We then averaged sensitivities (regression coefficients) for each species across the two watersheds. The sensitivity is thus in units of days per soil moisture deviation, with positive values indicating delayed flowering with wetter soils, and negative values indicating earlier flowering with wetter soils.

We included all sensitivities—whether based on significant underlying models or not—in our analyses. Results were similar, however, when we set all sensitivities with $p > 0.1$ to 0; this is not surprising given that the magnitude of sensitivities tended to decrease with decreasing model significance. Temperature sensitivities vary between negative values (species advance flowering with warming) or positive values (species delay flowering with warming). Because the most common temperature sensitivity in our results is negative, when we refer to “greater” sensitivities hereafter, we mean “more negative,” that is, earlier flowering with warming. When we refer to positive sensitivities, we specifically mention this and their relationship with delayed flowering.

Phylogenetic trees—Until very recently, analyses of community-wide phenological data sets that demonstrate species’ long-term responses to climate change (Visser, 2008) have lacked a phylogenetic framework (Davis et al., 2010). Our rationale for including phylogeny in studies of phenological response to climate change is two-fold: closely related species are not statistically independent owing to their shared evolutionary history (Felsenstein, 1985; Harvey and Pagel, 1991; Fisher and Owens, 2004) and knowledge of the phylogenetic distribution of species traits can provide a better assessment of the impact of climate change on biodiversity (Davis et al., 2010; Mazer et al., 2013, in this issue).

We initially assembled a phylogeny for all of the species included in our analyses using the program Phylomatic, version 2 (<http://phylodiversity.net/phylomatic/>) (Webb and Donoghue, 2005). Phylomatic trees were assembled assuming the APG III backbone (Bremer et al., 2009), which provides resolution to the family level only, and divergence times for families were calibrated in Myr using dates from Wikström et al. (2001). This phylogeny is advantageous because it includes all species in our analysis, but is disadvantageous because it provides only an approximate degree of relatedness—relationships, especially within genera, are left unresolved. Hence, much of this Phylomatic tree lacks phylogenetic resolution. This is problematic because recent theoretical and empirical studies have shown that a lack of resolution in a community phylogeny may mask significant patterns by reducing statistical power (Kress et al., 2009; Schaefer et al., 2011), or, alternatively, suggest significant phylogenetic patterns that are not supported by more completely resolved phylogenies (Davies et al., 2012).

To alleviate these concerns, we set about to infer a maximum likelihood (ML) phylogeny based on all available DNA sequence data from GenBank for all species included in our analyses. This has the advantage of estimating a phylogeny directly from DNA sequence data at all phylogenetic depths/ranks, but the disadvantage that sequences are not available for all species. To obtain phylogenies for our five study areas, we used two mega-trees produced for a worldwide study of the effect of phylogenetic distances on invasiveness (H. Schaefer et al., unpublished manuscript). For that study, GenBank nucleotide data for 17 DNA regions were downloaded, and data matrices for the entire flora of the continental United States and for the German flora were assembled and aligned using the PHLAWD computer package (Smith et al., 2009). These DNA matrices were then analyzed using maximum likelihood as implemented in RAxML v7.2.8 (Stamatakis et al., 2008) on the High Performance Computing cluster at Harvard University.

We present analyses here with branch lengths for the Phylomatic trees computed via the BLADJ algorithm in the program Phylocom (<http://phylodiversity.net/phylomatic/>) and using the given branch lengths from the program PHLAWD. To further evaluate sensitivity to phylogenetic branch lengths, we also explored analyses with BLADJ-adjusted branch lengths for the PHLAWD trees, as well as with all branch lengths set to 1 for both the Phylomatic and PHLAWD trees. All analyses produced similar results (results not shown).

Results were generally similar between Phylomatic and PHLAWD trees, or when they differed it was correlated with species sampling artifacts between the two tree designs (i.e., the PHLAWD trees were restricted to species present in our megatrees, see online Appendix S1G for species numbers in PHLAWD). Thus, we present the Phylomatic results here and provide all results, considering both tree constructions, in the Appendix S1. All trees are available through the Knowledge Network for Biodiversity (Wolkovich, 2013).

Statistical analyses—We performed all analyses in the program R 2.12.0 (R Development Core Team, 2010), using the packages *car* version 2.0-6 (Fox and Weisberg, 2011), *nlme* version 3.1-97 (Pinheiro et al., 2012), and *picante*

version 1.2-0 (Kembel et al., 2010). To compare differences in phenological variables (mean annual flowering time, interannual temperature sensitivity, and flowering time shift) between native and exotic species and relationships between variables across sites, we used mixed-effects (ME) models with site treated as random. Within sites, we used basic linear regression models (LM) with type II sums of squares. We excluded one outlier species (*Chenopodium glaucum* L., assessed by normal quantile plots) from the Fargo data, which did not dramatically alter our results. We reported results for Fargo with and without this species in supplemental tables (Appendices S1C and S1D using Phylomatic trees, Appendices S1J and S1K using PHLAWD trees).

We also performed the same tests but accounting for phylogenetic nonindependence by using a phylogenetic general linear model (PGLM). This model includes a variance-covariance structure based on evolutionary distance to control for phylogenetic structure in the data (Freckleton et al., 2002). Because this model suffers from very high type I error rates when the model residuals have little phylogenetic structure (Revell, 2010), we used a version of the model that includes the maximum likelihood estimate of λ (Pagel, 1999), defined as the transformation of the phylogeny that makes the data best fit a Brownian motion model of evolution. This model converges on the output of a basic linear model when λ is close to 0; in contrast, it applies a very strong phylogenetic correction to the model when λ approaches 1. We used an early version of R code for PGLM, which has now been released as part of the R package *caper* (personal communication, D. Orme). For all tests, we set $\alpha = 0.1$ to determine significance, but report all p -values explicitly; further, we only report significance when this level was met for both LM and PGLM analyses. We present results within and across sites; however, because our two models of interest likely operate at the level of co-occurring species, we focused mainly on site-level results.

Finally, we performed two tests on subsets of the data. First, for Concord, estimates of species’ abundances (six levels corresponding from rare to very common) were available, which allowed us to test for the role of shifts in abundance affecting estimates of changes over time in first-flowering dates (as population sizes increase, detection rates also may increase, which can shift first flowering dates earlier, even if, overall, the population flowering time is unchanged, see Miller-Rushing et al., 2008). For this model, we included abundance as a categorical main effect with three levels (increase in abundance, no change in abundance, or decrease in abundance), alongside native/exotic status and the interaction between the two. We additionally tested whether differences between native and exotic species were unique to their introduced range. Invasion biology theory suggests that if phenology drives the success of exotic species, then any phenological differences we observe between native and exotic species should only occur in the introduced range and should not be mirrored when we compare those exotic species in their native range with the rest of their native community (Davis, 2009). For this exercise, we contrasted Concord and Chinnor because these two sites have high species overlap and similar climates (Table 1). Using 42 species that were exotic at Concord but native to Chinnor, we compared differences (1) between these 42 species using their phenological data from Concord (introduced range) and the native community of Concord, and (2) between these 42 species using their phenological data from Chinnor (native range) and the rest of the native community at Chinnor. Ideally, we would also compare whether the phenological attributes of the 42 species themselves vary when measured at Concord vs. when measured at Chinnor. Such a direct comparison would provide one test for evidence of genotypic shifts following invasion, or for the presence of different genotypes from other source populations (i.e., the source population from the native range for the introduction to Concord may have come from somewhere geographically and/or genotypically distinct from Chinnor, or from multiple source populations). The underlying climate and data structure of the two sites (Table 1), however, prevented this comparison for all but temperature sensitivity. Because the climate is milder at Chinnor, and thus the growing season is longer, the flowering dates of these shared species would be expected to be earlier based on a completely plastic, temperature-driven model of flowering phenology. Additionally, the difference in time scales of the two data sets required us to calculate flowering time shift using different methods for each site and preventing direct comparison. For comparison of the temperature sensitivities, we performed a sign test (exact binomial) on the difference for each species in the calculated temperature sensitivity at Chinnor vs. Concord.

RESULTS

Variation in flowering between native and exotic species—Mean annual flowering time (day of year) was the only phenological

variable to show strong phylogenetic structure (sensu Revell, 2010) when considering its variation between native and exotic species (λ values ranging 0.58, at Washington, D.C. to 0.99 at Konza, see online Appendix S1). All other considered relationships showed relatively weak phylogenetic structure ($\lambda < 0.1$) save for one case that did not alter nonsignificant results (the temperature sensitivity at Konza). Thus, we focus on the PGLM results for flowering time and basic linear model (LM) results for all other variables. Complete results of PGLM and LM side-by-side are given in Appendix S1.

Across sites, exotic species flowered earlier (ME model: $F_{1,1797} = 4.31$, $P = 0.038$) and were more sensitive to temperature (ME model: $F_{1,1797} = 7.71$, $P = 0.0056$) than native species. This pattern, however, was not consistent when considering each site individually. We found trends in mean annual flowering time and temperature sensitivity between native and exotic species at the three mesic sites—Chinnor, Concord, and Washington, D.C.—but not the two grassland sites, Fargo and Konza. Exotic species tended to flower earlier than native species at the three temperate mesic sites (Fig. 2A, B, E), but differences were marginally significant only at Concord (PGLM: $F_{1,475} = 3.79$, $P = 0.052$, Fig. 2B). At the two grassland sites, flowering times were nearly identical between the native and exotic species (Fig. 2C, D). Similarly, exotic species tended to have greater temperature sensitivities (advanced their flowering dates more per °C) at the three mesic sites (Chinnor: $F_{1,373} = 7.08$, $P = 0.0081$, Concord: $F_{1,475} = 3.64$, $P = 0.057$, Washington, D.C.: $F_{1,446} = 2.75$, $P = 0.10$, Fig. 3A, B, E), but there were no significant trends at Fargo or Konza (Fargo: $F_{1,303} = 2.29$, $P = 0.13$, Konza: $F_{1,196} = 0.41$, $P = 0.52$, Fig. 3C, D); at Fargo, however, and in contrast to the other four sites, exotic species tended to be less temperature sensitive than native species (Fig. 3C).

Of the four sites (Chinnor, Fargo, Konza, Washington D.C.) where we fit climate sensitivity models including a precipitation term, only the two grassland sites—Fargo and Konza—showed trends between native and exotic (Fig. 4). Fargo showed significant variation between native and exotic species in flowering time responses to interannual precipitation variation ($F_{1,303} = 3.99$, $P = 0.047$, see also Appendix S1C), such that exotic species advanced their flowering dates with increased precipitation while native species delayed (Fig. 4A). For Konza, the trend was reversed—though nonsignificant: both precipitation ($F_{1,196} = 2.22$, $P = 0.14$, exotic species mean: 5.39 d per standardized precipitation unit, native species: -1.37) and soil moisture ($F_{1,196} = 2.47$, $P = 0.12$, Fig. 4B) sensitivities suggested that exotic species tended to delay flowering with increased moisture, while native species tended to advance (Fig. 4B).

Across the four sites (Concord, Chinnor, Fargo, Washington, D.C.) with sufficient long-term data, including periods of anthropogenic climate change (post-1970), exotic species showed greater advances in flowering times compared to native species (greater flowering time shifts, ME model: $F_{1,1281} = 8.35$, $P = 0.0039$). At Chinnor and Concord, exotic species have shifted significantly more than native species (Chinnor: $F_{1,369} = 3.61$, $P = 0.058$, Concord: $F_{1,360} = 9.39$, $P = 0.0023$, Fig. 5A, B), while at Washington, D.C., there was a similar, but nonsignificant trend ($F_{1,448} = 1.64$, $P = 0.20$, Fig. 5D). In contrast, at Fargo, there was no appreciable trend for shifts in flowering time ($F_{1,104} = 0.96$, $P = 0.33$), though exotic species have generally delayed their flowering over time (Fig. 5C). At the three North American sites, shifts of native species' flowering were close to or overlapped with zero (Fig. 5B–D), while at the Chinnor site, both native and exotic species have advanced over time (Fig. 5A).

Relationships between phenological variables—The temperature sensitivity of species scaled positively with their mean annual flowering times across all sites (ME model: $F_{1,1797} = 82.89$, $P < 0.0001$) except Fargo, such that early-season species showed the greatest sensitivity to temperature (Fig. 6). At Chinnor, Konza, and Washington, D.C., this relationship was consistent across exotic and native species (Chinnor: main effect of FFD: $F_{1,371} = 87.24$, $P < 0.0001$, interaction: $F_{1,371} = 0.13$, $P = 0.72$; Konza: main effect of FFD: $F_{1,194} = 17.90$, $P < 0.0001$, interaction: $F_{1,194} = 0.017$, $P = 0.90$; Washington, D.C.: main effect of FFD: $F_{1,444} = 8.59$, $P = 0.0036$, interaction: $F_{1,444} = 1.49$, $P = 0.22$): at Concord, the relationship varied with native/exotic status (main effect: $F_{1,473} = 8.90$, $P = 0.0030$, interaction: $F_{1,473} = 3.43$, $P = 0.065$). In the latter, exotic species showed a steeper relationship (slope of 0.067) compared to native species, which had sensitivities that were almost unchanging across the season (slope of 0.020, Fig. 6B). The estimated slopes of the three sites were highly similar (Chinnor: 0.064, Concord exotic species: 0.067, Washington, D.C.: 0.051). At Fargo there was no relationship between flowering time and temperature sensitivity (Fig. 6C).

As expected, species' flowering time shifts varied with their temperature sensitivities (ME model: $F_{1,1281} = 255.36$, $P < 0.0001$). The directionality of this relationship, however, varied between sites (Fig. 7). At Chinnor and Concord, temperature sensitivity scaled positively with flowering time shifts, such that the most temperature-sensitive species also showed the greatest advances in flowering times (Chinnor: main effect: $F_{1,367} = 301.17$, $P < 0.0001$, Concord: main effect: $F_{1,357} = 377.31$, $P < 0.0001$, Fig. 7A, B). At Chinnor, the relationship was similar for exotic and native species (Fig. 7A, interaction: $F_{1,367} = 0.037$, $P = 0.85$). In contrast, at Concord, exotic species have tended to shift more than native species over time given the same temperature sensitivity (Fig. 7B, interaction: $F_{1,357} = 8.90$, $P = 0.0030$). There was more extreme variation between native and exotic species at Fargo, where shifts in flowering over time were negatively related to temperature sensitivity (i.e., species with positive temperature sensitivities, meaning they delay flowering with warming, tended to advance their flowering over time and vice versa for species with negative temperature sensitivities) for exotic but not native species (main effect: $F_{1,102} = 10.00$, $P = 0.0021$, interaction: $F_{1,102} = 24.56$, $P < 0.0001$, Fig. 7C). At Washington D.C., a similar negative relationship was found (main effect: $F_{1,444} = 25.31$, $P < 0.0001$, interaction: $F = 13.51$, $P = 0.0027$), but in this case, it occurred for native species (Fig. 7D).

Relationships with abundance—As predicted, changes in species' abundances at Concord related to species' flowering time shifts such that species that had increased in abundance also shifted earlier over time (main effect of abundance: $F_{2,304} = 5.53$, $P = 0.0044$). Importantly however, exotic species still showed significant differences from native species (main effect of native vs. exotic: $F_{1,304} = 4.12$, $P = 0.043$)—suggesting that the greater shift in flowering times cannot be explained solely by a sampling artifact. Additionally, exotic species tended to shift their flowering times more with increased abundance compared to native species (interaction: $F_{2,304} = 2.84$, $P = 0.060$).

Comparisons in the native vs. introduced range—Finally, we tested for phenological differences between the shared 42 (Appendix S2) species that are native to Chinnor and exotic to Concord. To review, at Concord when considering all exotic species ($n = 98$), we found that exotic species flowered earlier, had greater

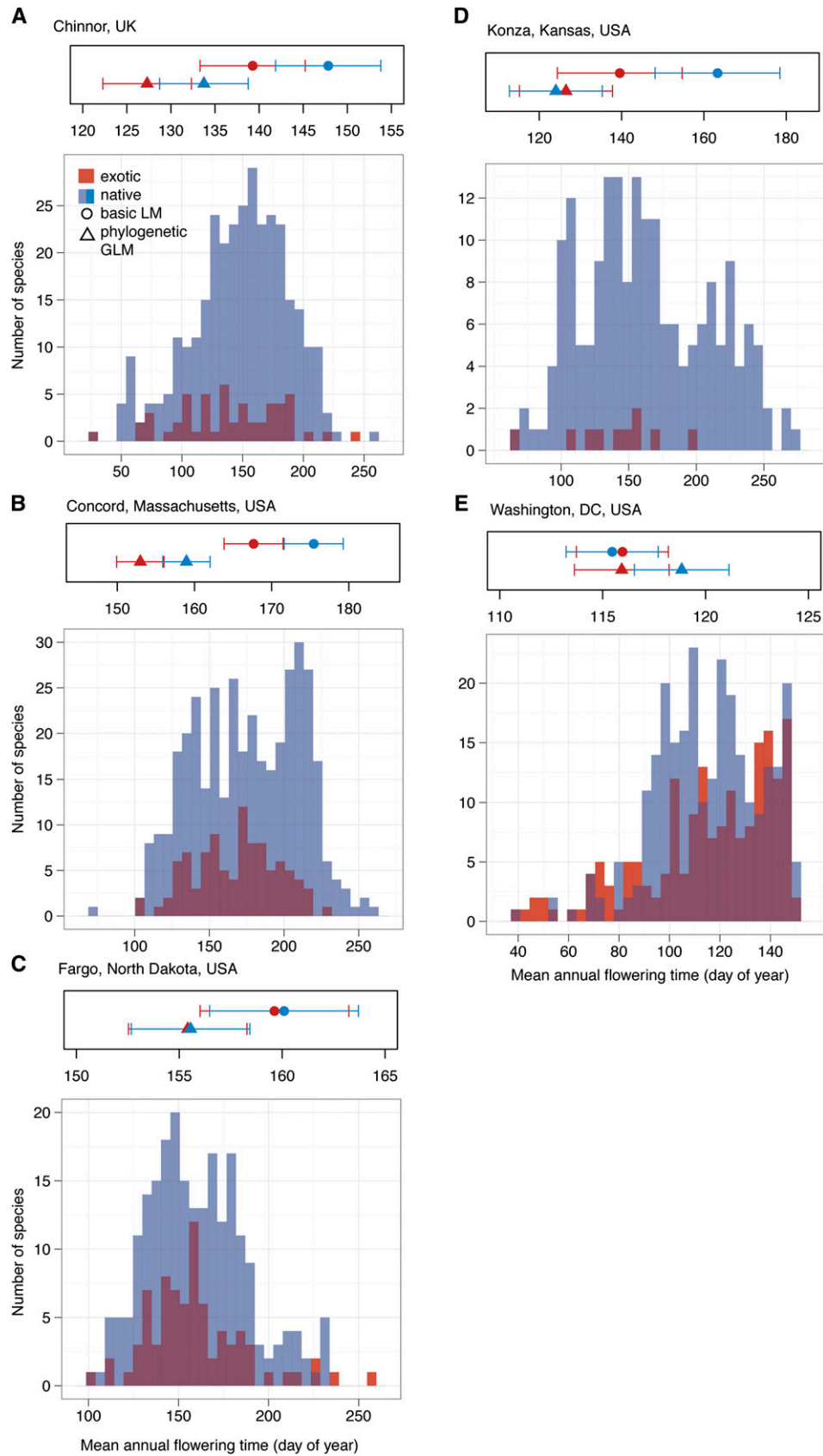


Fig. 2. Comparisons of mean annual flowering times (based on first flowering dates) of exotic and native species across sites. In each panel, we first show mean and standard errors from simple linear models and phylogenetic general linear models, then histograms where darker shading represents areas of overlap.

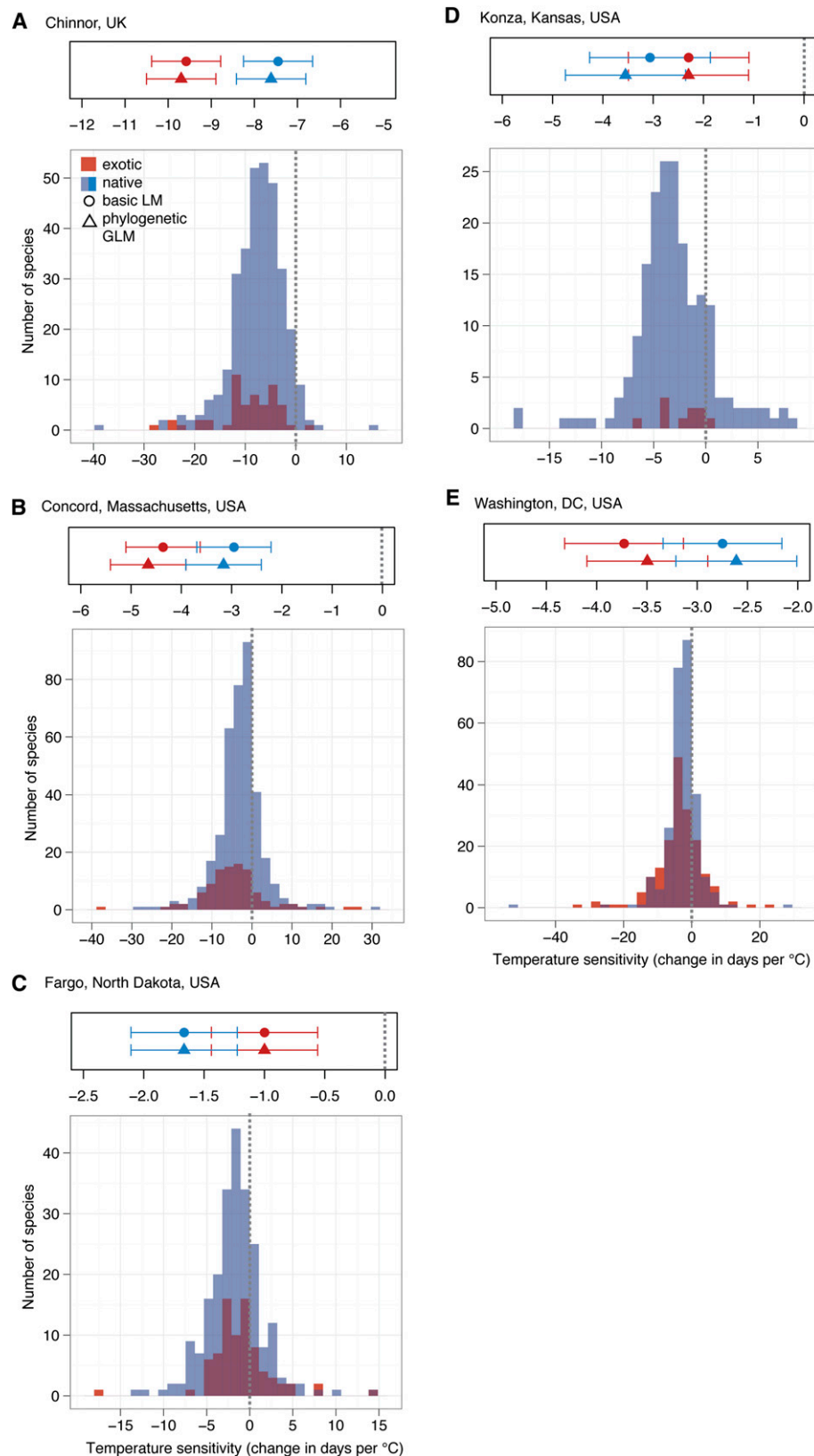


Fig. 3. Comparisons of temperature sensitivities of exotic and native species at each site. In each panel, we first show mean and standard errors from simple linear models and phylogenetic general linear models, then histograms where darker shading represents areas of overlap. Temperature sensitivity was calculated as a regression of first flowering date vs. mean annual temperature; results using sensitivities calculated via other methods were similar (online Appendix S1).

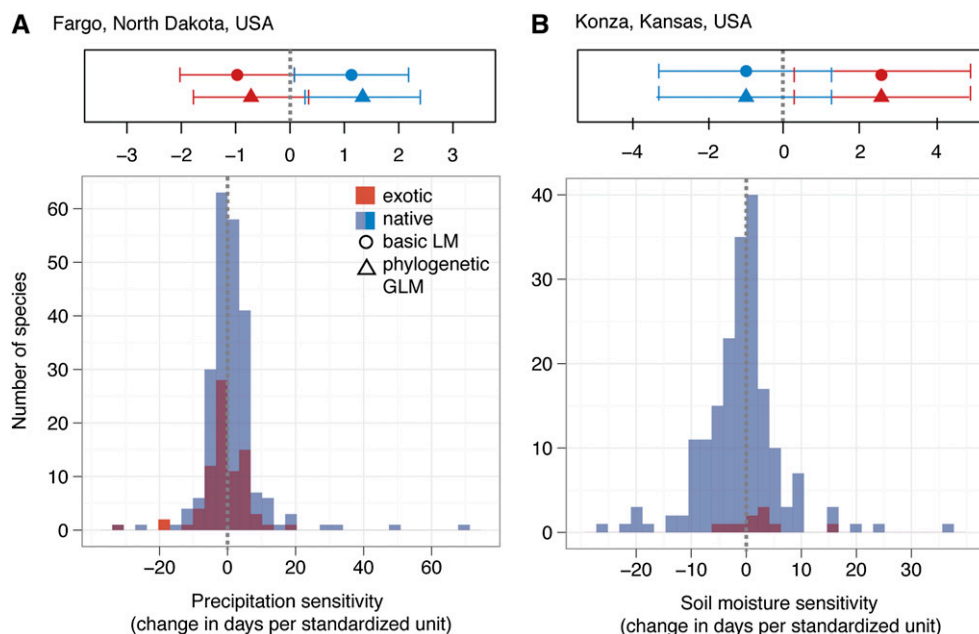


Fig. 4. Comparisons of moisture sensitivities of exotic and native species at (A) Fargo and (B) Konza. In each panel, we first show mean and standard errors from simple linear models and phylogenetic general linear models, then histograms where darker shading represents areas of overlap. Because soil moisture data were only available for Konza, we show precipitation sensitivities for Fargo. For full details on how these were calculated, see *Climate data and climate sensitivities* section of Materials and Methods.

temperature sensitivities, and showed greater flowering time shifts compared to the native community. These results were similar when we examined only the 42 exotic species that were shared with, and native to, Chinnor (Table 2). In the reduced analysis, the 42 exotic species flowered significantly earlier and showed much greater flowering time shifts than the native community; they were also more temperature sensitive, though this was not significant (Table 2). In contrast, at Chinnor these 42 species flowered at the same time as the rest of the community (or, though not significant, slightly later) and were highly similar in their temperature sensitivities and flowering time shifts (Table 2). This variation in the relative differences of these 42 species with their native and with their introduced communities suggests that these species do not establish due solely to unique attributes (e.g., earliest flowering or most temperature sensitive), but that they may invade based on these attributes relative to those of the introduced community. The temperature sensitivities for the species calculated at Chinnor were similar to those calculated at Concord ($n = 42$, $p = 0.64$), suggesting there has been no directional shift in the temperature sensitivities of these species following invasion. We cannot, however, rule out that these differences between the 42 species when analyzed within the native (Chinnor) vs. introduced (Concord) communities are due in part to adaptive shifts of the 42 species after introduction or differing source populations for the introduced range (also see later Discussion section *Unraveling phenology and plant invasions: Future directions*).

DISCUSSION

Our analyses revealed support for both the vacant phenological niche and phenological flexibility models. Considering all sites collectively, exotic species tended to flower earlier than native

species, supporting the vacant phenological niche model. They also showed greater temperature sensitivity and greater flowering time shifts (tending to advance their flowering dates over time concurrent with climate change) compared to native species. These findings of greater temperature sensitivity and flowering time shifts support the phenological flexibility model, which suggests that species with flexible phenologies may be the most successful invaders with climate change (though our results cannot differentiate between whether this flexibility is caused by phenotypic plasticity or local adaptation). Tests comparing species in their introduced and native ranges (Table 2) support that these phenological differences are only present in the introduced range: exotic species considered in their native range did not flower earlier, shift their flowering more over time, nor were they significantly more sensitive to temperature when compared to their native community. This suggests that identifying when phenology will play a role in invasion requires both information on the invader and the introduced community.

We observed important variation between sites, however, which suggests that the role of phenology in facilitating species invasions is contingent upon the local climate regime. Phenological research has tended to focus on mesic, temperate sites (Pau et al., 2011), where soil moisture is unlikely to limit growth, and phenology is strongly controlled by temperature (Nemani et al., 2003; Cook et al., 2012). Thus, trends observed in mesic temperate sites may not extrapolate to sites where soil moisture or other factors are limiting. Indeed, while our overall findings were consistent across the three mesic sites: exotic species tended to flower earlier, and show both greater temperature sensitivities and flowering time shifts, these results did not extend to the two grassland sites. Exotic species at Konza and Fargo flowered at the same time as native species and tended to vary in their sensitivities to moisture, not temperature. Thus, the role of phenology in contributing to species'

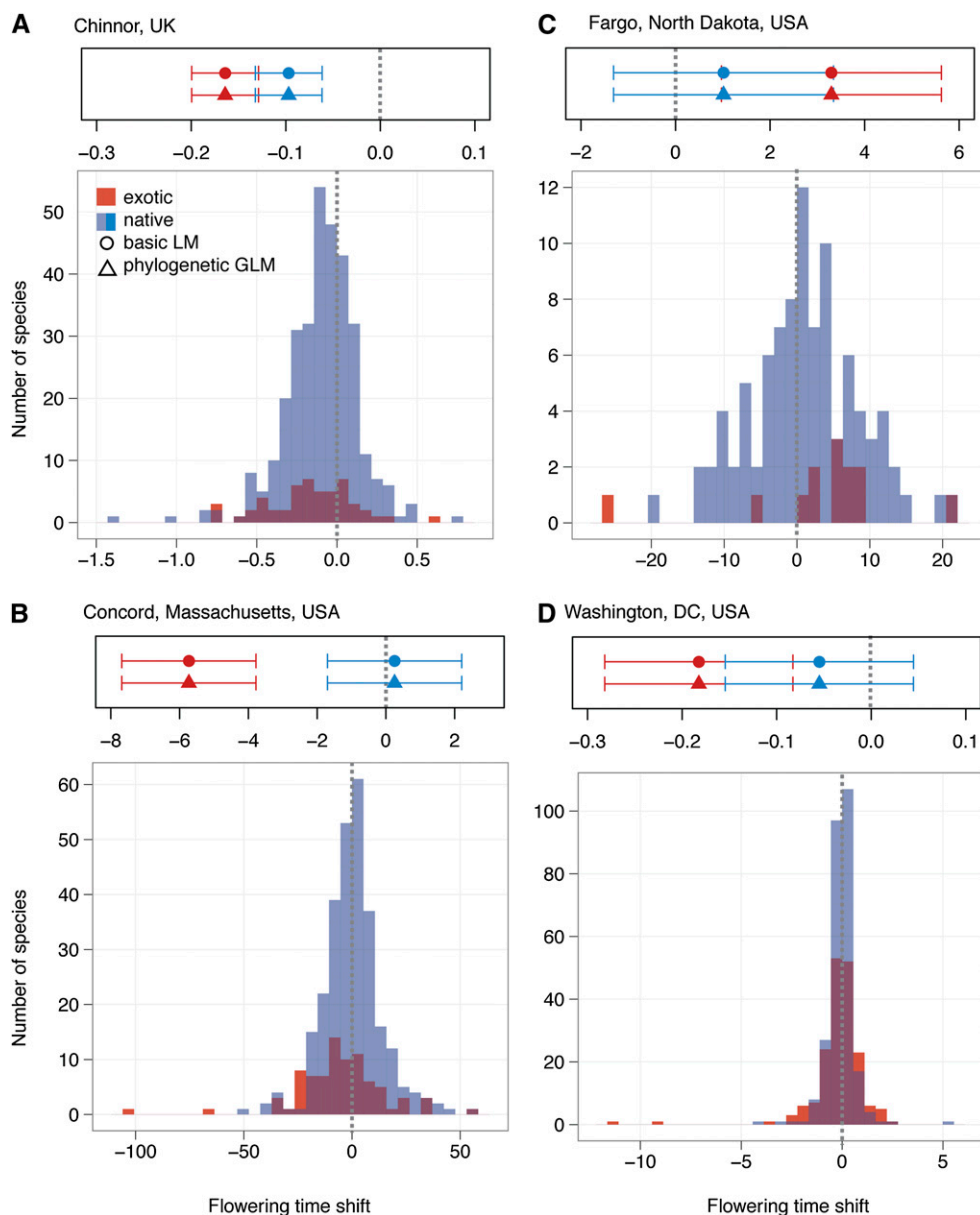
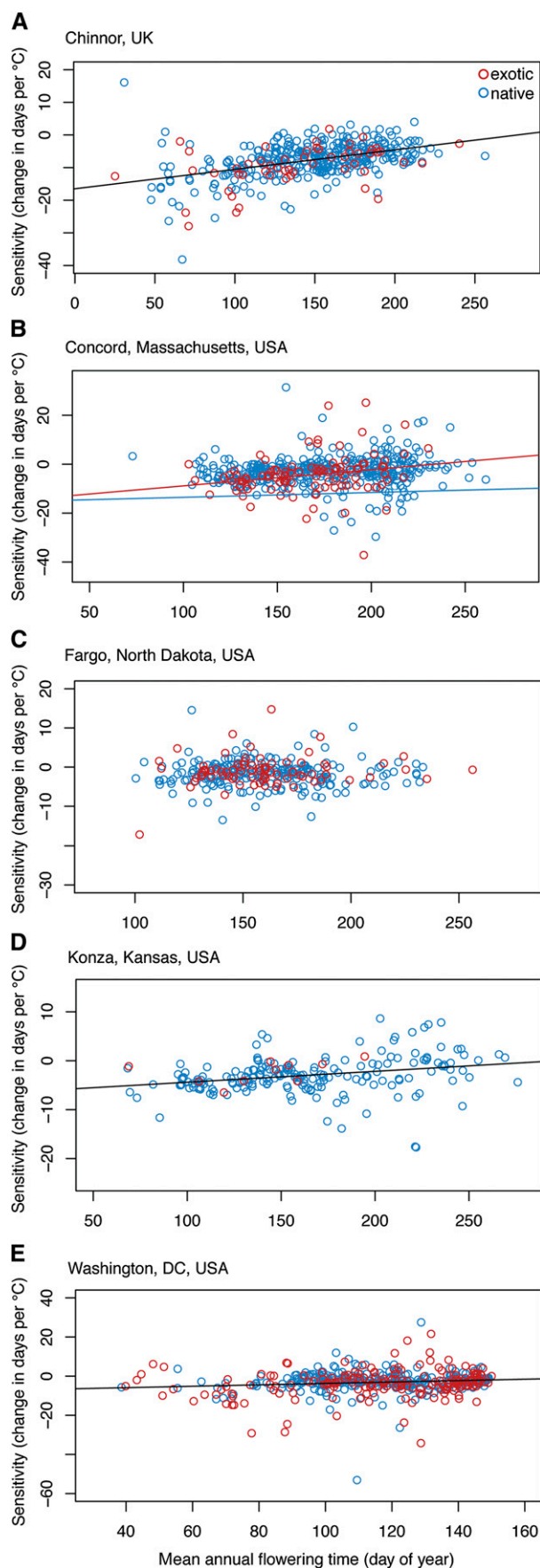


Fig. 5. Comparisons of shifts in flowering time of exotic and native species over time concurrent with climate change at each site. In each panel, we first show mean and standard errors from simple linear models and phylogenetic general linear models, then histograms where darker shading represents areas of overlap. Negative numbers indicate that a species has shifted earlier in recent years. For Konza, we did not have enough data to calculate this; for additional details on exactly how we calculated flowering time shifts for each site, see flowering time shift calculations section of Materials and Methods: *Phenological data*.

invasions into grassland systems may be most dependent on soil moisture regimes. In comparison to temperature, however, our understanding of how soil moisture controls phenology and how it will shift with climate change is especially depauperate, suggesting this is a critical area for further research.

Differences between mesic and grassland systems—Exotic species at the three temperate mesic sites studied here—Chinnor (UK), Concord and Washington, D.C. (USA)—yielded patterns predicted by the vacant niche and phenological flexibility models. They flowered earlier on average than native species. They were not, however, always the first species to flower: the earliest flowering species at Concord was a native species

(Fig. 2B), and native and exotic species together shared the earliest flowering times at Chinnor (Fig. 2A) and at Washington, D.C. (Fig. 2E). Thus, if these species are succeeding in their introduced habitats via early phenology it is not only by occupying a vacant temporal niche. Instead, exotics are likely exploiting multiple niche dimensions (Fargione and Tilman, 2005), of which phenology represents just one niche axis. Exotic species additionally were more sensitive to warming across these three sites—tending to advance their flowering more days per °C of interannual temperature variation (Fig. 3)—and showing greater flowering time shifts (Fig. 5). The strength of these trends varied between sites, however, with the climatically mildest site, Washington, D.C. (Table 1), showing the weakest



trends. This is perhaps not surprising because selection for earlier flowering and close climate tracking may be weaker when climate is milder, and thus the growing season is longer, because the fitness consequences for mistiming phenology are less severe (Pau et al., 2011). We thus hypothesize that the benefit of greater temperature sensitivities is most advantageous to exotic species establishing in systems with the shortest growing seasons, which are often the systems undergoing the most radical temperature shifts with climate change (Trenberth and Josey, 2007).

The two temperate grassland sites—Konza and Fargo—displayed phenological differences between native and exotic species that contrasted with other sites. At both grassland sites, exotic and native species tended to flower at similar times (Fig. 2C, D), rejecting the vacant phenological niche model. Additionally, while exotic species did not significantly differ from native species in their temperature sensitivity, exotic species were more sensitive in their phenological responses to moisture (Fig. 4).

At Fargo, we found that native species tended to delay their flowering with increasing precipitation. This delay may be related to the persistent winter snowpack at Fargo, such that higher precipitation leads to greater snowfall, later snowmelt, and hence later phenology (e.g., Inouye, 2008). Greater snowfall can also increase soil moisture throughout the growing season (O’Leary and Seastedt, 1994), potentially allowing native species to delay flowering to invest in greater growth (Heschel and Riginos, 2005; Kigel et al., 2011; Ivey and Carr, 2012) and thus, later reproduction in years with high precipitation. In contrast, exotic species at Fargo tended to advance flowering with increased precipitation, which may suggest that they do not have a similar strategy.

At Konza, native species tended to advance flowering with greater precipitation but this difference was not significant. In contrast to Fargo, Konza lacks a persistent winter snowpack and is appreciably warmer (Table 1) leading to a dominant midsummer drought that generally occurs around day 215 each season (Craine et al., 2012). The advance of native species with greater precipitation may help avoid summer drought. Exotic species, in contrast to native species, tended to delay their flowering with greater precipitation (following the general pattern of precipitation sensitivities seen in species at the temperate mesic sites; see Appendix S1), and few exotics begin flowering after the midsummer drought (all flowering before day 215, Fig. 2d). A similar dip in exotic flowering was documented at Konza by Craine et al. (2012). Thus, we hypothesize that exotics have adopted an alternative drought avoidance strategy by flowering before moisture becomes limiting. Understanding what drives this decline in exotic flowering surrounding the midseason drought at Konza may be critical to predicting how changes in midseason droughts in other systems will contribute to new invasions. Across two different systems—a temperate grassland and subalpine meadow—warming has led to an increased flowering gap surrounding greater midseason droughts (Sherry et al., 2007; Aldridge et al., 2011), which has been hypothesized

Fig. 6. Relationships between temperature sensitivity and mean annual flowering time (based on first flowering dates). We show a single regression line when only the main effect of first flowering date was significant, regression lines for both the native and exotic species separately when the main effect and interaction were significant, and no line when there was no significant relationship.

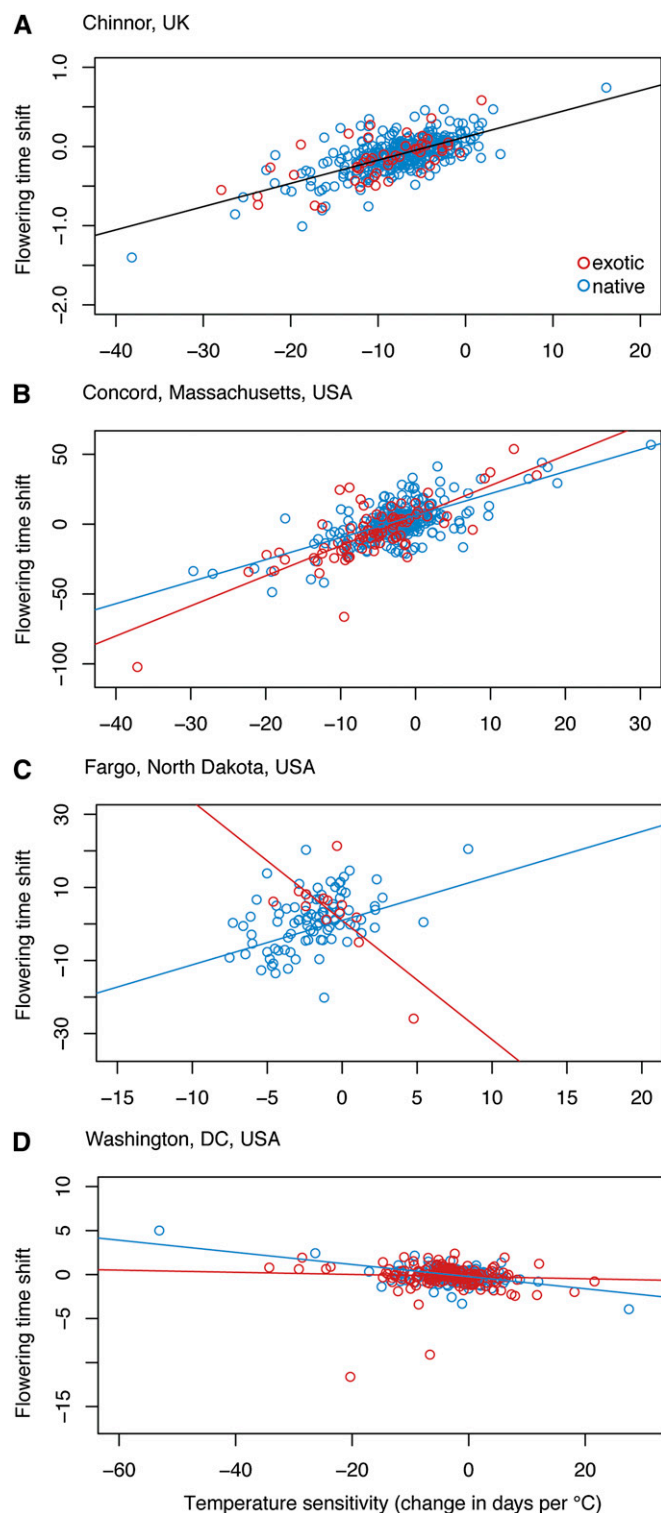


Fig. 7. Relationships between flowering time shifts and temperature sensitivity. We show a single regression line when only the main effect of temperature sensitivity was significant, and regression lines for both the native and exotic species separately when the main effect and interaction were significant.

(Sherry et al., 2007) to possibly promote future invasions via a vacant phenological niche.

Taken together, our results provide additional support that, while temperature control may dominate as the main climate predictor in temperate mesic sites (Cook et al., 2012), temperate grassland systems have additional important precipitation controls. At Fargo, precipitation influences snowpack, and native species delay flowering in years with high precipitation, while at Konza native species advance flowering with greater precipitation to avoid summer drought. In addition, variability in temperature sensitivities at Konza increases markedly around the time of the summer drought (Fig. 6D), suggesting temperature may become a less dominant, or more nuanced, controller on phenology as soil moisture becomes limiting. Our results for Konza, however, are based on relatively limited species sampling (only 10 exotic species) compared to other studies (Craine et al., 2012), and the phenological data span only 9 yr (Table 1). Thus, our power to detect a significant trend may be lower compared to other sites. Nonetheless, our analysis supports the need for improved modeling of responses to precipitation (e.g., Craine et al., 2009; Crimmins et al., 2011). Moisture and precipitation controls on plant phenology are poorly understood, and studies to date suggest contrasting phenological responses to precipitation across systems and species (Fay et al., 2003; Shinoda et al., 2007; Lesica and Kittelson, 2010; Lambert et al., 2010). Our modeling approach was limited to comparing first flowering dates to monthly average volumetric soil moisture or seasonal precipitation summations, but models incorporating snowpack, soil moisture, soil temperature, and the type (snow or rainfall), pattern, timing, and consistency of precipitation may clarify the role of precipitation in grassland systems such as Konza and Fargo.

Phenological responses to climate change and correlations of phenological variables—Our results suggest that in North America the much-heralded “earlier springs” (Abu-Asab et al., 2001; Schwartz et al., 2006; Ellwood et al., 2013) may be driven especially by exotic species’ responses, and the signature of climate change-induced advances by native species, though present (Inouye et al., 2000; Cook et al., 2008), may be more muted in comparison to exotics. We found that flowering times of exotic species have advanced with climate change much more than native species at the three temperate mesic sites (greater flowering time shifts at Chinnor, Concord, and Washington, D.C., Fig. 5). Further, at the three North American sites for which data were available (Concord, Fargo, and Washington, D.C.), the mean flowering time shift of native species was close to zero (Fig. 5B–D), with the majority of native species showing little change and advances in some species countered by phenological delays in others (Fig. 5B–D). Only at the UK site (Chinnor) did native species show significant flowering time shifts earlier over time.

Documenting advances in flowering times of exotic species over time based on first-flowering data are precarious if exotic species are also increasing in abundance over the period of observation because the probability of observing a flowering event may be proportional to abundance (Miller-Rushing et al., 2008). Several lines of evidence, however, suggest our findings are robust to this bias. First, for the one site with abundance data (Concord), we found that trends between exotic and native species in their shifted flowering times persisted when changes due to abundance were included in the model (consistent with findings by Willis et al., 2010), and exotic species tended to advance

TABLE 2. Comparisons of 42 species present at both Concord, USA and Chinnor, UK (“shared species”) and their resident native species communities (“nonshared species”)—where the shared species are native at Chinnor, but exotic at Concord. This tests the general invasion biology principle that traits contributing to species’ invasions should vary distinctly in comparison with the community in the introduced range, but not in comparison with the community in the native range. Note that methods to calculate flowering time shift differed between Chinnor and Concord, based on differences in the data structure at each site, such that absolute values are not directly comparable between sites.

Site: Phenological variable	Mean of 42 shared spp.	Mean of nonshared spp.	df	F	p
Chinnor: mean annual flowering time (day of year)	154.50	146.83	320	1.37	0.24
Concord: mean annual flowering time (day of year)	165.79	175.42	422	4.13	0.08
Chinnor: temperature sensitivity	−5.79	−5.41	320	0.32	0.57
Concord: temperature sensitivity	−6.01	−4.35	422	1.70	0.19
Chinnor: flowering time shift	−0.12	−0.09	317	0.47	0.50
Concord: flowering time shift	−4.72	0.23	325	4.13	0.04

over time more than native species with similar population increases. Second, for species at Chinnor and Concord, advances in flowering showed strong and consistent relationships with species’ temperature sensitivities (Fig. 7A, B), as predicted if species are advancing in response to warming independently from any changes in abundance. Finally, this advance in flowering time response was not universal across sites, it was instead reversed at Fargo—where exotic species show delayed flowering over time (Fig. 5C), which would require a decrease in relative abundances of exotic species over time.

Strong relationships between our measured phenological variables (Figs. 6, 7) highlight that understanding how phenology influences plant invasions will require information on which variables drive community assembly at a particular site. For example, the consistent positive relationship between mean annual flowering time and temperature sensitivity at our three mesic sites indicates that early-flowering species may be inherently better able to track increasing temperatures (Cook et al., 2012; Mazer et al., 2013, in this issue), though recent work has also found the reverse of this trend (Iler et al., 2013, in this issue). Thus, in cases where exotics and natives differ in both flowering time and sensitivity to temperature, for example at Concord, identifying which factor (niche vs. flexibility) is most critical to invader success will require approaches that can disentangle the two.

Unraveling phenology and plant invasions: Future directions—Our findings suggest that the intersection of phenology and shifting climate plays an important role in understanding and, thus possibly predicting, successful invaders across temperate systems. In addition, they highlight that it will be critical to incorporate additional climate variables beyond temperature for understanding how native and exotic communities will be altered by shifting climate regimes. While we confirmed predictions relating phenology to species invasions—especially at temperate mesic sites—we also found that our understanding is notably weaker for sites where precipitation and soil moisture regimes structure communities, such as at the two grassland sites we examined. More specialized climate models and additional climate data, especially related to soil moisture, soil temperature and winter snowpacks, will be critical for generating more powerful phenological models that can be extrapolated to such systems. Overcoming current data limitations (such climate variables are rarely available) and extending the focus of most phenological models from predominantly mesic, temperate systems (Nemani et al., 2003; Cook et al., 2012) would improve understanding of how climate and climate change have influenced species invasions globally. Such developments are critical to predicting species invasions and community shifts in

moisture-limited grassland systems where both temperature and precipitation are expected to shift dramatically with climate change (Dai, 2013; Hansen et al., 2012). If climate shifts away from the long-term precipitation means to which native species’ flowering times appear adapted, we may expect a decline in native species, alongside new invasions into these systems.

Additionally, further work is needed to understand how, and by how much, flowering time shifts and temperature sensitivities of exotic species are a product of phenotypic plasticity vs. local adaptation (Richards et al., 2006). Common garden experiments exploiting clinal variation (Woods et al., 2012) and additional research in the native ranges of exotic species could contribute greatly to this. Such research would also provide more robust tests of whether divergent phenologies of exotic species compared to community means are indeed unique to the introduced range of exotic species, and not mirrored in their native ranges (e.g., Godoy et al., 2009). We provided one such comparison (Table 2), which found that the earlier-flowering, greater temperature sensitivity and greater flowering time shifts observed in the introduced range were not matched in the native range. This may be due to the attributes of the introduced community relative to the attributes of the invader; that is, that the introduced community was vulnerable to invasion by not having native earlier flowering, more temperature sensitive species. However, local adaptation of the exotic species following introduction (e.g., Colautti and Barrett, 2011), or effects of source populations (i.e., the exotic species present at Concord may come from a source population geographically and genotypically different than Chinnor) for the exotic species (Bakker et al., 2009) could also produce this finding. Common garden approaches or more directly comparable metrics could formally test these contrasting mechanisms; of particular utility would be approaches that identify the actual cues driving phenology and how these vary across introduced and native ranges. Our most directly comparable metric—temperature sensitivity—was similar as calculated at Chinnor and Concord suggesting that there has not been a dramatic change in temperature sensitivity of the species post-introduction.

Finally, understanding the absence of shifting flowering times with climate change in many North American native species (Fig. 5) is clearly an important area for future work. A failure to track changing climate in space or time might drive performance declines (Cleland et al., 2012) and future extinctions (Willis et al., 2008). In contrast to North American sites our one European site—Chinnor—showed advances in both native and exotic species over time (with exotics advancing more). Additionally, at Chinnor, there was no variation between exotic and native species in the relationship between temperature sensitivity and flowering time shifts (Fig. 7A). Taken together,

these results suggest the dynamics of how exotic species contribute to community shifts and longer growing seasons may be more extreme in North America where, compared with Europe, plant species invasions have been more recent and prolific (Niemela and Mattson, 1996; Simberloff, 2009). The phenological responses to shifting climate might therefore not only reflect within and between species interactions, but also the biogeographic history of regions. Because plant phenology fundamentally defines growing seasons—and contributes to global estimates of carbon and water balance—understanding how and where exotic species drive changes in the timing and length of seasons is a critical area for further study.

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