Phenology in a warming world: differences between native and non-native plant species

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Abstract

Phenology is a harbinger of climate change, with many species advancing flowering in response to rising temperatures. However, there is tremendous variation among species in phenological response to warming, and any phenological differences between native and non-native species may influence invasion outcomes under global warming. We simulated global warming in the field and found that non-native species flowered earlier and were more phenologically plastic to temperature than natives, which did not accelerate flowering in response to warming. Non-native species' flowering also became more synchronous with other community members under warming. Earlier flowering was associated with greater geographic spread of non-native species, implicating phenology as a potential trait associated with the successful establishment of non-native species across large geographic regions. Such phenological differences in both timing and plasticity between native and non-natives are hypothesized to promote invasion success and population persistence, potentially benefiting non-native over native species under climate change.

Introduction

Phenology, or the timing of life-history events, both responds to and serves as a major indicator of climate change (Peñuelas & Filella 2001, Fitter & Fitter 2002, Menzel 2002, Cleland et al. 2007, Parmesan 2007, Ovaskainen et al. 2013, CaraDonna et al. 2014, Thackeray et al. 2016). For plants, the timing of germination, leaf-out (or green-up), flowering, and fruiting, are frequently determined at least in part by environmental conditions likely to be affected by climate change (Bradshaw 1965, Sparks et al. 2000, Parmesan & Yohe 2003, Badeck et al. 2004, Visser 2008, Forrest & Miller-Rushing 2010, Wolkovich et al. 2013). Because phenology influences interspecific competition, resource access, vulnerability to herbivores, mating success, and ultimately, population and community dynamics (Rathcke & Lacey 1985, Visser & Both 2005, Parmesan 2007, Forrest & Miller-Rushing 2010, Wolkovich & Cleland 2011, Cleland et al. 2012, Thackeray et al. 2016), it is also likely to influence population persistence in the face of future climate change (Møller et al. 2008, Willis et al. 2008, 2010, Donnelly et al. 2011, Cleland et al. 2012, Wolkovich et al. 2013, Thackeray et al. 2016).

Both observational and experimental studies document shifts in phenology in response to global warming, with many species advancing leaf-out, flowering, or both (Arft et al. 1999, Bradley et al. 1999, Fitter & Fitter 2002, Dunne et al. 2003, Parmesan & Yohe 2003, Menzel et al. 2006, Cleland et al. 2007, Jarrad et al. 2008, Amano et al. 2010, Hoffman et al. 2010, Fridley 2012, Ovaskainen et al. 2013, Whittington et al. 2015, Thackeray et al. 2016, König et al. 2017, Zohner & Renner 2017). However, the direction and magnitude of these shifts differ, and some species exhibit delayed phenological responses to warming (Peñuelas et al. 2002, Sherry et al. 2007, Dunnell & Travers 2011, Cook et al. 2012, Liancourt et al. 2012) or no response to warming (Bradley et al. 1999, Peñuelas et al. 2002, Liancourt et al. 2012, CaraDonna et al.

2014). Variable responses to warming may result from differential effects of climate change on early- versus late-season flowering species (Sherry et al. 2007, Park et al. 2018) or variation among species in the degree to which phenology is regulated by photoperiod vs. temperature (Chuine et al. 2010). Furthermore, because species respond differently to climate change, global warming also may alter phenological synchrony, or the degree of overlap in the flowering times of interacting species (Harrington et al. 1999, Stenseth & Mysterud 2002, Visser et al. 2004, CaraDonna et al. 2014, Kharouba et al. 2018, Zohner et al. 2018).

Interestingly, some evidence suggests that native and non-native species may differ in both phenology and phenological responses to warming in ways that could influence biological invasions and favor non-native species in warmer environments (Willis et al. 2010, Wolkovich et al. 2013). Here, we experimentally simulate global warming to test four non-mutually exclusive hypotheses on the role of phenology in non-native species' success developed by Wolkovich and Cleland (2011), all of which may be influenced by global warming: vacant niche, priority effects, niche breadth, and plasticity. (1) The *vacant niche hypothesis* extends Elton's (1958) theory to predict that non-native plants invade when there is a temporally empty niche to exploit. In this scenario, non-native species leaf, flower, and/or fruit earlier or later than native species, allowing them to better utilize temporally available resources. As a result, if global warming increases phenological differences between non-native and native species because they differ in either the magnitude or direction of response, then global warming may increase the availability of vacant niches. A pattern of more asynchronous flowering for non-native species with other community members (i.e., filling more temporally available niches) would further support this hypothesis. (2) *Priority effects* predict that non-native species establish earlier in the season than native species, sequester resources first, and thus may be more competitive (Sale 1977). Consistent with this hypothesis, multiple studies find that non-native species leaf and flower earlier than native species (Crawley et al. 1996, Seabloom et al. 2003, DeFalco et al. 2007, Resasco et al. 2007, Xu et al. 2007, Pyšek & Richardson 2007, Godoy et al. 2009, Pearson et al. 2012, Wolkovich et al. 2013). Priority effects for non-native species may become more prevalent if non-natives exhibit stronger phenological advances in response to warming than natives. (3) The *niche breadth hypothesis* suggests that non-native species occupy a broader niche space, or have longer phenological phases (e.g., leaf or flower for longer periods) than native species and thus gain extended access to nutrients, light, and pollinators. Consistent with this hypothesis, in some systems non-natives flower longer than native species and extend their growing seasons later into the year (Gerlach & Rice 2003, Lake & Leishman 2004, Cadotte et al. 2006). If global warming causes non-native species to extend their growing season or flowering period more than natives, then global warming may increase non-native niche breadth to a greater extent than native species. Finally, (4) the *plasticity hypothesis* proposes that phenological plasticity may provide invaders an advantage in the warmer and increasingly variable climates predicted in the future (Nicotra et al. 2010). In two studies using observational long-term records, non-native species exhibit more plastic flowering times in response to temperature compared to native species (Willis et al. 2008, 2010, Wolkovich et al. 2013).

We experimentally simulated global warming in the field to test the effects of warming (+3°C) on flowering phenology of 42 native and non-native species that are common in western Michigan grasslands and old fields. We also compiled data from the literature and local botanical records to determine time since introduction to North America, current extent (geographic distribution), and reconstructions of species' phylogenetic relationships. Our approach complements prior studies using long-term observations to compare phenological responses of native vs. non-native taxa by allowing us to differentiate phenological responses to warming from other variables that have also changed over the past century. In addition to considering differences between native and non-native species' phenology, we consider differences in the responses of non-invasive exotic and invasive (here defined as widespread and damaging) species, which may help address the question of why only some non-native species become invasive and identify traits associated with increased invasiveness and spatial spread (Pyšek & Richardson 2007, Gallagher et al. 2015, Divíšek et al. 2018). We address the following specific questions: (1) Does the phenology of native and non-native species differ, as predicted by the vacant niche, priority effects, and niche breadth hypotheses, and does warming influence these differences? (2) In accordance with the plasticity hypothesis, do native and non-native species differ in their phenological responses to warming? (3) Do native and non-native species differ in phenological synchrony at the community level as predicted by the vacant niche hypothesis, and how does warming influence phenological synchrony? Finally, because phenology may influence non-native species success and because the ecological and evolutionary processes that influence invasion can change over space and time (Dietz & Edwards 2006, Schultheis et al. 2015), we ask (4) Are flowering time and phenological plasticity correlated with spread (geographic distribution in the introduced range) of non-native species, and is there evidence that non-native species have evolved increased phenological plasticity to temperature since their introduction?

Materials and Methods

Field warming experiment

We established this experiment within the warming array at the Kellogg Biological Station (KBS), which has run constantly over the growing season (April-October) since its establishment in 2008. The warming array uses infrared heaters to elevate temperatures 3°C above ambient temperatures, matching regional predictions for climate warming in this area by the end of the 21st century (0.3°C-4.8°C) (Stocker et al. 2013). The array consists of four 3m-diameter plots, each surrounded by six infrared ceramic heaters (Model FTE-1000, Kalglo, Inc.) that evenly raise temperature across similar heating arrays (Kimball et al. 2008). Dummy heaters are suspended above four additional control plots to control for shading effects. Heaters are regulated by a proportional-integrative-derivative (PID) control system, which allows for a consistently elevated temperature relative to focal control (no heater) plots {see Kimball et al. (2008) for a full description of the heating apparatus}. Such heating designs have been shown to be effective at maintaining temperatures within 0.5°C of the target level 75% of the time (Kimball et al. 2008, Fig. S1).

In spring 2012, we planted 52 species (25 native, 12 exotic, 15 invasive) into the background early successional community in each plot (n=3 replicates/species/plot). Of these, 42 species (20 natives, 22 non-natives {7 exotic, 15 invasive}) survived to flower in 2013 and were included in this study. Study species were all forb and grass species found in old field or grassland habitats and, when possible, were selected congener or confamilial triplets of native, exotic, and invasive species representing a broad range of phylogenetic diversity (Schultheis et al. 2015). To avoid unintentional introduction of new invasive species to the area, we only included species reported in Kalamazoo County (McKenna 2004). When possible, we chose species that had local seed available, either through our own collections or commercial seed sources (see Table S1 in Supporting Information). Variation among seed sources did not influence results as analyses that excluded seeds sourced from outside the Midwest or that controlled for seed source by including a factor for seed source both yielded qualitatively similar results to those presented below (data not shown). Species were considered native if they were present in Michigan prior to European settlement (McKenna 2004). The non-native species are all from outside the United States, based on herbarium or historical records (Michigan Flora [http://michiganflora.net], Consortium of Midwest Herbaria [http://midwestherbaria.org/portal/]). We further categorized non-native species as invasive or non-invasive exotic, because differentiating between these two types of non-native species can yield important information on the drivers of invasiveness (Agrawal et al. 2005, Stricker and Stiling 2014, Schultheis et al. 2015). Species were characterized as invasive (here defined as widespread and damaging non-native species) if they were listed on one or more of the following as of June 2014: (1) Michigan Natural Features Inventory (Borland 2009), (2) Czarapata (2005) list of “major invader[s] of natural areas” not needing disturbance to establish, (3) Wild Type Plants (http://www.wildtypeplants.com), and (4) the Michigan Seed Law (Act 329 of 1965) (http://www.michigan.gov/). Inclusion on these lists means a species has been categorized as invasive in the midwestern United States based on reports from land managers, inclusion on government invasive species lists, or published documentation of their impacts on native plant and animal communities (Schultheis et al. 2015). We note that there can be substantial disagreement about an “invasive” classification and that invasive status often depends on local biotic and abiotic factors. Because of these concerns, we present results for the native vs. non-native comparison in the main text and results for native, exotic, and invasive comparisons in Supporting Information.

We germinated seeds of all species in low-nutrient potting media in the greenhouse and then transplanted seedlings into randomly selected locations within each field plot. Seedlings were planted 20cm apart and watered as needed to facilitate establishment. During the 2013 growing season, we recorded the flowering stage of each plant (bud, flower, or fruit) at weekly intervals (starting 21 May 2013). From this data we determined four phenological variables relevant to the hypotheses proposed by Wolkovich and Cleland (2011): (1) days to first flower, (2) days to last flower, (3) duration of flowering period, and (4) days to first fruit.

Data analysis

Because of the nested structure of our experimental design and potential phylogenetic non-independence of our study species, we analyzed our data in two ways. First, we determined the effects of warming and status (native or non-native) on phenology using a linear mixed model (SAS Institute 2011, PROC MIXED). We included days to first flower, days to last flower, flowering period length, or days to first fruit as four separate response variables. We included warming (ambient or elevated), status (native or non-native) and the warming by status interaction as predictor variables in each model. Plot (nested within warming treatment) and species (nested within status) were included as random factors. Post-hoc contrasts were used to evaluate differences between statuses and warming treatments when the warming by status interaction was significant ($p \leq 0.05$). We used similar models to test the effects of warming, species, and the warming by species interaction to examine variation among species independent of status, with plot within warming treatment included as a random effect.

To control for phylogenetic non-independence between species in our study, we conducted additional analyses that accounted for phylogenetic relatedness. First, we retrieved nucleotide sequences for *ITS, matK*, and *rbcL* from NCBI Genbank for each species (accessed November 2016) (Table S1). Using the MUSCLE algorithm in Geneious v6.1.8 (Kearse et al. 2012) we aligned gene sequences. We trimmed the ends of each sequence and concatenated the three genes using the R function phyutility (Smith & Dunn 2008). We determined the optimal model of molecular evolution for the alignment using the Akaike Information Criterion (AIC), Bayesian Information Criterion (BIC), and Performance Based Selection (DT) using ModelTest2 v2.1.7 (Darriba et al. 2012). All three methods selected the General Time Reversible model, with rate heterogeneity including invariable sites and the rate of evolution at other sites as a gamma distribution (GTR + I + Γ), as the optimal model. Maximum likelihood (ML) analysis with 100 bootstrap replicates was implemented with the high-performance computing version of RAxML v8.1.17 (Stamatakis 2014). We included a partition file for ML analysis to account for gene regions in the concatenated alignment.

We then performed phylogenetic generalized least squares (PGLS) analyses with Brownian motion models of trait evolution (Garland et al. 1993, Martins & Hansen 1997). PGLS was implemented by incorporating the constructed phylogeny (Fig. S2) into the covariance structure using the R package ape (v3.1-4, Paradis 2012), after which the linear models were fit using the gls function in the R package nlme (v3.1-119, Pinheiro et al. 2015). Each of the four phenological measurements were included as separate response variables and warming, status, and the warming by status interaction were included as fixed predictor variables.

Results from the two analyses were similar, so for clarity we present mixed model results in the main text because they use the appropriate nested field replication and report PGLS results in Supporting Information (Table S3).

Phenological synchrony

We examined the effects of warming and status on phenological synchrony between individuals at the community level using Augspurger's (1983) method, which measures synchrony (X) as the amount of overlap between an individual's flowering days with those of all other individuals within some defined population or community. A score of X=1 indicates complete synchrony; a score of X=0 indicates complete asynchrony. We calculated phenological synchrony at the community level as the amount of overlap of a given individual's flowering days with all hetero- and conspecific individuals within the same warming treatment (X). We used a linear mixed model to examine the effects of status, warming, and their interaction on X and included species (nested within status) and plot (nested within treatment) as random factors. We performed all synchrony analyses in R (R Core Team 2016, v3.3.2).

Phenological plasticity, invasion spread, and invasion time

We examined whether phenological plasticity in flowering time is correlated with species' geographic spread. We calculated the phenological plasticity of each species as the difference in mean days to first flower between elevated and ambient temperatures. Geographic spread was determined by counting all United States counties in which a species is found and indicated as "introduced" in the USDA PLANTS database (https://plants.usda.gov). We determined the effects of phenological plasticity and status on geographic spread using a linear model with geographic spread (number of US counties) as the response variable and status (native or non-native), phenological plasticity, and the status by plasticity interaction as predictor variables. Flowering time bears on the role of priority effects in invasion, so we also examined whether flowering time is correlated with geographic spread. We used a linear model to examine the effects of days to first flower, status, and the status by days to first flower interaction on geographic spread (number of US counties).

We then examined whether time since introduction is correlated with phenological plasticity in non-native species. We calculated time since introduction as the number of years a species has been found in Michigan, based on the date of first collection recorded in the Michigan Flora database (http://michiganflora.net). We determined the effects of time since introduction and status (exotic or invasive) on phenological plasticity using a linear model, including phenological plasticity as the response variable and status, time since introduction, and the status by time interaction as predictor variables.

To account for shared ancestry, we performed PGLS with Brownian models of trait evolution using the same linear models for geographic spread and time since introduction described above. We performed all geographic spread and time analyses in R (R Core Team 2016, v3.3.2).

Results

Effects of warming on native and non-native species' phenology

Non-native species exhibited advanced phenologies compared to native species (days to first flower, days to last flower, and days to first fruit (all $p \leq 0.05$; Fig. 1; Table S2) and accelerated their phenology in response to warming more than native species (status × warming: flowering $F_{1,283}=4.73$, $p=0.03$; days to last flower $F_{1,283}=5.70$, $p=0.02$; days to first fruit $F_{1,281}=6.03$, $p=0.02$; Fig. 1; Table S2). Similar results were observed even after accounting for phylogeny (Table S3). For non-native species, warming significantly accelerated flowering by 11.42 ± 6.79 days ($F_{1,283}=12.42$, $p=0.0005$), days to last flower by 14.12 ± 6.95 days

($F_{1,283}$=16.65, p≤0.0001), and days to first fruit by 10.91 ± 6.47 days ($F_{1,281}$=14.83, p=0.0001). Native species did not respond phenologically to warming (all p≥0.6; Fig. 1) and thus flowered 38.76 ± 7.12 days later and fruited 32.95 ± 6.97 days later than non-native species under warming (compared to 28.45 ± 7.00 and 22.38 ± 6.91 days later than non-natives under ambient temperatures for flowering and fruiting respectively). Finally, because species shifted days to first and last flower similarly, no effects on flowering period were observed (Table S2). However, when phylogenetic relationships are accounted for, native, and non-native species differed in how flowering period responded to warming (Table S3). Nonnative species shortened their flowering periods by 2.74 ± 3.26 days while native species tended to maintain the same flowering periods regardless of temperature.

These differences between non-native and native species were likely driven by the strong phenological responses of invasive relative to exotic species (Fig. S3, Table S4-5). Of the 8 species that significantly accelerated flowering in response to warming, 5 were invasive, 0 were exotic, and 3 were native (Fig. 2, Table S6).

It is possible that these patterns were driven by the Poaceae because in this family all of the non-native species included in our study happen to be C_3 grasses while most included natives are C_4 grasses (with the exception of C_3 native *Bromus kalmii*); C_3 species may advance flowering in response to warming more so than C_4 species, as shown in C_3 *Chenopodium album* relative to C_4 *Setaria viridis* (Lee 2011). However, results were qualitatively similar when C_3 Poaceae species were excluded from analyses (data not shown). It is also possible that native origin of the non-native species influenced phenology; however, most species included in our study originated from Europe or Eurasia, and flowering dates did not differ between species from these regions ($F_{1,18}$=0.93, p=0.35).

Effects of warming and status on phenological synchrony

Warming increased the phenological synchrony of non-native, but not native, species with other community members (warming × status $X^2_{1,311}$=17.61, $p \leq 0.0001$; Fig. 3). As a result, non-native species flowered more synchronously with other community members than native species did in the elevated temperature treatment but not in the ambient temperature treatment. This pattern was likely driven by the increased synchrony of exotic species under elevated temperatures (Fig. S4).

Phenological plasticity, invasion spread, and invasion time

In non-native species, earlier flowering was significantly associated with wider geographic spread, whereas native species' flowering time was not correlated with their geographic distributions (status × days to first flower $F_{3,33}$=9.66, p=0.004; non-native R^2=0.37, p=0.004; native R^2=0.13, p=0.16; Fig. 4A; Table S7A). Phenological plasticity was not associated with geographic spread ($F_{3,30}$=0.19, p=0.66; R^2=0.23; Table S7B). Results for both phenological plasticity and flowering time were similar when controlling for phylogeny (Table S8A-B) and when excluding C_3 grasses (days to first flower [DFF]: status × DFF $F_{1,25}$=7.64, p=0.01; plasticity: status $F_{1,22}$=6.80, p=0.02). Our choice of scale may influence these patterns (e.g., northern ranges are truncated by not including Canada). Results are non-significant when we used number of Michigan counties as a local measure of geographic spread (Table S9), likely because many native species occupy more Michigan counties than non-native species do. Exotic and invasive species exhibited similar relationships between earlier flowering and spread (Table S10A).

We detected some evidence that longer time since introduction was associated with increased phenological plasticity for invasive species but not for exotic species (status × time $F_{1,14}$=4.04, p=0.06; Fig. 4B; invasive R^2=0.62, p=0.007; exotic R^2=0.02, p=0.7). This pattern remains significant after controlling for phylogeny (Table S8) and is not driven by invasive C_3 grasses (when excluded, patterns were similar but non-significant, likely because of the reduced power resulting from the exclusion of 13 species {Fig. S5}). While removing the highly plastic and early-invading outlier, *Lotus corniculatus,* eliminated the significant status × time interaction in the mixed model, suggesting that the pattern was heavily influenced by this outlier, the status × time interaction in the phylogenetically-controlled analysis remained significant even when this outlier was removed ($t_{1,12}$=5.87, p=0.03).

Discussion

In the 42 species studied here, non-native species flower and fruit earlier than native species, and warming increases these differences. Warming significantly accelerated both flowering and fruiting and increased phenological synchrony of non-native species. In contrast, warming did not alter native species' phenology. Earlier flowering, but not phenological plasticity, was associated with the geographic spread of non-native species, potentially suggesting that early phenologies may help promote successful establishment across large geographic ranges. Together these findings suggest potentially important differences in native and non-native species' phenologies and phenological responses to climate change, which may have implications for the future success of native vs. non-native species in a warming world.

Vacant niche/priority effects hypothesis

Non-native species flower and fruit earlier than native species, particularly under warming, consistent with the priority effects hypothesis proposed by Wolkovich and Cleland (2011). Earlier flowering may allow earlier access to pollinators and resources (Sale 1977, Wolkovich & Cleland 2011), help introduced species avoid warmer temperatures and limited precipitation later in the season (DeFalco et al. 2007, Sherry et al. 2007, Craine et al. 2012), and allow non-native, particularly widespread invasive, species to become more competitive within the invaded community. Early phenologies have been observed in several of the most problematic invasive species, including *Lonicera maackii* (Resasco et al. 2007, Xu et al. 2007), *Centaurea solstitialis* (Gerlach & Rice 2003), *Bromus tectorum* (DeFalco et al. 2007), California annual grasses (Seabloom et al. 2003), and exotic species dominating US grasslands (Wilsey et al. 2018). Other work suggests that non-native species benefit from priority effects by beginning growth earlier in the season than natives (Dickson et al. 2012, Fridley 2012, Wilsey et al. 2015). Supporting these studies, we find that non-native species with earlier flowering times have wider geographic distributions, suggesting that priority effects may play a role in invasion success. Global warming may increase the strength of priority effects favoring non-native species as non-natives shifted flowering earlier in response to rising temperatures while native species did not respond to warming, increasing the magnitude of difference in flowering time between native and non-native species.

While advanced flowering of non-native species may also be consistent with the vacant niche hypothesis, native and non-native species did not exhibit different patterns of phenological synchrony under ambient temperatures, perhaps suggesting that non-natives are not occupying vacant phenological niches for much of their flowering periods even though their phenologies are shifted substantially earlier than native species. Non-native species' (particularly exotics') flowering became even more synchronous under elevated temperatures. Synchronous flowering with other community members can increase pollinator visitation, thereby increasing reproduction and seed set (Bawa 1977, Augspurger 1981, Ollerton & Lack 1992, 1998, Brown & Mitchell 2001, Donnelly et al. 2011, Burkle et al. 2013), but also may increase competition for pollinators (Memmot et al. 2007, Cleland et al. 2012, Burkle et al. 2013). In contrast to our finding, other studies have detected decreased synchrony under warming in grassland plant species, European herbaceous and woody species, and bird populations (Sherry et al. 2007, Reed et al. 2013, Wang et al. 2016, Zohner et al. 2018). Further work is needed to understand how phenological synchrony will shift with climate change (Kharouba et al. 2018) and how synchrony changes will influence community composition and the success of individual populations under global warming.

Niche breadth hypothesis

Though a few species shifted the length of their flowering periods with warming, we find no evidence generally supporting the niche breadth hypothesis. Native and non-native species' flowering periods did not differ, and because species shifted days to first and last flower similarly under warmed and ambient treatments, warming minimally affected flowering duration (non-natives did significantly increase flowering period under warming when controlling for evolutionary history).

Plasticity hypothesis

Non-native (and especially invasive) species accelerated flowering in response to warming more than native species, supporting Wolkovich and Cleland (2011)'s plasticity hypothesis, a potentially worrisome result given previous observational work demonstrating that phenological plasticity was associated with increased abundance and/or performance over the past decades of warming temperatures (Willis et al. 2008, 2010, Cleland et al. 2012, Wolkovich et al. 2013, Lamarque et al. 2015). For example, Willis et al. (2010) found that non-native, but especially invasive, species shift flowering time more than native species in response to interannual variation in temperature and that this plasticity correlated with increases in abundance over a 100-year time-span, characterized by a 2.4°C temperature increase (Willis et al. 2008). Similarly, in cross-continental comparisons, *Acer negundo* populations from the invasive range demonstrate greater phenological sensitivity to temperature and increased growth than native range populations (Lamarque et al. 2015). Enhanced phenological plasticity in non-native and particularly widespread invasive species may be part of a broader pattern of increased phenotypic plasticity in a variety of traits that may enhance invasion success (Davidson et al. 2011), but studies linking phenological plasticity to fitness and population growth are needed.

Interestingly, early colonizing non-native species exhibited greater phenological plasticity than more recent colonizers, possibly as a result of post-introduction evolution as populations are selected to shift phenological cues to those that are more relevant to the novel invaded environment. However, this pattern was influenced by *Lotus corniculatus,* an exceptionally plastic invasive species that established early, and there are several additional viable hypotheses for this pattern. First, species that rely more on temperature than photoperiod as a flowering cue may be more successful at matching their phenology to novel conditions and may have established more quickly and earlier than other invaders. Second, phenological plasticity or early flowering may not be the target of selection; instead phenological traits may be correlated with another trait under strong selection post-invasion (e.g., height or specific leaf area) (Anderson & Gezon 2014, Cooper 2018). Third, early-flowering species have been shown to shift flowering earlier under warming temperatures relative to late-flowering species (Sherry et al. 2007). Because invaders flower earlier than natives, this general pattern could also explain the difference in plasticity between invaders and natives: however, early- and late-flowering species do not differ in their warming responses in our study (i.e., days to first flower was not correlated with phenological plasticity, R^2=-0.03 p=0.99).

In our study, we did not detect any effect of warming on the reproductive phenology of native species. Similar to the decline of bird species' whose spring migration does not track climate change (Møller et al. 2008), inability to track climate and adjust flowering time has been shown to be associated with declines in native plant species' abundance (Stenseth & Mysterud 2002, Willis et. al 2008) and biodiversity (Wolf et al. 2017). This may be due to challenges associated with maintaining mutualistic interactions with pollinators or dispersers that are also responding to climate change (Memmot et al. 2007, Cleland et al. 2012, Burkle et al. 2013) or avoiding negative interactions with predators and competitors, including invasive species (Tikkanen & Julkunen-Tiitto 2003, Willis et al. 2008). If species with weak phenological responses are more prone to population declines (Willis et al. 2008), then native species may be at higher risk of extinction as the climate warms.

Conclusion

Our results show that non-native species flower and fruit earlier than native species and that non-native, but especially invasive, species accelerate phenology under warming temperatures, providing support for the priority effects and plasticity hypotheses (Wolkovich & Cleland 2011) and suggesting that warming may promote invasion success. As a group, native species in our study did not significantly advance flowering under simulated warming. This may affect seed set and fitness if a failure to accelerate flowering disrupts interactions with pollinators or causes other mismatches between ideal abiotic conditions for flowering and flowering time (e.g., temperature stress can inhibit pollen viability; Brown & Mitchell 2001). Further experimental work is needed to determine whether phenological plasticity is associated with plant fitness and demographic effects of climate change in long-lived species and to investigate the relative importance of plasticity and adaptation in phenological responses. However, this study of 42 species suggests that native and non-native taxa differ in key phenological traits and that global warming magnifies these phenological differences. Our findings illustrate the potential importance of phenology to invasion success and also prompt concerns that these phenological differences could be a mechanism by which global warming will advantage non-native species and disadvantage natives.

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Supporting Information

Figures

Figure 1. Effect of warming on (A) days to first flower, (B) days to last flower, (C) flowering period duration (days), and (D) days to first fruit for native and non-native species (least square means ± SE; N = 20 native and 22 non-native species). Letters represent significant differences between groups (adjusted for multiple comparisons with a Tukey test, $p \leq 0.05$).

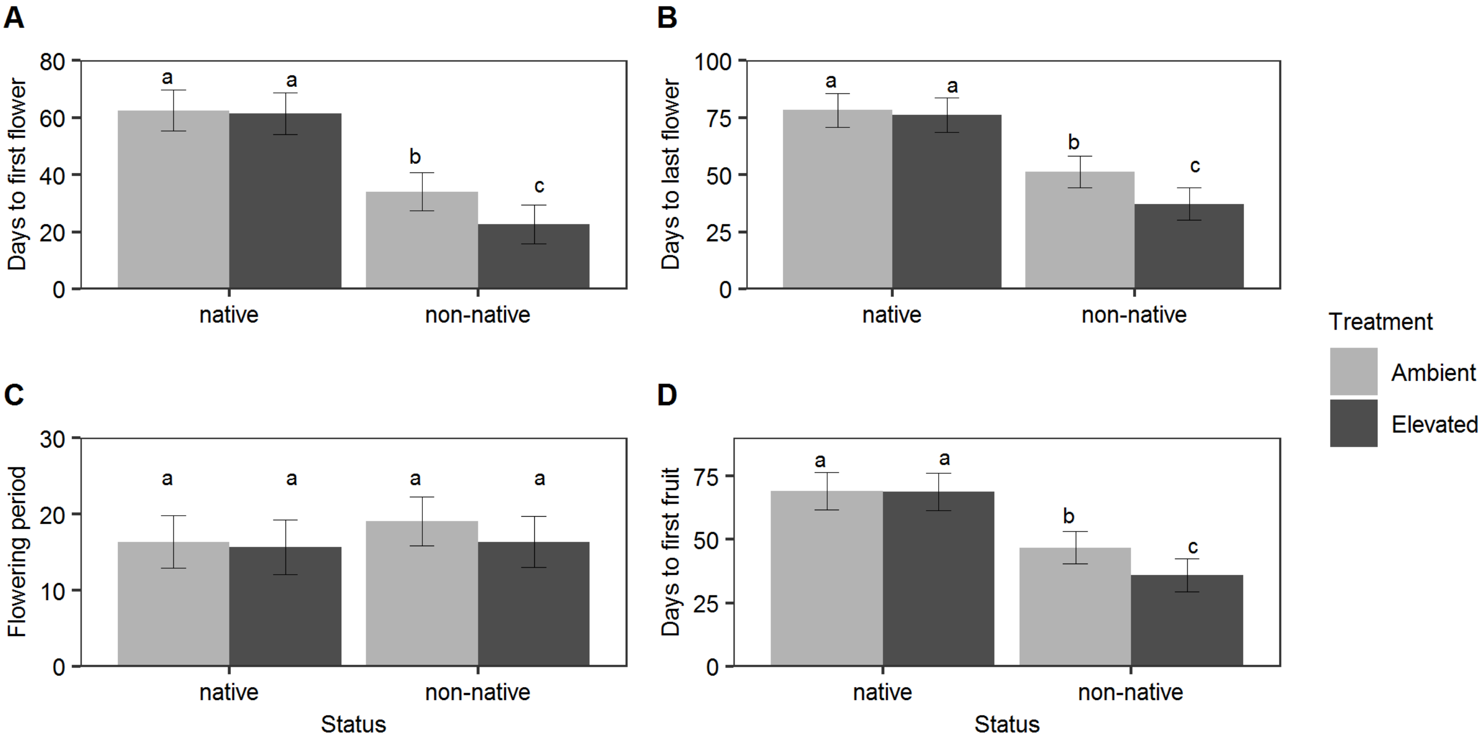


Figure 2. The effect of warming on flowering phenology of invasive, exotic, and native species. Each line represents the period between the Julian calendar date of first flower (DFF, left point) and the date of last flower (DLF, right point) (LSmeans ± SE). Gray and black bars represent ambient and elevated temperatures, respectively. Only species with data available for both DFF and DLF are included. * indicates a significant advance and ‡ represents a significant delay in DFF ($p \leq 0.05$).

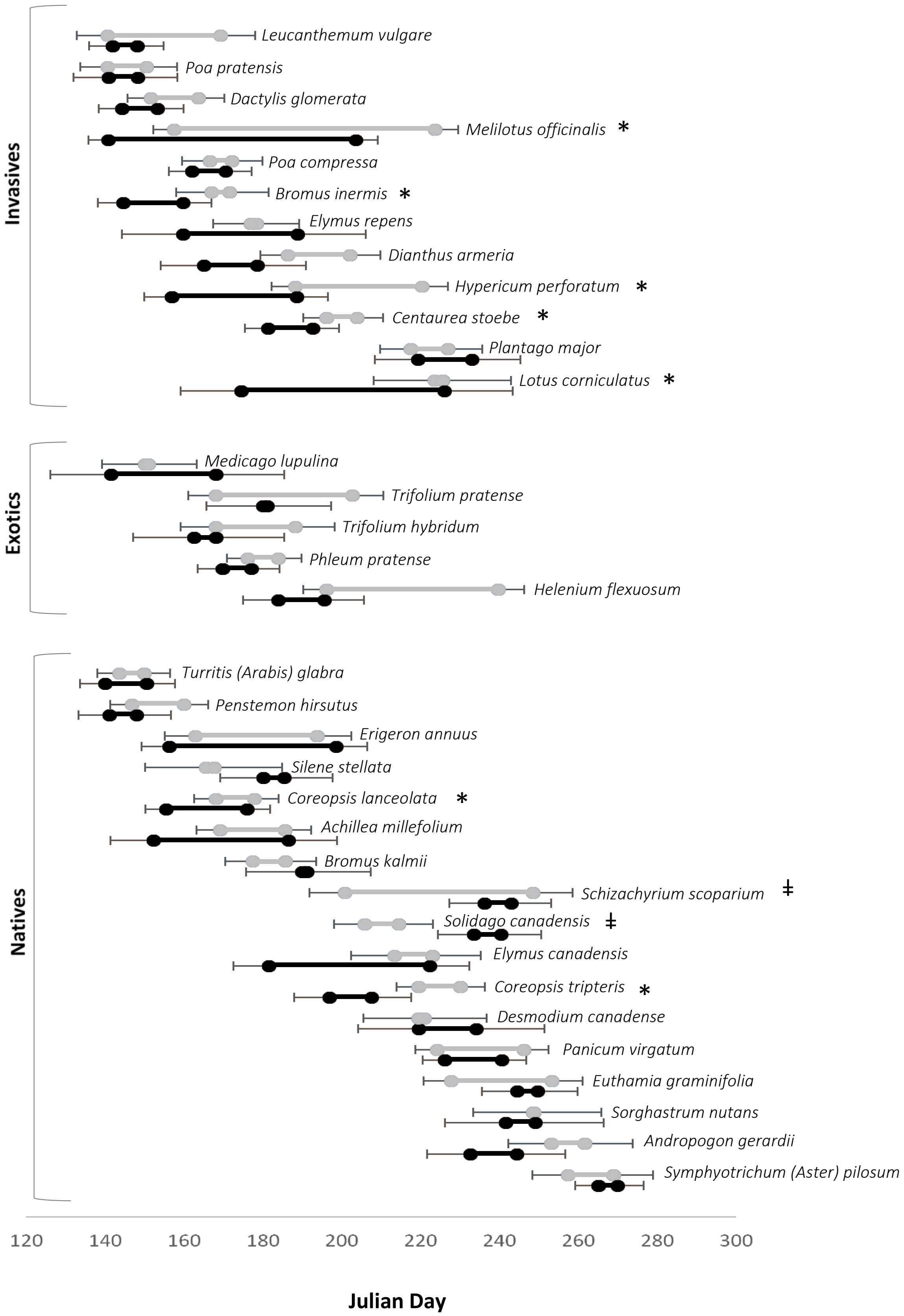

Invasives
Leucanthemum vulgare
Poa pratensis
Dactylis glomerata
Melilotus officinalis *
Poa compressa
Bromus inermis *
Elymus repens
Dianthus armeria
Hypericum perforatum *
Centaurea stoebe *
Plantago major
Lotus corniculatus *
Exotics
Medicago lupulina
Trifolium pratense
Trifolium hybridum
Phleum pratense
Helenium flexuosum
Natives
Turritis (Arabis) glabra
Penstemon hirsutus
Erigeron annuus
Silene stellata
Coreopsis lanceolata *
Achillea millefolium
Bromus kalmii
Schizachyrium scoparium ǂ
Solidago canadensis ǂ
Elymus canadensis
Coreopsis tripteris *
Desmodium canadense
Panicum virgatum
Euthamia graminifolia
Sorghastrum nutans
Andropogon gerardii
Symphyotrichum (Aster) pilosum
120
140
160
180
200
220
240
260
280
300
Julian Day

Figure 3. Phenological synchrony (X) (least square means ± SE) of native and non-native species under ambient and elevated (+3°C) temperatures. A phenological synchrony score of X=1 indicates complete synchrony among all individuals experiencing the same warming treatment, where all species start flowering at the same time and for the same length of time. A score of X=0 indicates complete asynchrony, or no overlap in flowering. Letters represent significant differences between groups (adjusted for multiple comparisons with a Tukey test, p≤0.05).

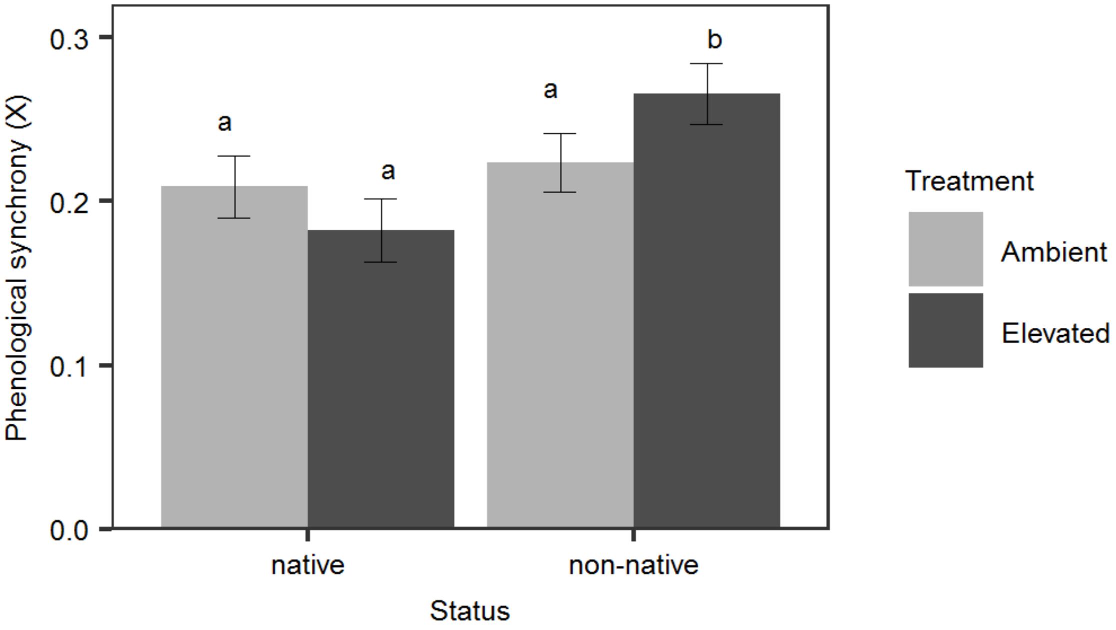
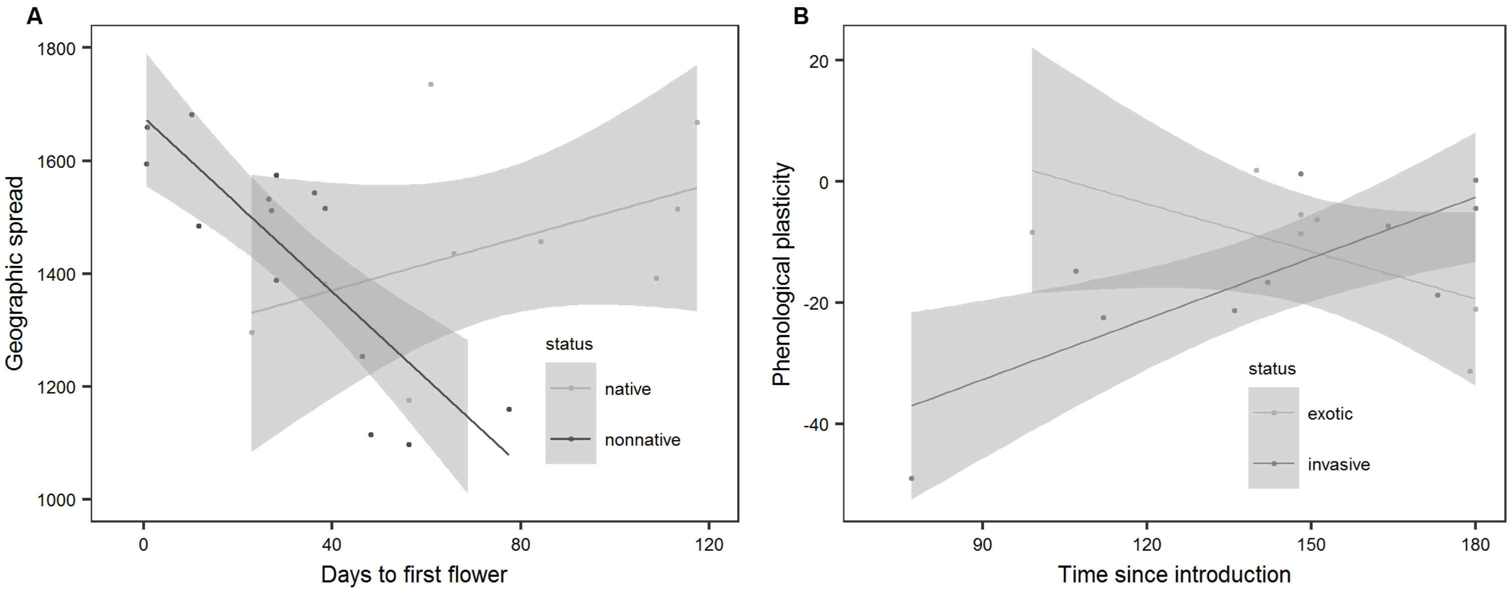


Figure 4. (A) Effect of flowering time (days to first flower under ambient conditions) on the geographic spread of native and non-native species (non-native R^2=0.38, p=0.004; native R^2=0.13, p=0.16). (B) Effect of time since introduction to Michigan (MI) (years) on phenological plasticity for invasive and exotic species (invasive R^2=0.62, p=0.007; exotic R^2=0.02, p=0.7). Gray areas represent 95% confidence intervals.



Supporting Information for "Phenology in warming world: differences between native and non-native plant species"

Figure S1. Air temperature in the warming array

Air temperature data (°C) in ambient and elevated plots in the warming array over the 2013 growing season (June-August). Heaters are set to raise temperatures by approximately 3°C. Sensors are hung above the center of the plot and measure daily mean temperatures.

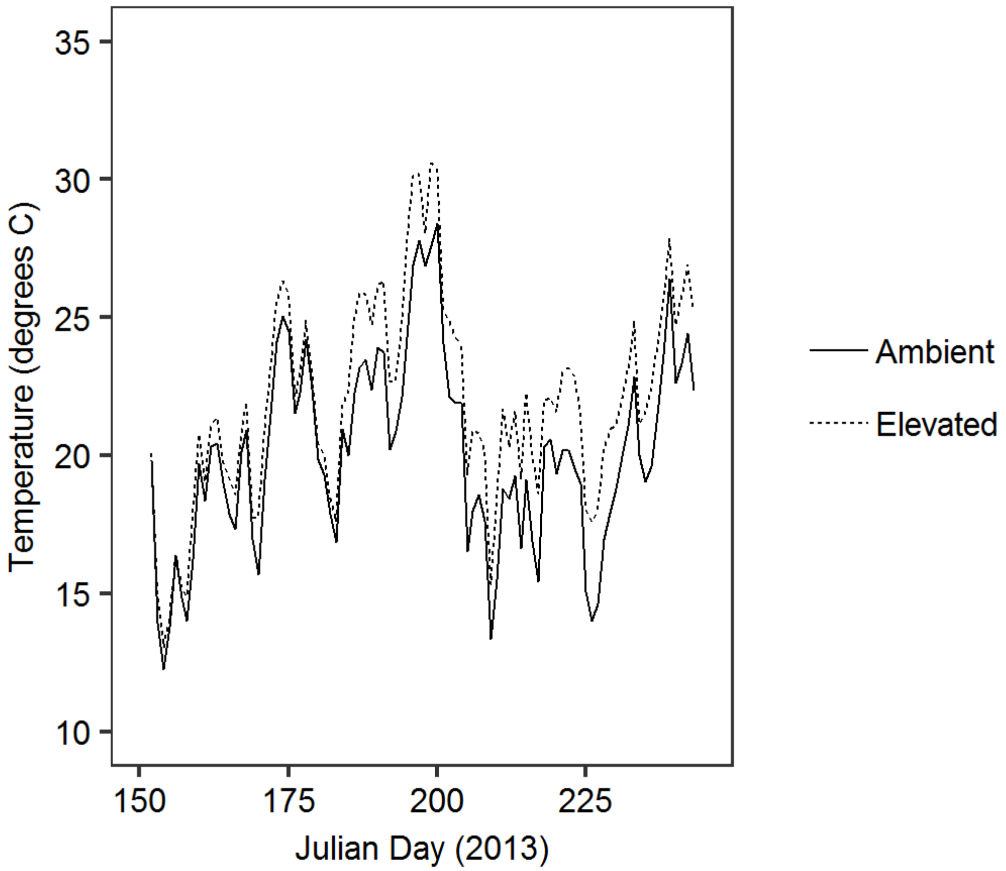
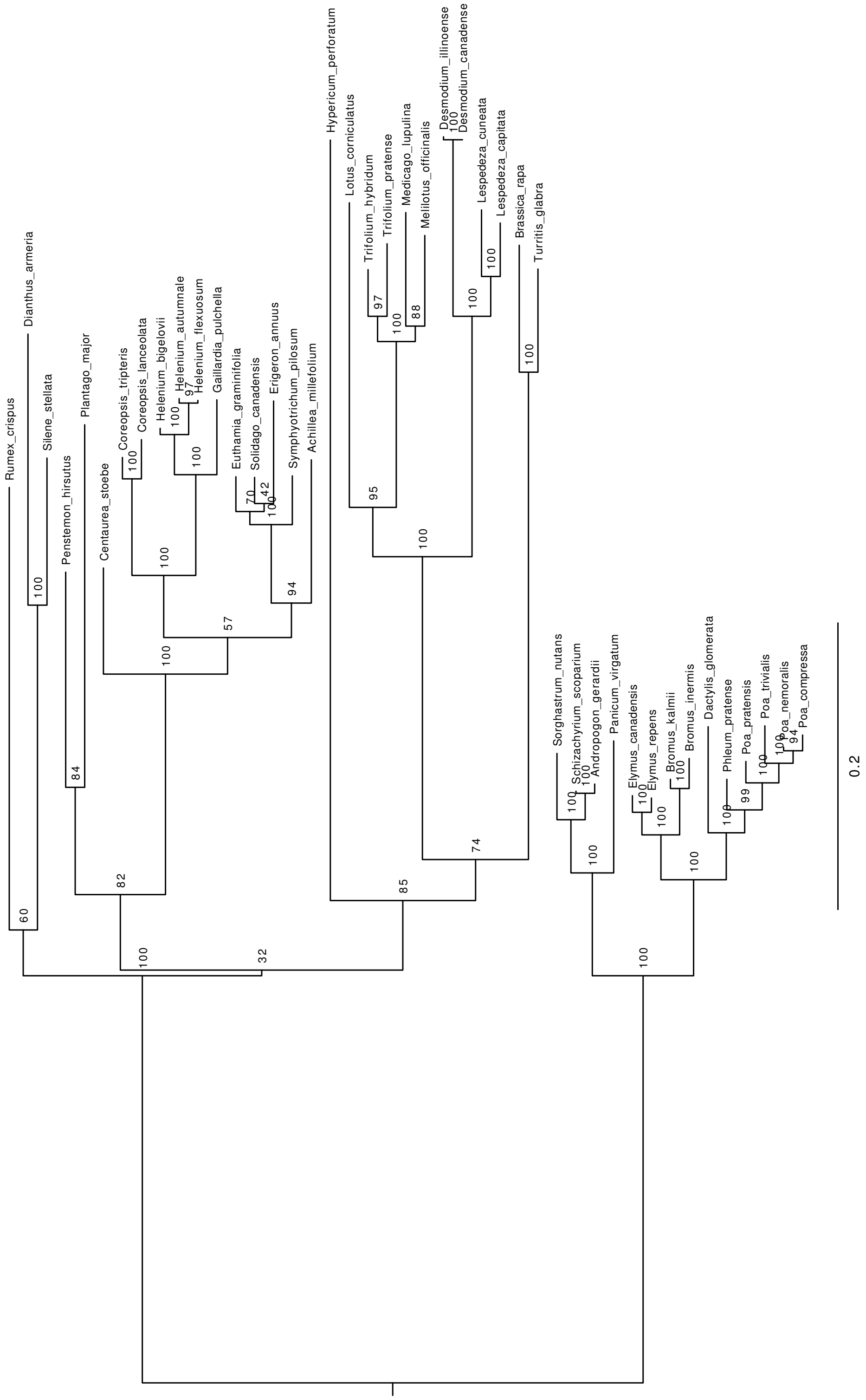


Figure S2. Phylogenetic relationships of native, exotic, and invasive species

The best-scoring ML tree from a rapid bootstrap analysis in RAxML from the analysis of concatenated sequences of *ITS, maK, rbcL*. ML bootstrap frequencies are the numbers associated with nodes, and branch lengths are proportional to the number of nucleotide changes.


Rumex_crispus
Dianthus_armeria
Silene_stellata
Penstemon_hirsutus
Plantago_major
Centaurea_stoebe
Coreopsis_tripteris
Coreopsis_lanceolata
Helenium_bigelovii
Helenium_autumnale
Helenium_flexuosum
Gaillardia_pulchella
Euthamia_graminifolia
Solidago_canadensis
Erigeron_annuus
Symphyotrichum_pilosum
Achillea_millefolium
Hypericum_perforatum
Lotus_corniculatus
Trifolium_hybridum
Trifolium_pratense
Medicago_lupulina
Melilotus_officinalis
Desmodium_illinoense
Desmodium_canadense
Lespedeza_cuneata
Lespedeza_capitata
Brassica_rapa
Turritis_glabra
Sorghastrum_nutans
Schizachyrium_scoparium
Andropogon_gerardii
Panicum_virgatum
Elymus_canadensis
Elymus_repens
Bromus_kalmii
Bromus_inermis
Dactylis_glomerata
Phleum_pratense
Poa_pratensis
Poa_trivialis
Poa_nemoralis
Poa_compressa
60
100
84
82
100
100
100
97
100
100
100
70
42
100
94
57
100
32
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97
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88
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100
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74
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100
100
100
99
100
100
94
100
0.2

Figure S3. Effect of warming on the phenology of native, exotic, and invasive species

Effect of warming on (A) days to first flower, (B) days to last flower, (C) flowering period duration (days), and (D) days to first fruit for native, exotic, and invasive species (least square means ± SE; N=20 native, 7 exotic, and 15 invasive species). Letters represent significant differences between groups (adjusted for multiple comparisons with a Tukey test, p≤0.05).

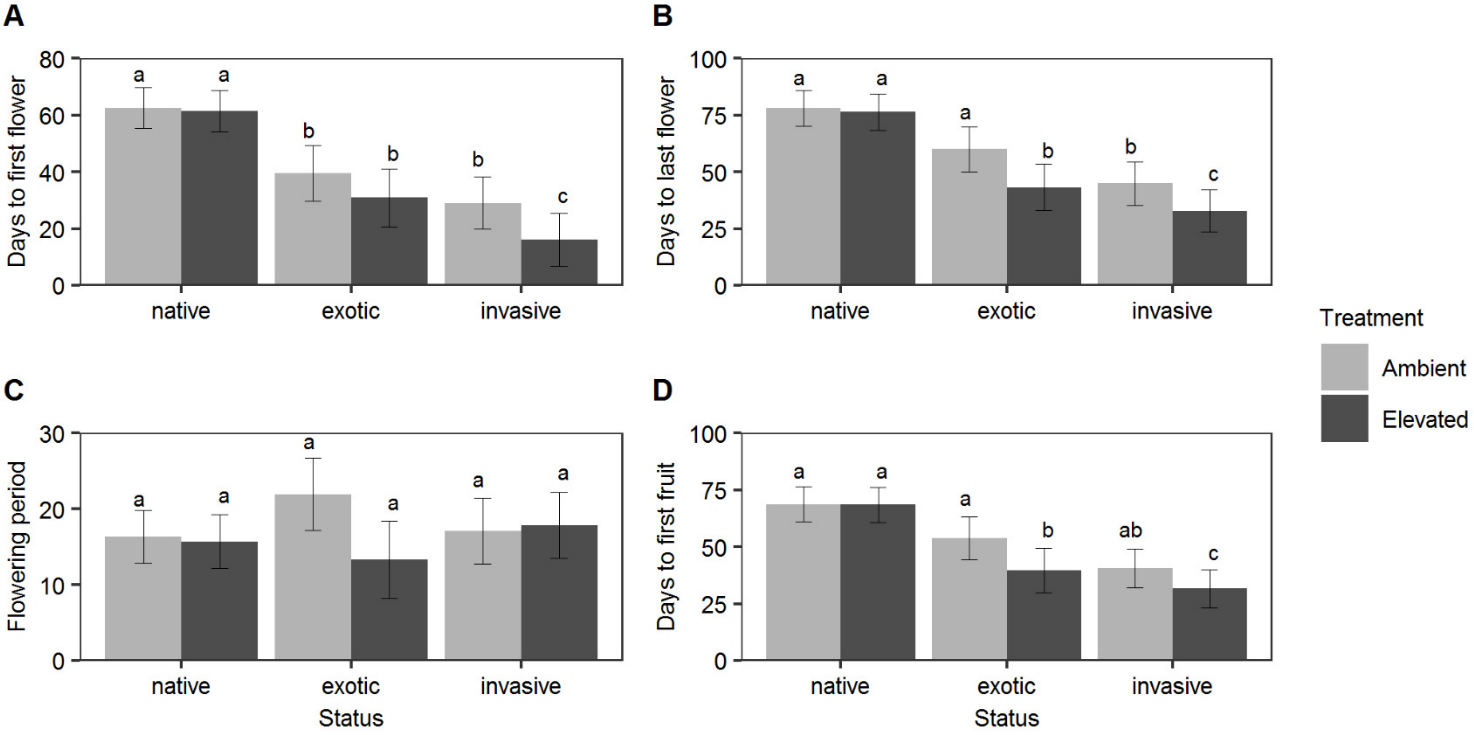

Figure S4. Phenological synchrony of native, exotic, and invasive species

Phenological synchrony (X) (least square means ± SE) of native, exotic, and invasive species under ambient and elevated (+3°C) temperatures. A phenological synchrony score of X=1 indicates complete synchrony among all individuals experiencing the same warming treatment, where all species start flowering at the same time and for the same length of time. A score of X=0 indicates complete asynchrony, or no overlap in flowering. Letters represent significant differences between groups (adjusted for multiple comparisons with a Tukey test, $p \leq 0.05$).

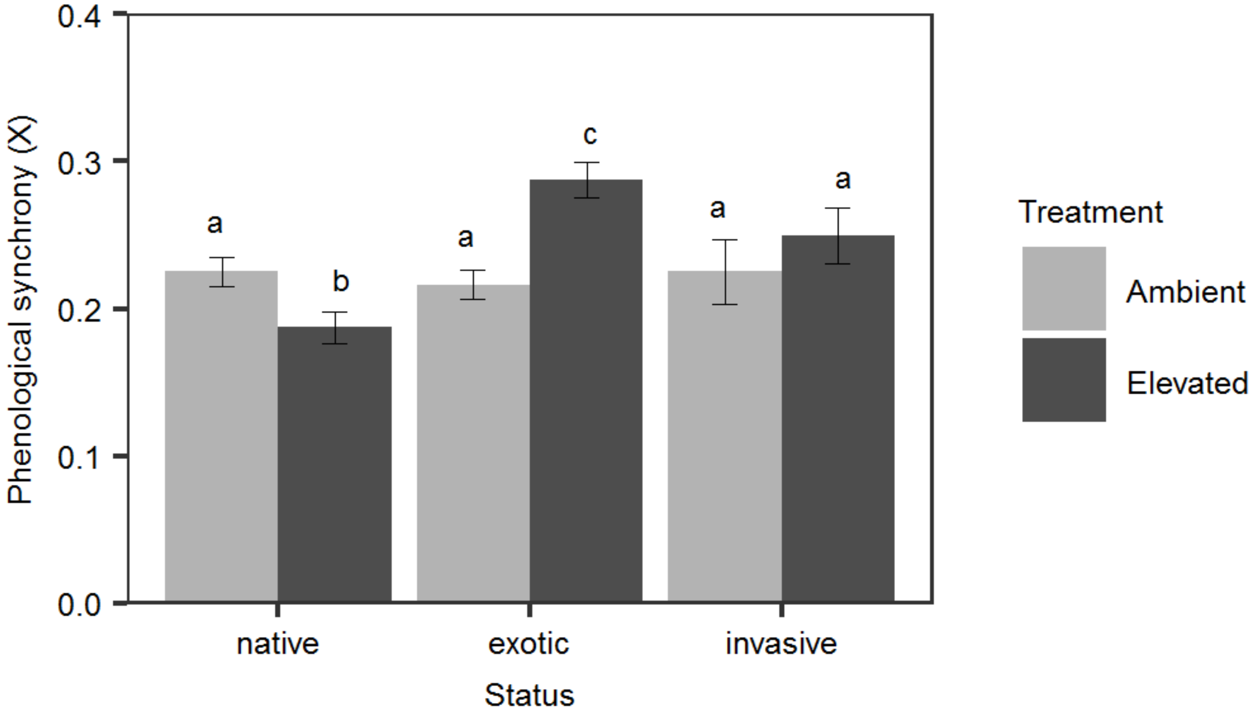

Figure S5. Effect of time since introduction on phenological plasticity, excluding C_3 grasses

Effect of time since introduction to Michigan (MI) (years) on phenological plasticity for invasive and exotic species, excluding C_3 grasses (invasive R^2=0.62, p=0.07; exotic R^2=-0.16, p=0.6). Gray areas represent 95% confidence intervals.

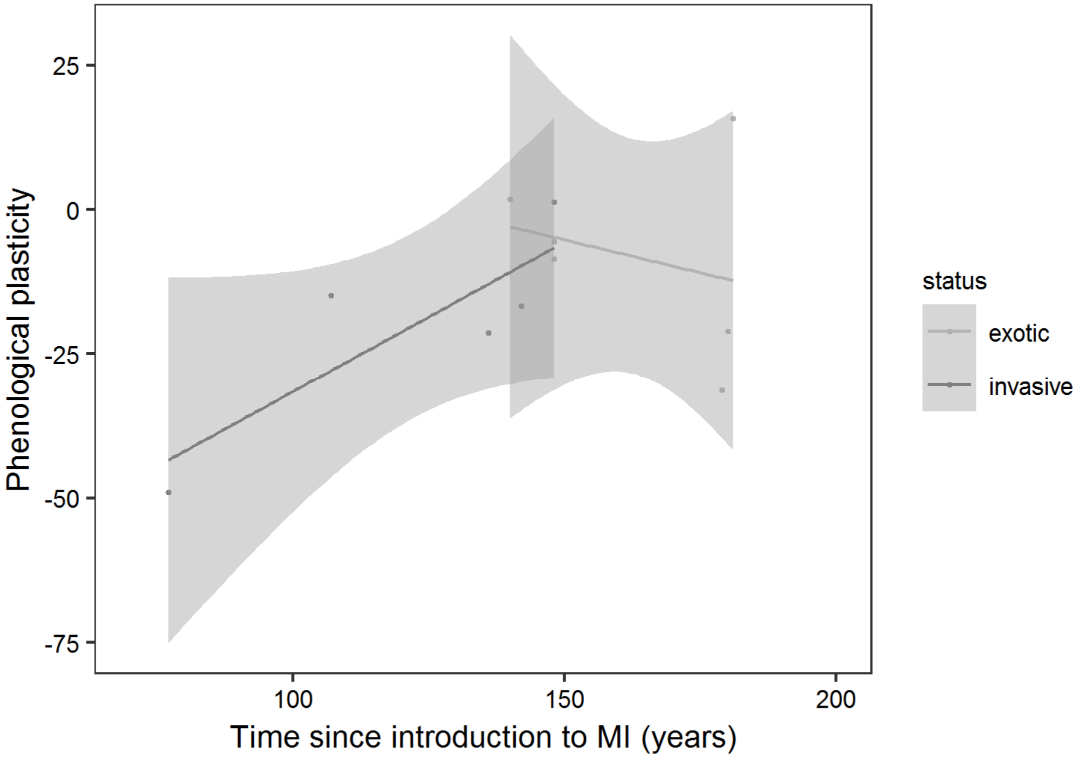

Table S1. Seed and phylogenetic information

Characteristics of the 42 species planted into the heating ring experimental plots in April 2012, including family, status (native, exotic, or invasive), and seed source. Field-collected seeds were from plants growing at the WK Kellogg Long-Term Ecological Research site. Purchased seed was from sources originally collected from MI (Michigan Wildflower Farm); OH, MN (Prairie Moon); PA, TX, CN, OR, WA (Ernst Seeds); NE (GRIN). GenBank accession numbers of genes (ITS, makK, rbcL) used for phylogenetic reconstruction are also provided.

Species name	**Family**	**Status**	**Source**	**ITS**	**makK**	**rbcL**
Achillea millefolium	Asteraceae	native	Field-collected	AY603185.1	EU385315.1	JX848399.1
Symphyotrichum (Aster) pilosum	Asteraceae	native	Field-collected	JQ360419.1	EU749444.1	EU677053.1
Centaurea stoebe	Asteraceae	invasive	Field-collected	JF914072.1	KC969492.1	KJ746252.1
Coreopsis lanceolata	Asteraceae	native	Michigan Wildflower Farm	KM347947.1	AY551495.1	HM849915.1
Coreopsis tripteris	Asteraceae	native	Michigan Wildflower Farm	KM347917.1	AY551499.1	
Erigeron annuus	Asteraceae	native	Field-collected	GU724302.1	HM989796.1	KJ841309.1
Euthamia graminifolia	Asteraceae	native	Field-collected	HQ142624.1	KJ592944.1	HQ590098.1
Gaillardia pulchella	Asteraceae	exotic	Ernst Seeds	KF607074.1	HM989787.1	HQ590105.1
Helenium autumnale	Asteraceae	native	Michigan Wildflower Farm	GU818553.1	GU817467.1, KJ772823.1	KJ773547.1
Helenium flexuosum	Asteraceae	exotic	Prairie Moon Nursery	KF607070.1	AY215804.1	AY215123.1
Leucanthemum vulgare	Asteraceae	invasive	Ernst Seeds	EF091600.1	HQ593344.1	KJ841377.1
Solidago canadensis	Asteraceae	native	Field-collected	HQ142591.1	EU749415.1	EU677023.1
Brassica rapa	Brassicaceae	invasive	Ernst Seeds	KF704394.1	AY541619.1	GQ184370.1
Turritis (Arabis) glabra	Brassicaceae	native	Prairie Moon Nursery	DQ310526.1	KP210444.1	HQ589958.1
Dianthus armeria	Caryophyllaceae	invasive	Field-collected	KX167086.1	KP210382.1	KT695582.1
Silene stellata	Caryophyllaceae	native	Prairie Moon Nursery	HQ334912.1	FJ589561.1	KP643867.1
Hypericum perforatum	Clusiaceae	invasive	Field-collected	JN811136.1	AB698447.1	HQ590139.1
Desmodium canadense	Fabaceae	native	Michigan Wildflower Farm	KM098891.1	HQ593266.1	KJ841264.1
Desmodium illinoense	Fabaceae	native	Ernst Seeds	KT459271.1	KT456906.1	KT458042.1

Lespedeza capitata	Fabaceae	native	Michigan Wildflower Farm	GU572172.1	KJ772888.1	KT695592.1
Lespedeza cuneata	Fabaceae	invasive	Ernst Seeds	GU572172.1	EU717416.1	EU717275.1
Lotus corniculatus	Fabaceae	invasive	Ernst Seeds	JN861076.1	HM049505.1	KJ841388.1
Medicago lupulina	Fabaceae	exotic	GRIN	JQ858257.1	HE966952.1	KJ841412.1
Melilotus officinalis	Fabaceae	invasive	Ernst Seeds	KJ999362.1	HE970723.1	KJ841414.1
Trifolium hybridum	Fabaceae	exotic	Ernst Seeds	AF053159.1	AF522125.1	KJ841632.1
Trifolium pratense	Fabaceae	exotic	Ernst Seeds	AF053171.1	EU749448.1	KJ841633.1
Plantago major	Plantaginaceae	invasive	Field-collected	AY101861.1	EU749328.1	EU676935.1
Andropogon gerardii	Poaceae	native	Michigan Wildflower Farm	DQ005015.1	AF144577.1	AJ784818.1
Bromus inermis	Poaceae	invasive	Field-collected	KF713194.1	AF164398.1	KJ841141.1
Bromus kalmii	Poaceae	native	Prairie Moon Nursery	AY367916.1		KT695565.1
Dactylis glomerata	Poaceae	invasive	Ernst Seeds	KJ598940.1	KF713137.1	HQ590058.1
Elymus canadensis	Poaceae	native	Michigan Wildflower Farm	KJ526335.1	HM770807.1	KC237138.1
Elymus repens	Poaceae	invasive	Field-collected	GQ365145.1	KF713125.1	HQ590076.1
Panicum virgatum	Poaceae	native	Michigan Wildflower Farm	DQ005062.1	EU434294.1	EF125135.1
Phleum pratense	Poaceae	exotic	Field-collected	HQ600524.1	HQ593382.1	KJ841460.1
Poa compressa	Poaceae	invasive	Ernst Seeds	KJ598896.1	KJ599232.1	KJ599121.1
Poa pratensis	Poaceae	invasive	Ernst Seeds	KJ598925.1	KJ599261.1	KJ599150.1
Poa trivialis	Poaceae	exotic	Ernst Seeds	GQ342555.1	FJ395369.1	JN893080.1
Schizachyrium scoparium	Poaceae	native	Michigan Wildflower Farm	DQ005072.1	FR832830.1	HE577863.1
Sorghastrum nutans	Poaceae	native	Michigan Wildflower Farm	DQ005080.1	EF137473.1	EF125121.1
Rumex crispus	Polygonaceae	invasive	Field-collected	KR537778.1	HQ593423.1	HQ590251.1
Penstemon hirsutus	Schrophulariaceae	native	Michigan Wildflower Farm	DQ531111.1		

Table S2. **Effect of warming and status on phenology of native vs. non-native species**

F-statistics and associated p-values for the effects of warming (ambient or elevated) and status (native or non-native) on reproductive phenology (days to first flower, days to last flower, flowering period, and days to first fruit) (linear mixed models, Gaussian distributions). Plot (nested in warming treatment) and species (nested in status) were included as random effects (estimates given as χ^2-values). Denominator degrees of freedom ranged from 6.91-283 for warming, from 32.4-40.6 for status, and from 281-294 for the interaction, depending on response variable. ***p≤0.0001, **p≤0.01, *p≤0.05, •p≤0.1.

Source	**df**	**Days to first flower F**	**Days to last flower F**	**Flowering period F**	**Days to first fruit F**
Warming	1	6.97**	10.09**	0.72	6.86**
Status	1	11.99**	11.12**	0.15	8.30**
Warming x Status	1	4.73*	5.70*	0.28	6.03*
Plot(treatment) (χ^2)		0.00	0.00	0.04	0.00
Species(status) (χ^2)		832.47	858.45	133.37	728.20
Residual		391.51	447.35	278.32	315.97

Table S3. **Phylogenetic analyses of the effect of warming and status on phenology of native vs. non-native species**

Results from phylogenetic generalized least squares (PGLS) testing the effects of status (native or non-native) and warming (ambient or elevated) on days to first flower, days to last flower, flowering period, and days to first fruit, while controlling for variance due to shared ancestry. ***p<0.0001, **p<0.01, *p≤0.05, ·p≤0.1.

Source **Brownian Motion**	**df**	**Days to first flower t**	**Days to last flower t**	**Flowering period t**	**Days to first fruit t**
Warming	1	-2.25*	-9.12***	-5.53***	-3.26**
Status	1	-0.03	-0.20	-0.14	0.00
Warming x Status	1	2.25*	11.52***	7.55***	2.34*
Residual	187	1135.65	1013.52	1207.57	17.06

Table S4. **Effect of warming and status on phenology of native, exotic, and invasive species**

F-statistics and associated p-values for the effects of warming (ambient or elevated) and status (native, exotic, or invasive) on reproductive phenology (days to first flower, days to last flower, flowering period, and days to first fruit) (linear mixed models, Gaussian distributions). Plot (nested in warming treatment) and species (nested in status) were included as random effects (estimates given as χ^2-values). Denominator degrees of freedom for warming ranged from 7.09-284 for warming, from 30.1-40.4 for status, and from 81.7-287 for the interaction, depending on response variable. ***p≤0.0001, **p≤0.01, *p≤0.05, •p≤0.1.

Source	**df**	**Days to first flower F**	**Days to last flower F**	**Flowering period F**	**Days to first fruit F**
Warming	1	8.85**	9.33*	1.88	10.02**
Status	2	6.41**	5.67**	0.06	4.55*
Warming x Status	2	2.55•	3.06*	1.54	2.66•
Plot(treatment) (χ^2)		0.00	10.68	0.00	2.32
Species(status) (χ^2)		833.46	874.85	134.54	716.85
Residual		392.46	296.2	258.9	129.1

Table S5. Phylogenetic analyses of the effect of warming and status on phenology of native, exotic, and invasive species

Results from phylogenetic generalized least squares (PGLS) testing the effects of status (native, exotic, or invasive) and warming (ambient or elevated) on days to first flower, days to last flower, flowering period, and days to first fruit, while controlling for variance due to shared ancestry. ***p<0.0001, **p<0.01, *p≤0.05, •p≤0.1.

Source **Brownian Motion**	**df**	**Days to first flower t**	**Days to last flower t**	**Flowering period t**	**Days to first fruit t**
Warming	1	-0.05	-0.06	-0.16	-0.08
Status	2	-1.81•	-3.13**	-4.54***	-4.56***
Warming x Status	2	1.81•	3.84***	8.53***	3.25**
Residual	153	1134.42	1053.92	1237.70	17.07

Table S6. Species-specific phenological responses to temperature

Species-specific phenological responses to temperature (linear mixed model, Gaussian distribution; plot nested in status included as a random factor). N is the number of individuals for each species that flowered. Values (least square means ± SE) represent the difference in each phenological variable (days to first flower DFF, days to last flower DLF, flowering period FP, and days to first fruit DFFr) between elevated and ambient temperatures. Negative values indicate that phenology was accelerated under elevated temperatures and positive values indicate that phenology was delayed under elevated temperatures. Significant values are in bold; ·p<0.1, *p<0.05, **p<0.01, ***p<0.0001 (Tukey's tests for warming x species).

Species name	N	Difference in DFF	Difference in DLF	Difference in FP	Difference in DFFr
Invasive species					
Bromus inermis	9	**-22.43 ± 7.67***	-11.69 ± 8.63	+10.82 ± 7.97	-10.58 ± 4.71
Centaurea stoebe	14	**-14.80 ± 5.91·**	-11.20 ± 6.63	+3.22 ± 6.09	**-10.67 ± 4.45·**
Dactylis glomerata	14	-7.29 ± 5.91	-10.32 ± 6.63	-3.00 ± 6.09	**-23.40 ± 4.10*****
Dianthus armeria	7	-21.30 ± 9.01	-23.49 ± 10.14	-2.86 ± 9.37	+5.90 ± 5.40
Elymus repens	3	-18.67 ± 13.27	+11.82 ± 14.94	+29.20 ± 13.87	+21.50 ± 9.65
Hypericum perforatum	12	**-31.25 ± 6.49****	**-31.69 ± 7.30****	-0.58 ± 6.70	**-39.23 ± 4.53*****
Leucanthemum vulgare	11	+1.25 ± 6.90	**-21.12 ± 7.75 ·**	**-21.85 ± 7.14 ***	-12.90 ± 5.40
Lotus corniculatus	2	**-48.98 ± 15.46***	+0.45 ± 17.42	+50.73 ± 16.20	
Melilotus officinalis	19	**-16.67 ± 6.12***	**-20.13 ± 5.74***	-3.33 ± 5.25	-7.60 ± 3.67
Plantago major	6	+1.83 ± 9.36	+6.09 ± 10.53	+4.06 ± 9.76	+9.60 ± 8.18
Poa compressa	12	-4.43 ± 6.47	-1.56 ± 7.27	+3.07 ± 6.69	-4.25 ± 3.88
Poa pratensis	8	+0.23 ± 7.94	-2.21 ± 8.93	-2.14 ± 8.26	+1.86 ± 4.96
Rumex crispus	6	+15.84 ± 11.24	-5.76 ± 12.65	-19.80 ± 11.74	+1.75 ± 8.48
Exotic species					
Helenium flexuosum	10	-12.20 ± 7.46	**-44.01 ± 8.38****	-32.06 ± 7.73	**-28.33 ± 5.40****
Medicago lupulina	3	-8.57 ± 13.20	+17.10 ± 14.87	+25.96 ± 13.81	
Phleum pratense	15	-6.32 ± 5.80	-6.81 ± 6.51	-0.59 ± 5.98	-5.54 ± 4.02
Trifolium hybridum	4	-5.49 ± 12.20	-20.12 ± 13.73	-14.94 ± 12.75	+1.33 ± 8.92
Trifolium pratense	6	+13.09 ± 11.25	-22.72 ± 12.66	**-34.12 ± 11.72·**	**+23.50 ± 8.48·**
Native species					
Achillea millefolium	9	-16.86 ± 8.44	+0.87 ± 9.50	+18.02 ± 8.77	+1.00 ± 8.92
Andropogon gerardii	4	-20.54 ± 10.94	-17.17 ± 12.31	+3.87 ± 11.43	-13.00 ± 9.65
Bromus kalmii	6	+13.69 ± 11.23	4.28 ± 12.64	-7.89 ± 11.71	-0.50 ± 6.31
Coreopsis lanceolata	17	**-12.62 ± 5.39·**	-1.84 ± 6.04	+10.70 ± 5.53	-5.97 ± 3.42
Coreopsis tripteris	11	**-22.58 ± 7.24***	**-22.43 ± 8.14·**	-0.43 ± 7.51	+2.83 ± 7.96
Desmodium canadense	2	-1.35 ± 15.47	14.65 ± 17.42	_14.33 ± 16.02	
Elymus canadensis	5	**-31.77 ± 9.97***	-0.68 ± 11.22	**+30.03 ± 10.40***	+3.25 ± 6.82

Erigeron annuus	9	-6.62 ± 7.42	4.88 ± 8.34	+12.18 ± 7.69	-0.45 ± 5.36
Euthamia graminifolia	8	+16.77 ± 7.98	-3.55 ± 8.97	**-20.82 ± 8.29·**	**+19.00 ± 6.53***
Helenium autumnale	5				-15.00 ± 8.92
Panicum virgatum	16	+1.89 ± 5.54	-5.62 ± 6.22	-7.50 ± 5.70	-1.66 ± 4.67
Penstemon hirsutus	12	-5.77 ± 6.66	-11.98 ± 7.48	-6.56 ± 6.89	**-24.22 ± 4.41****
Schizachyrium scoparium	6	**+35.46 ± 9.01****	-5.47 ± 10.13	**-40.98 ± 9.37****	+1.50 ± 7.26
Silene stellata	3	+14.61 ± 13.20	+17.79 ± 14.86	+4.67 ± 13.81	-5.00 ± 8.00
Solidago canadensis	7	**+27.64 ± 8.47***	**+25.98 ± 9.53·**	-2.89 ± 8.78	**+37.50 ± 9.65****
Sorghastrum nutans	2	-7.16 ± 15.46	+0.55 ± 17.41	+7.12 ± 16.21	
Symphyotrichum (Aster) pilosum	10	+7.78 ± 7.46	+1.03 ± 8.39	-6.11 ± 7.75	
Turritus (Arabis) glabra	14	-3.52 ± 5.98	+0.69 ± 6.92	+4.52 ± 6.36	+1.11 ± 3.49

Table S7. Geographic spread, phenological plasticity, and time since introduction

Effect of status (native or non-native) and (A) days to first flower (DFF) and (B) phenological plasticity (difference in DFF between elevated and ambient temperatures) on the geographic spread (number of US counties) of native and non-native species (linear models, Gaussian distributions). (C) Effect of status (exotic or invasive) and time since introduction to Michigan (years) on phenological plasticity for non-native species (linear model, Gaussian distribution). $^{**}p \leq 0.01$, $^{*}p \leq 0.05$, $\cdot p \leq 0.1$.

A) Source	**df**	**F**
Status	1	11.57**
DFF	1	3.01·
Status x DFF	1	9.66**
Residual	33	415.2

B) Source	**df**	**F**
Status	1	8.19**
Plasticity	1	0.19
Status x Plasticity	1	1.41
Residual	30	432.6

C) Source	**df**	**F**
Status	1	4.57*
Time since introduction	1	0.21
Status x Time	1	4.04·
Residual	14	12.2

Table S8. Phylogenetic analyses of geographic spread, phenological plasticity, and time since introduction

Results from phylogenetic generalized least squares (PGLS) testing the effects of status (native or non-native) and (A) days to first flower (DFF) and (B) phenological plasticity (difference in DFF between elevated and ambient temperatures) on the geographic spread (number of US counties) of native and non-native species. (C) Effect of status (exotic or invasive) and time since introduction to Michigan (years) on phenological plasticity for non-native species, while controlling for variance due to shared ancestry. **$p \leq 0.01$, *$p \leq 0.05$.

A) Source	**df**	**t**
Status	1	10.74**
DFF	1	1.75
Status x DFF	1	4.59*
Residual	28	625.55

B) Source	**df**	**t**
Status	1	10.74**
Plasticity	1	1.75
Status x Plasticity	1	4.59*
Residual	28	672.50

C) Source	**df**	**t**
Status	1	1.27
Time since introduction	1	5.68*
Status x Time	1	5.92*
Residual	12	16.22

Table S9. Effect of flowering time and phenological plasticity on geographic spread in Michigan

Effect of status (native or non-native) and (A) days to first flower (DFF) and (B) phenological plasticity (difference in days to first flower between elevated and ambient temperatures) on the geographic spread (number of MI counties) of native and non-native species (linear models, Gaussian distributions).

A) Source	**df**	**F**
Status	2	0.01
Phenological plasticity	1	0.16
Status x Plasticity	2	0.08
Residual	33	21.6

B) Source	**df**	**F**
Status	2	0.00
DFF	1	0.09
Status x DFF	2	0.14
Residual	30	19.7

Table S10. Effects of flowering time and phenological plasticity on the geographic spread of native, exotic, and invasive species

Effect of status (native, exotic, or invasive) and (A) days to first flower (DFF) and (B) phenological plasticity (difference in DFF between elevated and ambient temperatures) on the geographic spread (number of US counties) of native, exotic, and invasive species (linear models, Gaussian distributions). Exotic and invasive species demonstrate similar patterns for both plasticity and DFF (DFF: Tukey test for status × DFF p=0.45; plasticity: Tukey test for status p=0.97). **p≤0.01, *p≤0.05, •p≤0.1.

A) Source	**df**	**F**
Status	2	2.46
DFF	1	5.62**
Status x DFF	2	4.58*
Residual	31	425.50

B) Source	**df**	**F**
Status	2	3.84*
Plasticity	1	2.76•
Status x Plasticiy	2	0.86
Residual	28	444.50