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RESEARCH PAPER

Impacts of differing community composition on flowering phenology throughout warm temperate, cool temperate and xeric environments

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ABSTRACT

Aims Flowering phenology is well documented to restrict the distribution of many plant species. However, community-level shifts in flowering time may occur either through exclusion of species with unsuitably early or late flowering for local conditions (composition-derived phenological shifts) or through intraspecific phenological responses to climate variations over space. Although these mechanisms have quite different ecological implications, the relative contribution of composition-derived phenological shifts remains largely unknown. Therefore, determining the magnitude of composition-derived phenological variation is crucial for understanding the relationship between phenology and community assemblage over space, and for predicting the impacts of future climate change. This study will evaluate the contributions of compositional differences to spatial variation in community-level flowering times throughout the early, mid and late portions of the growing season and across a variety of temperate environments.

Location Continental United States.

Methods This study develops novel herbarium-based methods to separate intraspecific phenological variations over space from changes in flowering time derived from differences in community composition.

Results Although typically smaller than intraspecific variations, composition-derived shifts in flowering time explained up to 49.3% of overall phenological variation. Composition-derived changes in flowering time among late-flowering species also explained the greatest proportion of overall variation and were the most responsive to differing climate conditions. Xeric regions also exhibited composition-derived phenological shifts that were stronger and more closely tied to climate conditions (R^2 up to 0.553) than other regions.

Main conclusions These results indicate that interspecific differences in flowering time play a significant role in determining the composition of the plant community over space. However, the impact of flowering phenology on community assemblage varies considerably among seasons and climate regions, and appears to be strongest among xeric regions and among late-flowering species.

Keywords

Biogeography, climate, community ecology, flowering, herbarium records, phenology, plant biology.

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INTRODUCTION

The reproductive timing of plant species has been well documented to vary in response to changes in environmental conditions, both over space and interannually. The ability of individual species to adapt their phenology either plastically or genetically to differing environmental conditions has been found to have an impact on both the range limits (Chuine & Beaubien, 2001; Morin *et al.*, 2007) and persistence (Willis *et al.*, 2008) of many species, while differences in climatic conditions may influence both the composition (Morin *et al.*, 2007; Craine *et al.*, 2012) and invasibility (Willis *et al.*, 2010) of the plant community. However, when viewed from a community perspective, changes in mean phenological timing (pooled across a representative sample of local species) may occur either through phenological adaptations by individual species to varying conditions or through systematic changes in the composition of the plant community towards species with consistently earlier or later flowering times. These two mechanisms represent quite distinct ecological processes with very different implications for the composition of the plant community as a whole, but their relative contributions to overall patterns of community-level phenology remain poorly understood. Therefore, in order to interpret the repercussions of future climate variation on the plant community, it is essential to separate the mechanisms by which spatial variations in phenology occur and to determine the contributions of intraspecific and composition-derived phenological variation to overall community-level phenological variations.

To date, the majority of phenological research has focused on phenological responses to differing environmental conditions that occur within a single species (i.e. intraspecific phenological variation; Fig. 1a), and do not incorporate the effects of variations in the composition of the plant community. Intraspecific phenological responses may occur either through (1) phenotypic plasticity, which comprises the ability of plants to adapt their phenological timing to various climatic conditions through physiological, behavioural or morphological mechanisms that do not require genotypic variation (Bradshaw, 1965), or (2) local genetic adaptations resulting from selective pressure towards differing phenologies among populations that inhabit areas with distinct climatic conditions (Olsson & Agren, 2002; Jonzén *et al.*, 2007; Vitasse *et al.*, 2009a,b). Unfortunately, it is often quite difficult to disentangle interpopulation genetic adaptations from plastic phenological responses to differing conditions over space (Donnelly *et al.*, 2012), and this study will not attempt to distinguish between these two forms of intraspecific phenological variation.

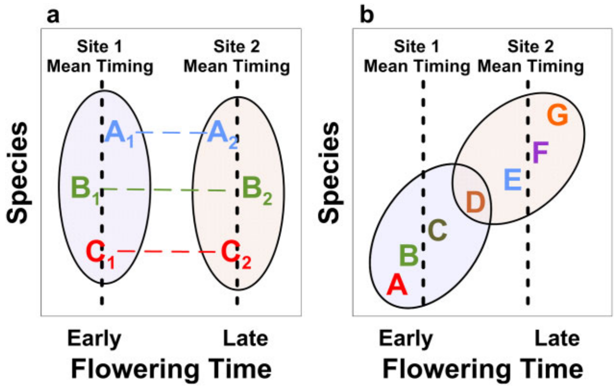

Figure 1 Models of purely intraspecific (a) and purely composition-derived (b) phenological variation over space. Species are denoted by capital letters. Locations are denoted by numerals and community composition at each location is indicated by ellipses. Vertical dashed lines represent the mean phenological timing for each location.

In contrast to phenological adaptations that occur within individual species, however, are changes in community-level phenology that result from differences in the mean flowering time across all species that collectively form the plant community at different locations over space. As the plant community changes over space or in response to climate gradients, species with maladapted traits or environmental tolerances may be filtered out of the plant community and replaced with different species that exhibit more suitable traits for the local environment (Keddy, 1992). In a similar fashion, species with unsuitable flowering phenology for a given location may be excluded, resulting in changes in the composition of the plant community that shift preferentially towards species that intrinsically flower earlier or later, as local conditions dictate (Fig. 1b). Such systematic shifts in the composition of the plant community over space have been found to result in community-level differences in mean flowering time across all species present in each location. Being driven purely by compositional differences, such variation occurs independently of phenological plasticity within individual species (Craine *et al.*, 2012). Community-level patterns of phenology across different locations may thus be affected both by differing intraspecific responses by species that are common across both locations and by the exclusion of species with flowering phenology that is unsuitable to local conditions at either location (e.g. composition-derived changes) (Primack *et al.*, 2009; Craine *et al.*, 2012). Individual species are typically only capable of plastic phenological responses to climate conditions that are historically present in their native ranges, and may be limited in their ability to adapt to more extreme conditions (Sparks *et al.*, 2000; Morin *et al.*, 2010). Hard limits in the range of climate conditions across which each species is capable of persisting are also typically present (Chuine & Beaubien, 2001; Morin *et al.*, 2007; Chuine, 2010). Unsuitable timing of flowering and fruiting that results in cold damage to reproductive tissues or premature termination of fruit development has been implicated as the primary mechanism for these climatic range limits, indicating that differences in flowering phenology are critical to changes in the composition of the plant community over space (Morin *et al.*, 2007). Thus, it is likely that intraspecific changes in flowering time, which cannot account for changes in community composition, represent only a portion of the overall phenological variation that occurs across broad climate gradients.

These two mechanisms also represent quite distinct processes with very different implications for the composition of the plant community. Composition-derived variations in community-level flowering phenology reflect the systematic exclusion of species that cannot adapt their reproductive timing to suit a given environment (resulting in timing that is too early or too late) and their replacement by other taxa that exhibit a more suitable reproductive timing. In contrast, phenological change that occurs intraspecifically represents the ability of individual species to adapt their phenology (plastically or through local genetic adaptation) in order for it to remain suitable across a range of environments without being excluded due to unsuitable reproductive timing. Increased intraspecific adaptation among the majority of species in a location would therefore be expected to reduce phenologically driven disruptions to community composition, while composition-derived phenological change directly reflects phenologically driven changes in community composition over space.

Thus, it is clear that simple examinations of community-level phenological variation that do not distinguish between these two mechanisms are limited in their ability to evaluate the relationships between community composition and reproductive phenology. Differences in community-level flowering time that result purely from systematic shifts in the composition of the plant community have been detected among both cold-temperate perennial grasslands in North America (Craine *et al.*, 2012) and among assemblages of species in bog, woodland and disturbed communities throughout Franklin County, ME, USA (Heinrich, 1976). Despite this, composition-derived phenological variation has rarely been examined separately from intraspecific variation, and its relative contributions to overall patterns of community-level phenology remain poorly understood. Further, no systematic comparison of intraspecific and composition-driven phenological change has been conducted at a spatial scale that is sufficient to extrapolate to regional and continental processes, or that is capable of comparing the role of such changes in community composition across broad climate regions.

Nevertheless, it is well documented that under changing climate conditions plant species must typically either adapt plastically, evolve rapidly to meet the changing environmental conditions, or face local extinction and replacement by species that are better adapted to the local environment (Aitken *et al.*, 2008). Research into phylogenetic patterns of species loss has already detected preferential decreases in abundance and increases in the risk of local extinction among those taxa with the lowest plasticity in flowering time under interannual climate variations and progressive warming in the Boston area, USA (Willis *et al.*, 2008). Additionally, process-based models have indicated that the primary climatic constraints on the ranges of temperate tree species arise from unsuitable timing of flowering and fruiting (Morin *et al.*, 2007). Thus, it is clear that the timing of reproductive phenology is closely tied to the composition of the plant community over space. Understanding the magnitudes of intraspecific and composition-derived changes in flowering phenology over space is crucial to evaluating how rapidly the composition of those communities is likely to shift under future climate changes.

Previous studies have also determined that the magnitude and direction of intraspecific phenological responses to climate cues vary significantly among the early, middle and late portions of the growing season (Fitter *et al.*, 1995; Miller-Rushing & Primack, 2008; Gordo & Sanz, 2010; Wolkovich *et al.*, 2012; Mazer *et al.*, 2013). Similarly, phenological sensitivity to temperature variations is often milder among warm temperate and subtropical regions than cool temperate regions (Borchert *et al.*, 2005), while xeric regions often exhibit delayed phenology in response to late rainfall (Ghazanfar, 1997; Peñuelas *et al.*, 2004; Gordo & Sanz, 2010). Thus, it is quite plausible that the relative contributions of intraspecific variation and phenologically deterministic shifts in species composition to patterns of overall variation in flowering time may differ both seasonally and among regionally distinct climate zones. Unfortunately, large-scale examinations capable of evaluating the magnitude of intraspecific and compositional changes in flowering phenology across broad regions and wide environmental gradients are lacking. Such large-scale studies are necessary, however, to determine the relative importance of compositional changes in flowering time for the assemblage of the plant community at continental and global scales, as well as to forecast the severity of phenologically driven disruptions to the composition of existing plant communities under additional climate change. This study will remedy this deficiency, and will use novel, herbarium-based methods to separate the contributions of intraspecific and composition-derived phenological variations to the overall timing of community-level flowering throughout the growing season and to evaluate the relative magnitudes of intraspecific and composition-derived shifts in flowering phenology along climate gradients throughout warm temperate, cool temperate and xeric environments.

Specifically, this research will address the following questions.

1. Do systematic, phenologically deterministic changes in the composition of the plant community over space account for a significant portion of overall spatial variation in flowering time throughout temperate environments at regional and continental scales?

2. Does the proportion of overall spatial variation in flowering time that can be explained through intraspecific variations differ among the early, middle- and late-flowering portions of the plant community, or among xeric, warm temperate and cool temperate environments?

3. Does the proportion of overall spatial variation in flowering time that can be explained through the effects of changes in community composition differ among the early, middle- and late-flowering portions of the plant community, or among xeric, warm temperate, and cool temperate environments?

4. Do intraspecific variations in flowering time exhibit different responses to seasonal temperature variations during the early, middle and late portions of the growing season, or among xeric, warm temperate or cool temperate environments?

5. Do the effects of changes in community composition on community-level flowering time along seasonal temperature gradients differ among the early, middle and late portions of the growing season, or among xeric, warm temperate or cool temperate environments?

METHODS

Data sources

Records of flowering phenology used in this study were drawn from the digital archives of the herbaria of Clemson University, the University of South Carolina, Florida State University, Arizona State University, the University of Arizona, the University of California-Riverside, the University of Texas and the Rocky Mountain Herbarium. This record included samples of trees, shrubs and herbaceous species collected from the years 1890 to 2012. Only samples that were collected in flower and documented the county of collection were included. Graminoid (grass-like) species were excluded due to a lack of discrimination between flowering and fruiting phenophases throughout most digital records. In order to ensure that only regions with sufficient sampling were included, only data in states that included over 1500 samples were evaluated based on empirical observation of sampling intensity. After all unusable data were excluded, the remaining record included 823,033 samples over a total of 24,105 species among 750 counties and 16 states, covering over 2.5 million km^2 (Fig. 2). Nevertheless, this sample was still restricted to those areas in which significant herbarium records were digitally available, and thus covered only 18% of the continental United States. Temperature data used in this study were drawn from US climate normals (1971–2000) developed by the PRISM Climate Group (Prism Climate Group, 2004). Köppen climate classification data was drawn from the 2006 world map of Köppen–Geiger climate classification (Kottek *et al.*, 2006).

Climate classes

Each county was assigned to one of three climate classes based on the Köppen–Geiger climate type that covered the majority of each county. Arid and semi-arid counties were placed into a single ‘xeric’ class (Köppen classes BWk, BWh, BSk, BSh). Humid subtropical (Cfa), dry subtropical (Csa, Csb) and maritime (Cfb) regions were combined into a ‘warm temperate’ class, while hemi-boreal (Dfb, Dsb) and boreal (Dfc) regions, along with two high-altitude alpine (ET) counties, were combined into a single ‘cool temperate’ class (Fig. 2).

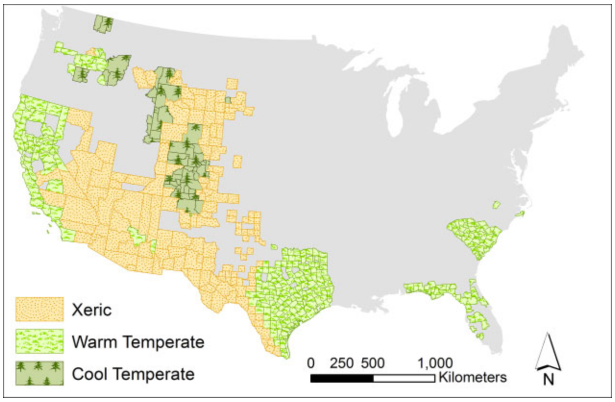

Figure 2 Study area and climate regions.

Seasonal classes

As patterns of flowering phenology may vary significantly throughout the growing season (Bradley *et al.*, 1999; Menzel, 2000; McEwan *et al.*, 2011), it was necessary to separate all species into seasonal classes for comparative analysis. Classes were assigned by calculating the mean DOY (day of year) in which samples of each species were collected in flower (Park, 2012) within each state for each species. Each species was then placed into one of seven quantile classes based on the relative order of flowering (from earliest to latest) of all species within each state. Seasonal classes were developed at the state level to ensure a sufficiently robust list of species for accurate ranking, while still compensating for major regional variations in the duration and onset of the growing season. Seven classes were empirically determined to be necessary for the separation of mid-season flowering from early and late-season flowering, which exhibited significantly different properties. However, this also resulted in the generation of intermediate classes that incorporated elements of both early, mid- and late-season flowering. Thus, only data from the second, fourth and seventh seasonal classes, which typified the major differences in intraspecific and composition-derived flowering phenology that occurred throughout the early, middle and late portions of the growing season, will be presented here. Data from the second-earliest class, which exhibited similar patterns of variation to the earliest class, is presented in preference to the earliest class due significantly improved sampling intensity in the second seasonal class.

Pairwise comparisons

As examinations of intraspecific and composition-derived phenological differences required separation of those species that remained common over space from those species that were excluded from various locations, it was necessary to develop novel methods in order to examine each element of phenological variation separately. Thus, all analysis of spatial variation throughout this study was conducted through pairwise comparisons of mean flowering times between each possible pair of counties using MATLAB. This permitted precise identification of all species that were common across each pair of locations as well as those species that were not, allowing a separation of the effects of intraspecific and compositional changes in flowering time throughout the study area. This method also facilitated comparisons of flowering phenology among all locations that included sufficient phenological documentation regardless of their proximity or dissimilarity of climate conditions, and was therefore not restricted to comparisons between adjacent or climatically similar locations.

Calculating overall differences in flowering time

In order to evaluate the overall differences in flowering time that occurred among each pair of counties, the mean flowering time (represented by the mean collection date of all flowering samples) was calculated for each species that was present within each county. The average timing of all species within a given class was then calculated for each county. In order to facilitate comparisons between flowering time among locations, pairwise differences in mean overall flowering time were calculated among each possible pair of counties, resulting in a measurement of the difference in overall flowering time among each pair of locations. This metric represents an estimate of the actual differences in flowering phenology over space, and incorporates the effects of both intraspecific and compositional changes over space.

Isolating intraspecific differences in flowering time

In order to evaluate the overall differences in flowering time that occurred among each pair of counties, the mean flowering time of each species (represented by the mean collection date of all flowering samples) in a given timing class was calculated within each county. For each possible pair of counties, all species that were present in both locations were then selected. For each of the two counties being compared, a community-level mean flowering time was then calculated based on the flowering times of only those species that were present within both counties. Differences in the resulting averages were then computed. Thus, by evaluating identical sets of species in each location, this metric isolated intraspecific phenological variation and excluded the effects of changes in species composition between each pair of counties.

Isolating composition-derived differences in flowering time

In order to evaluate the overall differences in flowering time that occurred among each pair of counties, the mean flowering time of each species (represented by the mean collection date of all flowering samples) in a given timing class was also calculated across all samples throughout its entire range. This resulted in a single estimate of flowering time for each species that was not influenced by any intraspecific responses to varying environmental conditions over space. For each possible pair of counties, all species that were present in only one of the two counties were then selected. For each of the two counties being compared, a community-level mean flowering time was then calculated based on the flowering times of only those species that were not shared with the other county. Differences in the resulting averages were then computed. Thus, by eliminating the effects of local environmental variation on the flowering times of each species, this metric isolated composition-derived differences in flowering time and excluded the effects of intraspecific phenological variation. It should be noted that while the proportion of species that were shared among each pair of counties was highly variable, the relative proportion of shared to unshared species had no significant impact on the overall magnitude of composition-derived phenological differences ($R^2 < 0.001$, $P = 0.419$, d.f. = 26113).

Comparison with overall flowering

The relationships of intraspecific and composition-derived variations in flowering phenology to variations in overall flowering time within each season and climate region were evaluated through linear regression analyses conducted within each seasonal class and climate region, as well as throughout the entire study area.

Responses to seasonal temperature variation

Additionally, intraspecific and composition-derived variations in flowering time within each season were compared with differences in county-level mean temperature estimates (based on 1971–2000 normals) over the 3-month period to which they showed the strongest relationship using linear regression analysis. As temperature variations during the same periods were most closely related to flowering times in each season across all climate regions, this resulted in comparisons of early season (class 2) flowering with mean temperatures from February to April, of mid-season (class 4) flowering with mean temperatures from May to July, and of late season (class 7) flowering with mean temperatures from August to October.

However, because of the pairwise nature of the methods used to estimate intraspecific and composition-derived differences in flowering time, estimates of intraspecific and composition-derived flowering phenology required a sufficient diversity of both shared and unique species within each county pair to represent mean, multispecies trends across the plant community. Therefore, all county pairs that included fewer than 10 species that were shared across both counties or fewer than 20 species that were unique to each of the two counties were excluded from analysis. Despite this restriction, comparisons were still possible among surprisingly distant communities, and included county pairs separated by over 4500 km, and over 11.5° in latitude. Further, this requirement appeared to be sufficient to eliminate any biases that resulted from variable sample intensity among locations, as the number of collections showed no significant effect on timing estimates ($R^2 < 0.001$, $P = 0.717$, d.f. = 2132). Previous studies have also confirmed that herbarium-based estimates of flowering phenology typically exhibit minimal collector bias and can accurately predict *in situ* observations of flowering time (Miller-Rushing *et al.*, 2006; Bowers, 2007; Robbirt *et al.*, 2011; Zalamea *et al.*, 2011). As this record evaluated spatial rather than temporal phenological variation and therefore pooled samples over many decades and collectors at each location, resulting estimates of intraspecific or composition-derived variation in flowering phenology should be particularly resistant to the influence of collector bias or variable sampling intensity.

RESULTS

Contributions to observed variation in overall flowering time

Intraspecific variations in flowering time were closely related to overall variations in flowering time, explaining over 50% of observed variation in overall flowering in all cases and over 75% of overall early season variation (Fig. 3, Table 1). Regression analysis also found that intraspecific changes in flowering time were similar in magnitude to overall variations in flowering time, and actually exceeded the mean overall responses in flowering time during the early and middle portions of the growing season (Fig. 3, Table 1).

In contrast, linear regressions of differences in composition-derived and overall flowering times found that the ratio of composition-derived variations in flowering time to overall variations in flowering time was less than 0.34 in all cases (Figs 4–6, Table 2) and that composition-derived phenological differences explained under 50% of overall variation in flowering (up to 49.3% among early flowering xeric communities; Table 2). However, the relationship between composition-derived and overall variations in flowering time often remained highly significant, and exhibited considerable seasonal variation. Composition-derived differences in flowering time also showed minimal contributions to differences in overall flowering time during the middle portion of the growing season (Fig. 4b), but explained over 25% of the observed variation among late-flowering species ($R^2 = 0.278$; Fig. 4c, Table 2). Examination of spatial patterns of composition-derived variation in late-season flowering phenology were also surprisingly similar in both distribution and magnitude to overall patterns of variation in flowering time (Figs 5 & 6).

The role of composition-derived phenological changes in determining overall variations in flowering time also appeared to vary considerably among climate regions. Composition-derived variations in early season flowering were minimally connected to overall flowering times in warm temperate areas, but were strongly correlated to overall early season flowering in xeric regions, explaining nearly 50% of the observed variation ($R^2 = 0.493$, $B = 0.20$, $P < 0.001$; Table 2). Interestingly, composition-derived variations in early spring flowering in xeric regions also exhibited strong correlation to intraspecific variations ($R^2 = 0.40$, $P < 0.001$, d.f. = 1195), even though such relationships were modest ($R^2 \leq 0.081$) throughout all other seasons and regions.

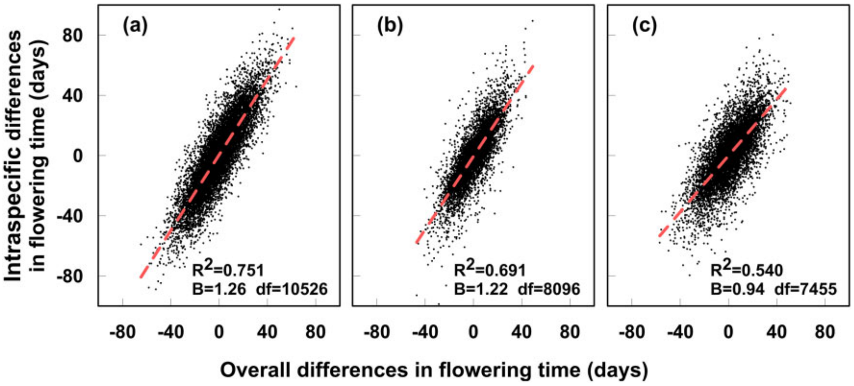

Figure 3 Intraspecific versus overall differences in flowering phenology over space among early flowering (a), mid-season flowering (b), and late-flowering portions of the plant community (c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. *B* is used here to indicate the slopes of linear relationships between intraspecific and overall phenological variations.

Table 1 Contributions of intraspecific phenological variation to overall differences in flowering time within xeric, warm temperate and cool temperate environments. Significant correlations are indicated using bold text.

Intraspecific versus overall variation in timing of flowering	Overall	Xeric	Warm temperate	Cool temperate
Early season				
Percentage of explained variance	**75.1%**	**78.7%**	**69.2%**	**76.0%**
ΔIntraspecific/ΔOverall	**1.26**	**1.24**	**1.17**	**1.02**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
No. of samples	10527	1194	6311	26
Mid season				
Percentage of explained variance	**69.1%**	**77.1%**	**58.3%**	**86.9%**
ΔIntraspecific/ΔOverall	**1.22**	**1.27**	**1.20**	**1.15**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
No. of samples	8097	1400	1857	1172
Late season				
Percentage of explained variance	**54.0%**	**58.5%**	**53.4%**	**53.3%**
ΔIntraspecific/ΔOverall	**0.94**	**0.88**	**0.93**	**1.06**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
No. of samples	7456	987	5283	14

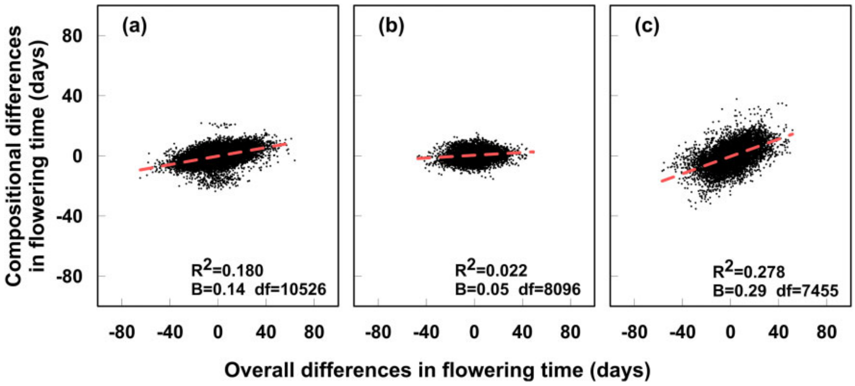

Figure 4 Compositional versus overall differences in flowering phenology over space among early flowering (a), mid-season flowering (b), and late-flowering portions of the plant community (c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. *B* is used here to indicate the slopes of linear relationships between composition-derived and overall phenological variations.

Table 2 Contributions of composition-derived phenological variation to overall differences in flowering time within xeric, warm temperate and cool temperate environments. Significant correlations are indicated using bold text.

Compositional versus overall variation in timing of flowering	Overall	Xeric	Warm temperate	Cool temperate
Early season				
Percentage of explained variance	**18.0%**	**49.3%**	**6.8%**	**22.2%**
ΔCompositional/ΔOverall	**0.14**	**0.20**	**0.10**	**0.34**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**0.013**
No. of samples	**10527**	**1194**	**6311**	**26**
Mid season				
Percentage of explained variance	**2.2%**	**0.4%**	**4.3%**	**5.3%**
ΔCompositional/ΔOverall	**0.05**	**–0.02**	**0.05**	**0.08**
P-value	**< 0.001**	**0.018**	**< 0.001**	**< 0.001**
No. of samples	**8097**	**1400**	**1857**	**1172**
Late season				
Percentage of explained variance	**27.8%**	**20.7%**	**30.3%**	15.3%
ΔCompositional/ΔOverall	**0.29**	**0.34**	**0.25**	0.25
P-value	**< 0.001**	**< 0.001**	**< 0.001**	0.150
No. of samples	**7456**	**987**	**5283**	14

Responses to seasonal temperature variations

Across the entire study area, early season flowering exhibited rapid intraspecific shifts towards earlier flowering under warmer February to April temperature ($R^2 = 0.433$, $B = –4.53$ days °C$^{–1}$, $P < 0.001$; Fig. 7a, Table 3). In comparison, mid-season flowering exhibited milder shifts towards earlier flowering in response to increasing May–July temperature ($R^2 = 0.144$, $B = –1.67$ days °C$^{–1}$, $P < 0.001$; Fig. 7b, Table 3). While late-season flowering did show significant intraspecific shifts towards later flowering in response to increasing temperatures from August to October, correlations between intraspecific variations in flowering time and differences in autumn temperature were minimal ($R^2 = 0.042$, $B =$ 1.31 days °C^{-1}, $P < 0.001$; Fig. 7c, Table 3). Intraspecific responses to temperature variations within each season were consistently lower in warm temperate regions than either xeric or cool temperate regions (Table 3). Additionally, cool temperate regions exhibited substantially stronger responses to temperature variations by both mid- and late-season flowering than occurred in either of the other climate regions, although estimates of late-season responses may be somewhat unreliable due to the small sample size in cool temperate regions (Table 3).

While intraspecific responses to seasonal temperature variations were typically strongest among early flowering species, composition-derived responses to changing temperatures were strongest among late-flowering species (Fig. 8). Although early and mid-season compositional responses to temperature variations were significantly weaker and less deterministic than intraspecific responses, late-season composition-derived shifts towards later flowering time among locations with warmer temperatures from August to October were both more consistent ($R^2 = 0.258$) and more rapid ($B = 1.39$ days °C$^{–1}$) than intraspecific responses to autumn temperature changes (Figs 7c & 8c, Tables 3 & 4). Additionally, both early and late-season compositional responses to temperature variations were strongest in xeric regions: these responses were not only much more deterministic than intraspecific responses to seasonal temperature variations (Tables 3 & 4), but also exhibited much more rapid delays in late-season flowering ($B = 1.58$ days °C$^{–1}$; Table 4) than occurred through intraspecific mechanisms ($B = 0.98$ days °C$^{–1}$; Table 3). However, composition-derived phenological responses to differing temperatures during the middle portion of the growing season remained minimal throughout all regions ($R^2 \leq 0.077$; Fig. 8b, Table 4), as well as

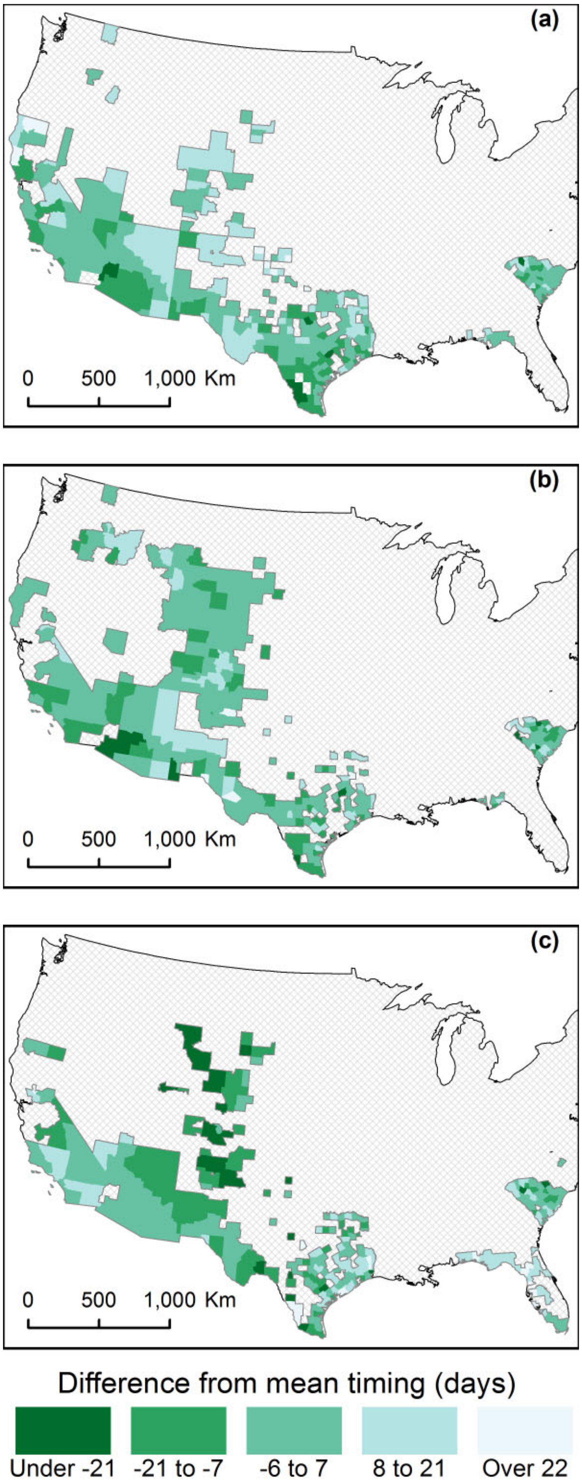

Figure 5 Variations in overall flowering time over space among early flowering (a), mid-season flowering (b), and late-flowering portions of the plant community (c). County-level estimates of mean flowering time were derived from mean flowering times of each species within each county.

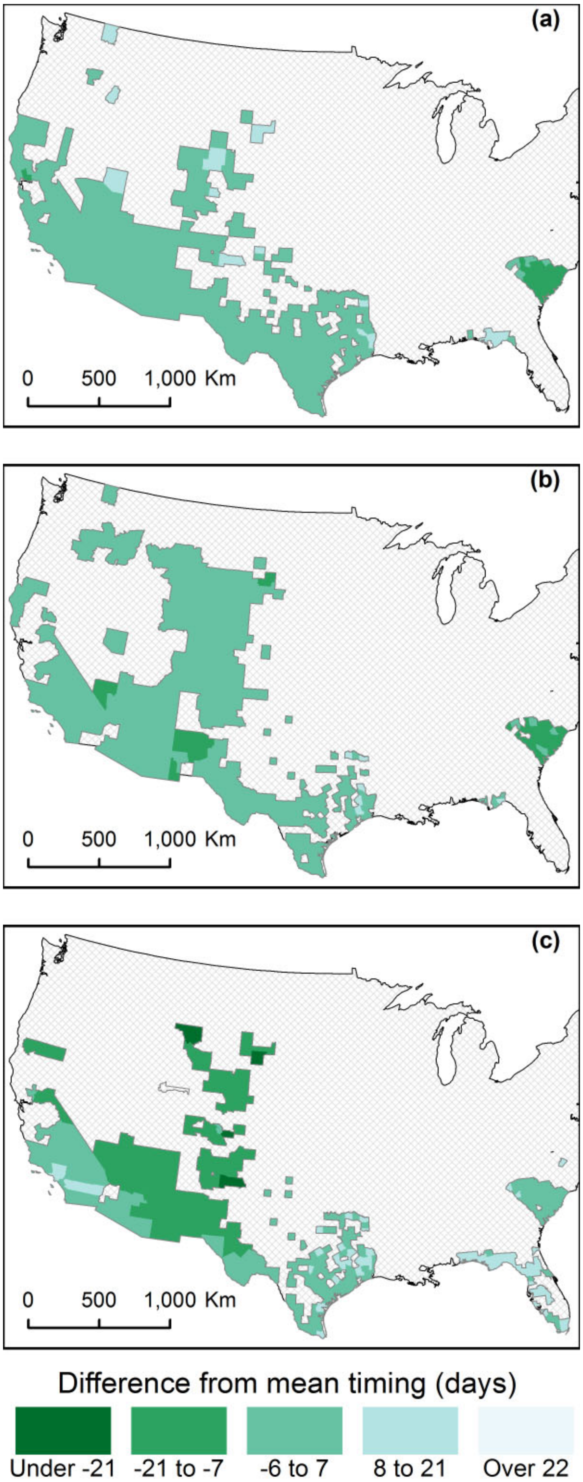

Figure 6 Composition-derived variations in flowering time over space among early flowering (a), mid-season flowering (b), and late-flowering portions of the plant community (c). County-level estimates of flowering time were derived purely through the mean flowering of each species within a county across its entire documented range.

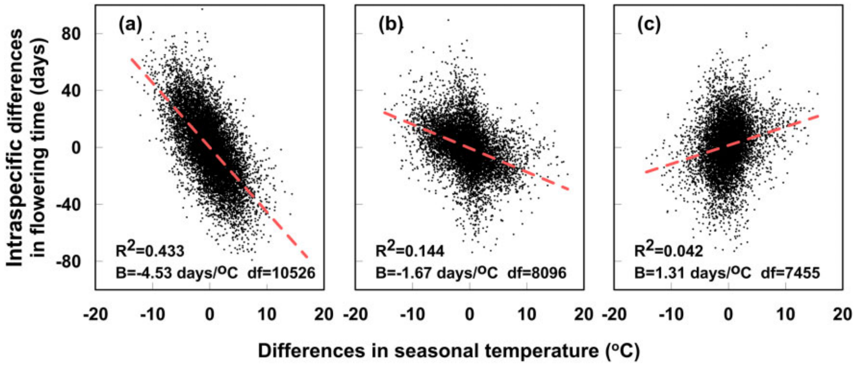

Figure 7 Intraspecific responses to differences in seasonal temperature among early flowering (a), mid-season flowering (b), and late-flowering portions of the plant community (c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. *B* is used here to indicate the slopes of linear relationships between intraspecific phenological timing and seasonal temperature variations.

Table 3 Intraspecific phenological responses in flowering time to spatial variations in seasonal temperature throughout xeric, warm temperate and cool temperate environments. Early season flowering was compared with mean temperature from February to April. Mid-season flowering was compared with mean temperature from May to July, and late season flowering was compared with mean temperature from August to October. Significant correlations are indicated using bold text.

Intraspecific responses to spatial variations in temperature	Overall	Xeric	Warm temperate	Cool temperate
Early season				
Percentage of explained variance	**43.3%**	**55.3%**	**31.3%**	**51.8%**
Days °C^{-1}	**–4.53**	**–4.20**	**–4.36**	**–2.26**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
No. of samples	**10527**	**1194**	**6311**	**26**
Mid season				
Percentage of explained variance	**14.4%**	**13.2**	**5.1%**	**39.1%**
Days °C^{-1}	**–1.67**	**–1.53**	**–1.91**	**–2.24**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
No. of samples	**8097**	**1400**	**1857**	**1172**
Late season				
Percentage of explained variance	**4.2%**	**9.6%**	**1.8%**	**73.2%**
Days °C^{-1}	**1.31**	**0.98**	**0.93**	**2.41**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.001**
No. of samples	**7456**	**987**	**5283**	**14**

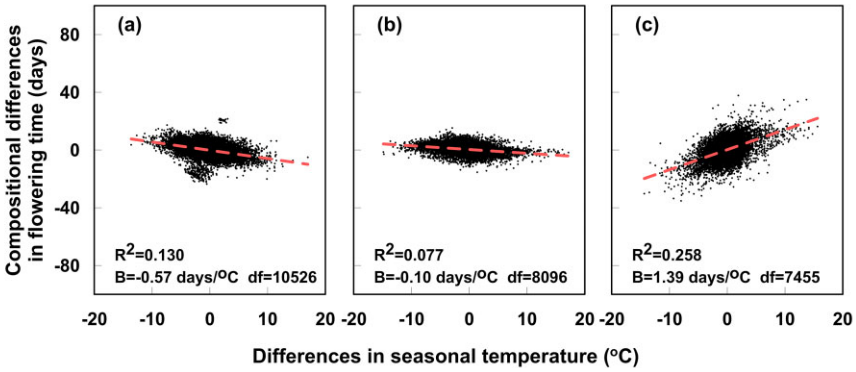

Figure 8 Compositional responses to differences in seasonal temperature among early flowering (a), mid-season flowering (b), and late-flowering portions of the plant community (c). Dots represent comparisons between a county pair, while dotted lines indicate a significant linear trend. *B* is used here to indicate the slopes of linear relationships between composition-derived phenological timing and seasonal temperature variations.

within warm temperate regions throughout all seasons ($R^2 \leq 0.09$ in all cases; Table 4).

DISCUSSION

Collectively, it is clear that both intraspecific and composition-derived changes contribute significantly to the overall pattern of spatial variation in flowering timing that occurs throughout the United States, and that the isolation of composition-derived phenological variation reveals important differences in community-level phenology and its relationship to community composition along environmental gradients. Intraspecific variations in flowering time are sufficient to explain the majority of overall variation in flowering time throughout all seasons and within each climate region, although the percentage of overall variation in flowering times that could be explained purely through intraspecific responses was greatest in spring and reduced among later portions of the bloom display. In contrast,

Table 4 Compositionally derived phenological responses in flowering time to spatial variations in seasonal temperature throughout xeric, warm temperate and cool temperate environments. Early season flowering was compared with mean temperature from February to April. Mid-season flowering was compared with mean temperature from May to July, and late season flowering was compared with mean temperature from August to October. Significant correlations are indicated using bold text.

Compositional responses to spatial variations in temperature	Overall	Xeric	Warm temperate	Cool temperate
Early season				
Percentage of explained variance	**13.0%**	**34.0%**	**2.0%**	**29.0%**
Days °C^{-1}	**–0.57**	**–0.69**	**–0.30**	**–1.06**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.004**
No. of samples	**10527**	**1194**	**6311**	**26**
Mid season				
Percentage of explained variance	**7.7%**	**7.0%**	**7.2%**	< 0.1%
Days °C^{-1}	**0.10**	**–0.26**	**–0.53**	–0.01
P-value	**< 0.001**	**< 0.001**	**< 0.001**	0.153
No. of samples	**8097**	**1400**	**1857**	1172
Late season				
Percentage of explained variance	**25.8%**	**49.4%**	**9.0%**	**37.9%**
Days °C^{-1}	**1.39**	**1.58**	**1.00**	**0.81**
P-value	**< 0.001**	**< 0.001**	**< 0.001**	**< 0.015**
No. of samples	**7456**	**987**	**5283**	**14**

however, the magnitude of composition-derived phenological changes differed significantly, both among climate regions and along a seasonal gradient. Therefore, these results indicate that phenological timing plays a significantly more important role in determining the composition of some plant communities than others, and that such communities may experience more rapid phenologically driven changes in composition through species loss, invasions or range shifting under additional climate change than other communities that exhibit lower composition-derived shifts in flowering phenology.

Seasonal differences in mechanisms underlying phenological variation

While intraspecific variation explained the majority of overall spatial variations in flowering time, reduced intraspecific responses to temperature variations were detected later in the growing season, particularly among late-flowering species. This supports previous *in situ* research which found reduced intraspecific responses to temperature variations during the mid and late portion of the growing season (Fitter *et al.*, 1995; Gordo & Sanz, 2005; Cook *et al.*, 2012). Similarly, *in situ* examinations of mean responses to interannual temperature variations throughout North America and Europe found that autumn flowering species exhibited milder and more variable responses to interannual temperature variations than spring flowering species (Wolkovich *et al.*, 2012).

In contrast to intraspecific variations, however, composition-derived phenological differences exhibited stronger responses to temperature variations over space and explained a larger percentage of variation in overall flowering time among late-flowering species. Collectively, these results indicate that the portion of the plant community that flowers towards the end of the growing season may experience a higher degree of phenologically driven range limitation than species that flower earlier in the year. Phenological studies which only examine intraspecific phenological variation may therefore underestimate the magnitude of responses to climate change in late-season flowering phenology.

Mid-season flowering typically exhibited the mildest composition-derived phenological variation, and explained only a small percentage of observed variation in overall flowering. This pattern is compatible with previous research into the mechanisms underlying phenologically derived range limitation, as most species were found to be range limited either by cold damage to flowering structures through late frosts, to which early flowering species would be most vulnerable, or by cold damage to fruiting structures prior to seed maturation, to which late flowering species would be most susceptible (Morin *et al.*, 2007; Chuine, 2010). Thus, it appears that additional warming is less likely to produce phenologically driven changes in the composition of that portion of the plant community which flowers during late spring or summer.

Composition-derived phenological variation across climate regions

In addition to seasonal differences, the role of flowering phenology in determining community composition also appeared minimal throughout warmer temperate regions. As warm temperate regions represented the areas with the mildest climate, this may reflect a region where damage to poorly timed blooms by cold or drought is often insufficient to exclude those species. Thus, it appears likely that warm temperate regions may be less prone to phenologically enforced changes in composition than xeric or cool temperate regions, and may be more resilient to future climatic changes.

In xeric regions, however, the plant community appears to be highly susceptible to phenologically enforced changes in composition, as xeric regions exhibited the most rapid composition-derived changes in the timing of both early and late-season flowering across a temperature gradient. Composition-derived phenological changes among early flowering species were also strongly responsive to temperature shifts and highly correlated to overall phenological variations. Interestingly, it would also appear that composition-derived phenological changes among early flowering species in xeric regions were also strongly correlated to intraspecific shifts in flowering time. Collectively, this may reflect an increased pressure to avoid frost damage (Inouye, 2008) and drought (Ghazanfar, 1997; Peñuelas *et al*., 2004; Gordo & Sanz, 2005, 2010; Prieto *et al*., 2008; Mission *et al*., 2011; Ferdenández-Martínez *et al*., 2012) within xeric regions that enforces highly coherent flowering times among early flowering species.

CONCLUSIONS

These results clearly show that herbarium records may be used successfully to evaluate the magnitude of intraspecific and composition-derived shifts in flowering phenology in response to changing climatic conditions over space, and represent a new means of estimating the magnitude of disruption to the composition of existing plant communities that would result from changes in optimal reproductive timing under additional climate change. Unlike previous methods, which relied upon *in situ* observation (Craine *et al*., 2012), this method may easily be extended to any region that includes significant digital herbarium records and some form of spatial temperature and climate characterization, and may also be further expanded to continental and global scales as herbarium records are digitally processed and become available. While this study primarily focused on broad climatic regions throughout North America, these results also have significant implications for a range of temperate environments and may easily be adapted to any region of the globe for which both significant herbarium records and basic climate information are available.

Still, this research represents only a preliminary examination of the mechanisms underlying spatial variations in flowering phenology throughout North America. Further research will expand this work to evaluate the magnitude of intraspecific and compositional variations in flowering phenology among plants that exhibit differing morphologies and physiological adaptations. A fuller understanding of the mechanisms which underpin observed patterns of variation in flowering phenology is critical for predicting the resilience of the plant community to future climate perturbations. Thus, future work will expand this method to separate intraspecific variations in flowering time into variations caused through either phenotypic plasticity or interpopulation genetic adaptation. While this work remains at the preliminary stages, it is clear that community-level changes in flowering phenology are closely tied to changes in the composition of the plant community over space. Evaluation of the various mechanisms that contribute to spatial differences in community-level flowering phenology represents a critical next step forward for predicting future changes in the ranges and local persistence of plant species that occur throughout the globe.

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