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Climate affects the rate at which species successively flower: Capturing an emergent property of regional floras

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Abstract

Aim: Climate affects the flowering time of many species. Little is known, however, about how climate influences the properties of regional floras, including the rate at which taxa flower sequentially throughout the flowering season. This study is the first to detect geographical variation in this rate across North America. In addition, we tested for the independent effects of intraspecific variation in flowering time and taxonomic composition on the rate of sequential flowering among regional floras distributed across a temperature gradient.

Location: North America.

Time period: This study examined >59,000 herbarium specimens that were collected in flower from 1901 to 2013.

Major taxa studied: 2,803 angiosperm taxa.

Methods: We identified 51 climatically homogeneous regions across the continental, mostly western states of the USA, in each of which ≥100 species were represented by herbarium specimens. We then examined the effects of mean annual temperature (MAT) on the rate of sequential flowering among species in each region. We also evaluated whether geographical variation in the rate of sequential flowering was attributable to intraspecific variation in the flowering time and/or the taxonomic composition of regional floras.

Results: As MAT increased over space, the rate of sequential flowering (standardized by the absolute length of the flowering season in each region) increased among relatively early-flowering taxa but decreased among the latest-flowering taxa. Both intraspecific variation and shifts in taxonomic composition among floras contributed to this pattern.

Main conclusions: Among floras throughout North America, the rate of sequential flowering among co-occurring taxa changes with MAT. Intraspecific phenological variation primarily affects the rate of sequential flowering during the first half of the growing season, consistent with the inference that future warming will most strongly affect flowering synchrony among early-flowering taxa.

KEYWORDS
climate change, flowering time, herbarium specimen, phenology

1 | INTRODUCTION

Many plant species alter the timing of their flowering in response to local climate conditions, which can influence the mean flowering date (MFD), the duration and the termination of flowering by individuals, populations and species (Bock et al., 2014; Cook, Wolkovich, & Parmesan, 2012; Fitter, Fitter, Harris, & Williamson, 1995; Panchen & Gorelick, 2016; Post, Pedersen, Wilmers, & Forchhammer, 2008; Szabó, Vincze, & Czúcz, 2016; Wolkovich et al., 2012). The effects of climatic conditions on the collective properties of plant communities and floras, however, have rarely been examined. For example, local or regional climatic conditions might influence the duration of the flowering season (defined here as the portion of the year during which 90% of species flower; Park, 2016), either compressing or extending it (Diez et al., 2012).

When considered from the perspective of a plant community or regional flora, geographical variation in climate may be associated with changes in a variety of collective properties related to the local flora as a whole. Just as the flowering times of individual species vary spatially in response to local climate conditions (Borchert, Robertson, Schwartz, & Williams-Linera, 2005; Lavoie & Lachance, 2006; Menzel, Estrella, & Fabian, 2001), so too the phenological properties of plant communities may shift over space in response to differences in local climate (CaraDonna, Iler, & Inouye, 2014; Diez et al., 2012). For example, changes in the percentage of co-occurring species that have begun to flower as the flowering season progresses may differ among floras that occupy climatically distinct regions. Although previous studies have determined that the seasonal distribution of flowering times may differ among floras (Diez et al., 2012) and that the rate at which temperature increases during spring may control the synchrony of spring flowering (Wang, Tang, & Chen, 2016), no comprehensive assessment of the relationship between local climate and the distribution of flowering times across the growing season has yet been attempted. Here, we examine, for the first time, a property of regional floras, namely the rate at which angiosperm species initiate flowering in sequence among successive stages of the flowering season, and how this property is influenced by local climatic conditions.

In any flora, the percentage of species that has initiated flowering increases from zero to 100 throughout the flowering season. The rate at which this percentage increases as the flowering season progresses (hereafter referred to as the rate of sequential flowering) may have strong ecological consequences (Pau et al., 2011). For example, the rate at which species successively flower may influence the diversity of co-flowering species. If this rate changes across the flowering season, there may be periods during which the flowering times of many species are highly synchronous (i.e., when a large number of species begin flowering in rapid succession, potentially resulting in a period of relatively high floral diversity). Conversely, there may be periods during which the synchrony of flowering is low (i.e., more time elapses between the flowering times of successively flowering species, potentially resulting in periods of relatively low floral diversity).

Seasonal variation in the species diversity of flowers can affect plant reproductive success owing to both interspecific competition among plant taxa for pollinator visitation (Feldman, Morris, & Wilson, 2004; Rathcke, 1988a, 1988b; Waser, 1978) and facilitative or mutualistic interactions (Feldman et al., 2004; Laverty, 1992; Mitchell, Flanagan, Brown, Waser, & Karron, 2009). For example, increases in the number of species with overlapping flowering periods may result in intensified competition for pollinator services (Stone, Willmer, & Rowe, 1998), thus reducing reproductive success. Accordingly, historical patterns of interspecific flowering phenology in many floras limit synchrony among plant species that might otherwise compete for pollinator visitation (Rathcke, 1988a; Reader, 1975; Stiles, 1975; Whalen, 1978). In other cases, however, reductions in the number of co-flowering species may disrupt mutualistic flowering displays among taxa, thereby reducing the frequency of pollinator visits per species or per individual (Staggemeier, Diniz-Filho, & Morellato, 2010; Tachiki, Iwasa, & Satake, 2010).

It is well documented that the diversity of species in flower varies throughout the flowering season (Aldridge, Inouye, Forrest, Barr, & Miller-Rushing, 2011), differs among communities that occupy contrasting habitats (Heinrich, 1976) and may be affected by inter-annual climate variation (Aldridge et al., 2011). The effects of local climatic conditions on the rate of sequential flowering, however, remains unknown. Here, we examine these effects during successive stages of the flowering season.

It is important to note, however, that two distinct mechanisms may generate variation among plant communities in the rate at which sequentially flowering species initiate flowering. First, variation among communities in the seasonal distribution of flowering times may be attributable to shared species exhibiting different flowering times at different locations (Lacerda, Araújo Barros, Almeida, & Rossatto, 2017; Panchen & Gorelick, 2016; Park, 2014). If the flowering times of species that occur across a temperature gradient exhibit different magnitudes (or directions) of change in response to local climatic conditions, this will result in geographical variation in the rate at which sequentially flowering species begin to flower as the flowering season progresses (Panchen & Gorelick, 2016; Prevéy et al., 2017). Second, differences among communities in the seasonal distribution of flowering times may be attributable to geographical variation in taxonomic composition, which may also be influenced by climatic conditions. Both these mechanisms have previously been documented to play a role in determining community-level phenological mean flowering dates across broad climate gradients (Park, 2014).

It is likely that both these mechanisms (species-specific responses to local climatic conditions versus geographical variation in community composition) also play a role in determining the seasonal distribution of flowering within floras distributed along similar climate gradients. However, these two mechanisms differ in their implications for our ability to predict community-level shifts in phenology in response to climate change. If geographical variation in the rate of sequential flowering is attributable primarily to intraspecific variation, then spatial variation in current climatic conditions that

affect the rate at which species flower successively may be used to predict changes in this rate in response to projected climate change. In contrast, if geographical variation in the rate of sequential flowering is attributable primarily to differences among regions in species composition, then it will be more difficult to predict, for a given location, how future climate change will affect the rate of sequential flowering. Thus, examining the effect of each of these processes on the rate of floral accumulation (i.e., the rate of at which sequentially flowering species flower) over space is crucial to understanding the implications of future climate change on the future rates of floral accumulation under projected climate warming.

Examinations of the rate of sequential flowering and its relationship to local climate require information on flowering time across a taxonomically diverse and spatially heterogeneous set of floras. With the advent of digitally available specimen data, herbarium records now represent a powerful resource with which to examine the phenology of a large number of taxa distributed across an unparalleled geographical area (Callinger, Queenborough, & Curtis, 2013; Willis et al., 2017). Although herbarium collections have been found to exhibit some biases in their taxonomic and spatial focus and to under-sample seasons corresponding to extreme inclement weather (e.g., winter, Daru et al., 2017), herbarium data have been well documented to provide an accurate account of flowering phenology across a wide range of species (Davis, Willis, Connolly, Kelly, & Ellison, 2015; Jones & Daehler, 2018). Although potentially less accurate than estimates of the date of flowering onset based on in situ observations, herbarium-based estimates of mean flowering time have been determined to remain robust even when the number of observations is low (Bertin, 2015) and are less influenced by collector bias than estimates of first or last flower (Robbirt, Davy, Hutchings, & Roberts, 2011). Furthermore, estimates of mean flowering time that were derived from herbarium-based phenological data in Boston were found to provide accurate estimates of mean flowering time that exhibited similar patterns of variation to in situ observations and to remain accurate among taxa with both short and long flowering durations (Primack, Imbres, Primack, Miller-Rushing, & Del Tredici, 2004).

Here, we examined 59,096 electronically available herbarium records to investigate whether regional climatic conditions affect the rate of sequential flowering among species in floras distributed across a broad climate gradient throughout North America. In addition, we identified the role of mean annual temperature (MAT) in generating geographical variation in the rate of sequential flowering, in addition to the mechanisms that generate such changes. To begin, we used specimen-based data to estimate the mean flowering dates (MFDs) of a total of >2,800 plant taxa distributed across the continental USA in each of 51 climatically homogeneous local climate regions (LCRs; defined below). We then used these MFDs to estimate the amount of time required for successively flowering portions of the species in each LCR to flower (each portion representing 15% of the flowering taxa in the LCR). Finally, these values were used to test the hypothesis that regional MAT affects the rate at which the angiosperm taxa within an LCR successively flower as the flowering season progresses and to evaluate the roles of intraspecific variation versus changes in taxonomic composition in response to MAT in

generating geographical variation in this property. Collectively, our analyses revealed that warmer climates are associated with increases in the rate of sequential flowering among the first 50% of species to flower and reductions in the rate of sequential flowering among the last 20% of species to flower. Both intraspecific phenological variation and changes in species composition contribute to the observed effects of MAT on the rate of sequential flowering, although these two mechanisms differ in importance and may reinforce or oppose each other during different portions of the growing season.

2 | MATERIALS AND METHODS

2.1 | Herbarium data

Records of flowering phenology used in this study were drawn from the digital archives of 72 herbaria throughout North America (see Acknowledgements). This study examined 7,300,614 digital records of herbarium specimens and ultimately retained for analysis 59,096 specimens that were recorded in flower and met all additional criteria for analysis. These records included trees, shrubs and herbaceous angiosperm taxa collected from 1901 to 2013. All specimens that were collected while not in flower or that did not explicitly document their phenological status, the latitude and longitude of the collection site or the date of year (DOY) of collection were excluded from further analysis. A specimen was considered to be collected in flower if its digitized record explicitly included phenological status and recorded the specimen as being in flower. This assessment was based on a visual examination of the specimen by herbarium staff, typically at the time of digitization. Although the method for scoring the phenological status of a specimen might have differed among taxa and herbaria, the phenological assessment of all specimens was consistently intended to identify those that were collected while at least one flower was open. These records represent second-order phenological data in the classification scheme developed by Yost et al. (2018). The DOYs of collection of these herbarium specimens were used to estimate the mean flowering time (MFD) of each taxon in each LCR, as described below (Bertin, 2015).

Given that taxonomic nomenclature was not always consistent among specimens, species names were standardized and synonymies resolved using taxonomic records from The Plant List, the International Legume Database and Information Service, the Global Compositae Checklist, and Tropicos.org using the Taxonomic Name Resolution Service iPlant Collaborative, v.4.0 (accessed 4 April 2017; http://tnrs.iplantcollaborative.org; Boyle et al., 2013). Specimens that could not be identified unambiguously were eliminated from further analysis, as were duplicate specimens (i.e., one or more specimens that were collected on the same date and location as another specimen of the same taxon). For this study, we treated subspecies as independent taxa.

2.2 | Defining local climate regions

In this study, our objective was to evaluate the pace of the flowering season throughout the continental USA at geographical scales

broad enough to include a sufficiently large number of herbarium records and angiosperm taxa for rigorous analysis, but fine enough to discriminate among climatically distinct regions and floras. To accomplish this, we divided the continental USA into a series of LCRs, each of which represents a climatically homogeneous area (Park, 2016). These LCRs were identified by overlaying grid-based estimates of MAT and mean annual precipitation (MAP) that were derived from 4 km long-term climate means produced using the Parameter-elevation Regression on Independent Slopes Model (PRISM) for the years 1901–2013 (PRISM Climate Group, Oregon State University; http://prism.oregonstate.edu; created 4 February 2004) such that each LCR spanned a contiguous region within which MAT across all grid cells fell within 0.5°C of the median value (e.g. from 0 to 1°C), within which mean annual precipitation fell within 1 cm of the median value (e.g. from 20 to 22 cm), and which spanned ≤ 1° in latitude or longitude. This led to polygons of various sizes, because climatically heterogeneous landscapes were composed of numerous smaller LCRs, but ensured that each LCR represented a distinct but climatically homogeneous region.

In order to ensure that each LCR contained a sufficient diversity of taxa to represent its local flora, we overlaid the coordinates of the herbarium specimens onto these LCRs and eliminated all LCRs that included <100 taxa (Supporting Information Tables S1 and S2). To reduce the effects of unusual climate conditions on MFD, only taxa that were collected in ≥2 years within a given LCR were included for analysis. We acknowledge that taxon-specific estimates of MFD in each LCR might not be highly precise when the sample size is low; 45% of local MFD estimates were derived from only two specimens, and only 1% of local MFD estimates were based on >10 specimens (Supporting Information Figure S1). However, the outcome variables investigated here (defined in Sections 2.5, 2.7, and 2.8) do not depend on the estimated MFD of any given taxon being highly accurate; they depend on the collective attributes of the MFDs among taxa in a given LCR. The criteria we imposed for inclusion of a given taxon in the dataset analysed here represented a trade-off between sample size and taxonomic diversity. To address concerns that differences in sampling intensity among LCRs might affect the values of our outcome variables and therefore their association with MAT, we tested for significant correlations among LCRs between taxonomic diversity and MAT and between sample size (the mean number of herbarium specimens per taxon) and MAT. Taxonomic diversity and MAT were independent among LCRs ($r = 0.03$, $p > 0.245$, $n = 51$), and the mean number of specimens per taxon was also independent of MAT ($r = 0.04$, $p > 0.167$, $n = 51$). Consequently, we could be confident that sampling intensity was not confounded with MAT when testing for relationships between MAT and the outcome variables examined here.

The remaining dataset spanned 51 LCRs distributed across the continental USA, with a mean LCR area of *c.* 1,000 km^2. The LCRs used in this study ranged from 32 to 49° N latitude and from 1 to 23°C MAT and included data from 2,803 distinct taxa, representing 59,096 herbarium specimens (Supporting Information Table S1). The distribution of MATs among the selected LCRs did not differ significantly from normal (Shapiro–Wilk test: $W = 0.956$, $p = 0.059$, d.f. = 51). Although the higher density of phenologically assessed herbarium specimens in the western USA led to the majority of LCRs in this study being located in this region ($n = 39$), our dataset also included LCRs in the midwestern ($n = 2$), gulf coast ($n = 2$) and northeastern portions of the USA ($n = 9$; Figure 1). Shrublands, evergreen forest and mixed or deciduous forests were the dominant vegetation domains throughout the majority of these LCRs, as estimated from the National Land Cover Database 2011 (Supporting Information Table S1; Homer et al., 2015).

2.3 | Calculating taxon-specific mean flowering date

The annual mean flowering date of each taxon was then calculated for each year and LCR in which specimens of that taxon were collected. The MFD for each taxon within each LCR was then calculated as the mean of all annual MFD estimates for that taxon within that LCR.

2.4 | Identification of percentile classes

To compare LCRs with respect to the rate at which sequentially flowering taxa reach their MFD, we divided the flora of each LCR into groups of successively flowering species that could be compared directly among LCRs. Given that LCRs differed in species richness, these groups were defined so that they made up equal proportions of the flora of each LCR rather than a specific number of taxa. To achieve this, in each LCR, we ranked all taxa with respect to their MFD and then assigned each taxon a percentile rank, with the earliest-flowering taxa assigned the lowest ranks. We then divided the flora of each LCR into six sequential percentile classes, each of which represented one-sixth of the successively flowering taxa within a local flora; we excluded the first 5% and the last 5% of taxa to initiate flowering in each LCR because these were considered to flower outside the flowering season (Park, 2016). The six percentile classes were defined as follows within each LCR: taxa that exhibited
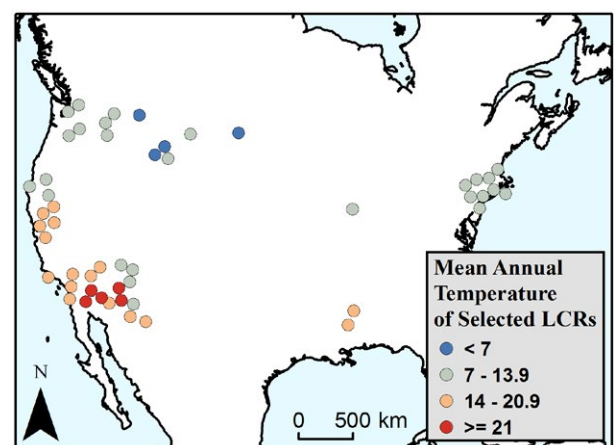

FIGURE 1 Study area and climate regions. Circles indicate local climate regions (LCRs). The colour of each circle indicates the mean annual temperature (MAT) within each LCR based on 1901–2013 PRISM climate means

MFDs within (a) the 5th–19.9th percentile (i.e., the earliest-flowering taxa); (b) the 20th–34.9th percentile; (c) the 35th–49.9th percentile; (d) the 50th–64.9th percentile; (e) the 65th–79.9th percentile; and (f) the 80th–94.9th percentile (i.e., late-flowering taxa). Each percentile class therefore included 15% of sampled taxa in an LCR (i.e., 16.7% of taxa that flower within the flowering season, which excludes the first and last 5% of taxa). The proportion of the flowering season in an LCR that was required for all the species within a given percentile class to flower was inversely proportional to the rate of flowering among the successively flowering species in that percentile class (see Section 2.5).

These six classes, although somewhat arbitrary, represent a trade-off between identifying enough classes to capture seasonal differences in the rate of sequential flowering and including a sufficient number of taxa within each class to represent its flowering behaviour. In order to ensure that the results of this study were not unduly influenced by the division of each local flora into six percentile classes (instead of some other number), all analyses were repeated using nine percentile classes (with each class representing 10% of the flowering taxa in each LCR) and five percentile classes (with each class representing 18% of the flowering taxa in each LCR).

It should also be noted that within each LCR, the set of taxa that constitute each percentile class is unique; each taxon appears in only one percentile class. In contrast, one or more of the taxa in a given percentile class within a given LCR may also appear in other LCRs, either in the same or in different percentile classes. Additionally, given that percentile classes were defined as a proportion of each local flora rather than by a set period of flowering, the rate of sequential flowering often differed among percentile classes within an LCR; that is, successive percentile classes within a given LCR generally differed with respect to the time that elapsed between the MFD of the earliest- and latest-flowering taxa (Figure 2; Supporting Information Table S1).

2.5 | Estimating rates of sequential flowering: MFD accumulation rates

In this study, we used the MFDs of the taxa in each LCR to examine a collective property of each percentile class: the percentage of the flowering season in the LCR required for all taxa within that class to flower in succession. The way in which this variable can change over the course of the flowering season in an LCR can be illustrated by an accumulation curve of its MFDs (Figure 2). The percentage of the flowering season required for all taxa within a percentile class to flower provides an estimate of the rate of successive flowering among taxa in each LCR throughout its flowering season; lower values of the former indicate a faster rate of sequential flowering among taxa. Below, we refer to this rate as the "MFD accumulation rate", while emphasizing that high rates of MFD accumulation correspond to relatively low percentages of the flowering season required for all taxa to reach MFD.

For each percentile class in each LCR, we first subtracted the MFD of the earliest-flowering taxon from the MFD of the last taxon to flower, producing a raw value representing the "duration" of the percentile class. Given that the duration of the entire flowering season differs among LCRs, however, we standardized the duration of each percentile class in each LCR by converting it into a percentage of the total flowering season within that LCR (Park, 2016). This was accomplished by dividing the duration of a given percentile class in a given LCR by the total length of the flowering season in the LCR (estimated as the number of days between the MFDs of the 5th and 95th percentile of flowering taxa within the LCR), and multiplying the resulting value by 100. Given that each percentile class represents one-sixth (16.7%) of the taxa that flower during the flowering season, the time required for all taxa in a given percentile class to reach MFD would occupy one-sixth of the flowering season if the
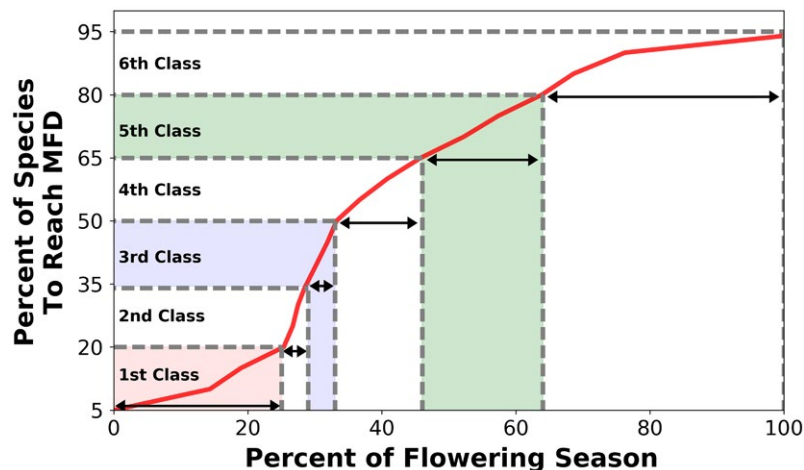

FIGURE 2 Example of a mean flowering date (MFD) accumulation curve (red line) for a single local climate region (LCR). Within each percentile class of sequentially flowering taxa (e.g., the third percentile class, representing the 35th–49.9th percentile of species is represented by the blue shaded area), the slope of the continuous line represents the rate at which the species begins to flower. The lengths of double-headed horizontal arrows indicate the proportion of the flowering season that passes between the MFD of the earliest- and latest-flowering species within each percentile class. For example, the first species of the third percentile class begins to flower when 29% of the flowering season is complete, and the last species in this percentile class begins to flower when 33% of the flowering season is complete

MFD accumulation rate were constant across the flowering season. Shorter durations would indicate a higher MFD accumulation rate within that percentile class than would occur given a constant rate of MFD accumulation (and therefore greater synchrony in the MFD of the taxa constituting that percentile class; Figure 2). Conversely, longer durations would indicate a slower MFD accumulation rate (and therefore lower synchrony in the MFD of the taxa constituting that percentile class).

2.6 | The effects of local climate on the MFD accumulation rate

For each percentile class, we determined the effect of MAT (based on 1901–2013 climate means) on the MFD accumulation rate by regressing, among LCRs, the percentage of the duration of the flowering season required for all taxa in that class to reach their MFD as a function of MAT ($y = Bx + ab$, where y is the percentage of the entire length of the flowering season in an LCR that was required for all taxa in that class to reach their MFD, x is the MAT, B is the slope of the relationship between MFD and MAT, and a is the intercept). In this framework, a regression slope significantly greater than zero would indicate that warmer climates are associated with an increase in the percentage of the duration of the flowering season required for all taxa to reach flowering (i.e., a lower MFD accumulation rate and lower synchrony of MFD) in that percentile class. In contrast, a significant negative relationship would indicate that warmer climates are associated with a reduction in the percentage of the duration of the flowering season required for all taxa in a given percentile class to reach their MFD, or higher MFD accumulation rates, and therefore higher synchrony in MFD among taxa. To ensure that the direction and strength of these relationships were not qualitatively

affected by the decision to divide the flowering season into six percentile classes, this analysis was also conducted using alternative sets of percentile classes in which the growing season was divided into different numbers of percentile classes that represented 10% of taxa (i.e., nine classes) and 18% of taxa (i.e., five classes).

2.7 | Isolating the influence of intraspecific phenological differences on temperature-mediated MFD accumulation

We examined whether intraspecific changes in MFD along a temperature gradient contributed to geographical variation in the MFD accumulation rate in each percentile class. This was accomplished by identifying every pair of taxa that co-occurred in two or more LCRs in the same percentile class and measuring the dissimilarity between their MFDs (i.e., the absolute value of the difference in their MFDs as a percentage of their local flowering season) within each LCR (Equation 1).

$$| (MFD_{Taxon\,A} - MFD_{Taxon\,B}) | / \text{Duration of flowering season} = \text{Dissimilarity} \quad (1)$$

The change in the difference between the MFDs of the two taxa (ΔDissimilarity; Equation 2) between each pair of LCRs in which both taxa occurred was then calculated, as was the difference in MAT ($\Delta MAT = MAT_{warmer\,LCR} - MAT_{cooler\,LCR}$) between each pair of locations.

$$\text{Dissimilarity}_{warmer\,LCR} - \text{Dissimilarity}_{cooler\,LCR} = \Delta\text{Dissimilarity} \quad (2)$$

This ΔDissimilarity value was calculated for all pairs of taxa that co-occurred in multiple LCRs (Figure 3c). Given that this analysis
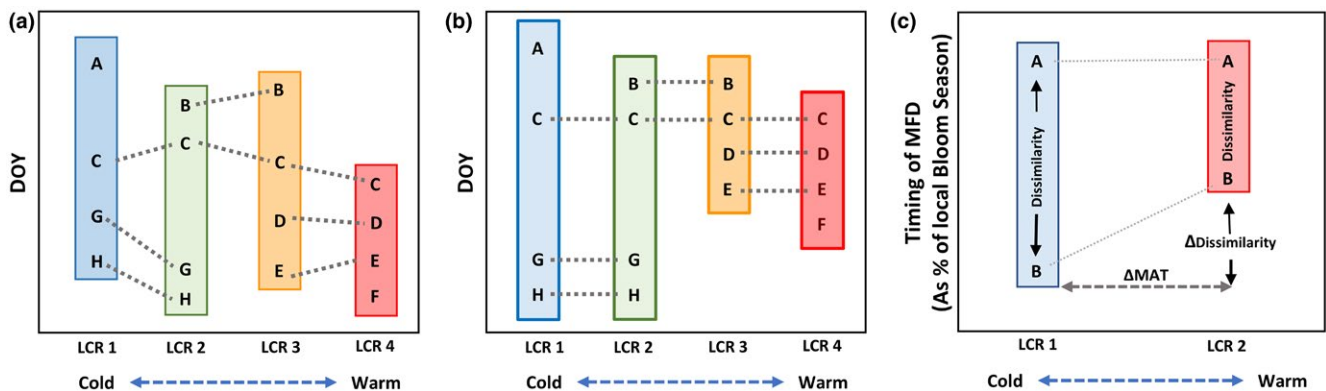

FIGURE 3 Conceptual models illustrating two mechanisms that might contribute to geographical variation in the percentage of the flowering season required for all taxa within a percentile class to flower: changes in species composition versus intraspecific variation in mean flowering date (MFD) among local climate regions (LCRs). Capital letters within each panel represent the date of year (DOY) of hypothetical taxa with a given percentile class. The length of each vertical bar represents the time required for all taxa in a percentile class to flower within a given LCR. (a) changes in taxonomic composition and intraspecific phenological variation both cause a decline in the time required for all taxa to flower with increasing mean annual temperature (MAT); the DOYs of the MFDs represent the observed MFD of each taxon within each LCR. (b) Changes in taxonomic composition across LCRs alone cause a decline in the time required for all taxa to flower with increasing MAT; the DOYs of the MFDs are based on the mean, nationwide MFD of each taxon (estimated using all herbarium specimens). (c) Intraspecific phenological variation is the sole cause for the decline in the time required for all taxa to flower with increasing MAT; in this example, the synchrony of MFDs among co-occurring species within a given percentile class increases as MAT increases

was designed to evaluate changes in the synchrony of MFDs within each percentile class, only cases in which both taxa flowered within the same percentile class in both LCRs were considered for analysis. Values of ΔDissimilarity greater than zero indicate cases where the MFDs of a given pair of taxa became less synchronized (i.e., more dissimilar) in the warmer of the two LCRs in which it occurred, whereas values less than zero indicate cases where a pair of taxa became more synchronized in the warmer LCR. For each percentile class, we used the values for all pairs of taxa that occurred in two or more LCRs to conduct linear regressions of ΔDissimilarity versus ΔMAT. A positive slope of this regression would indicate that the MFDs of the two taxa became more dissimilar (i.e., less synchronous) in warmer LCRs. A negative slope would indicate that the MFDs of co-occurring taxa became more similar in warmer LCRs.

2.8 | Isolating the effect of species composition on temperature-mediated MFD accumulation

To examine the contribution of species composition to variation in the MFD accumulation rate among LCRs that differed in MAT, we compared the time required for all taxa to reach MFD (in each percentile class) among LCRs in the absence of intraspecific variation in MFD. To remove the effects of intraspecific variation in local MFDs across LCRs, we first calculated a single estimate of the mean MFD for each taxon across all locations in which it was collected (including specimens outside the LCRs used in this study). Using these LCR-independent estimates of MFD, we recalculated the MFD accumulation rate for each percentile class within each LCR. This step eliminated any effect of intraspecific changes in MFD among LCRs on the MFD accumulation rates (Figure 3b).

Within each percentile class, we then conducted linear regressions, among LCRs, of the percentage of the flowering season required for all taxa to reach flowering (using the temperature-independent estimates of MFD for each taxon) versus MAT. Having eliminated intraspecific variation from this constrained dataset, any significant relationship between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT could be attributed to differences among LCRs in floristic composition. Significant positive relationships between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT would indicate that, among LCRs in warmer locations, the taxonomic composition changed such that either some taxa that exhibited highly synchronous MFDs were removed (thereby requiring the temporal bounds of the percentile class to be extended to ensure that it continued to retain 15% of the taxa in the LCR) or some taxa that exhibited less synchronous MFDs were added. Significant negative relationships between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT would indicate that, among LCRs in warmer locations, the composition of the local flora changed in a manner that increased the synchrony of the MFDs. Given that this analysis eliminated all intraspecific variations in MFD that might have occurred in response to differences in local temperature among LCRs, any differences among LCRs with respect to

the MFD accumulation rate for a given percentile class could therefore be attributed solely to differences in species composition.

3 | RESULTS

3.1 | Mean flowering date accumulation rate versus climatic conditions

Significant relationships were detected among LCRs between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT within the second, third and sixth percentile classes. This relationship was negative for both the second (R^2 = 0.30, p < 0.01; Figure 4b) and third (R^2 = 0.15, p < 0.01; Figure 4c) percentile classes; the synchrony of MFDs increased with MAT. Conversely, a significant positive relationship was detected between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT in the sixth percentile class (R^2 = 0.10, p = 0.03; Figure 4f); warmer temperatures were associated with reduced synchrony among the MFDs of the taxa constituting this class. No significant relationships were detected between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT for the first, fourth or fifth percentile classes (p > 0.17 in all cases; Figure 4a,d,e). Analogous relationships were detected when similar analyses were conducted after dividing the flowering season into both smaller (Supporting Information Figure S2) and larger (Supporting Information Figure S3) numbers of percentile classes. Across all temperature regimes, the rate of MFD accumulation was found to increase sharply during the second percentile class (Figure 5).

3.2 | The influence of intraspecific variation on the synchrony of MFDs between co-occurring taxa

Significant relationships were detected between the pairwise difference in MFDs among co-occurring taxa (ΔDissimilarity) and the difference in MAT between the LCRs in which they occur (ΔMAT). In the first percentile class, higher ΔMAT was associated with increasingly dissimilar MFDs among pairs of co-occurring taxa (R^2 = 0.06, p = 0.03; Figure 6a), indicating that warmer temperatures were associated with intraspecific shifts in phenology that reduced the synchrony of MFDs among the earliest-flowering taxa. However, in the second percentile class, this relationship was negative (R^2 = 0.18, p = 0.05; Figure 6b); warmer temperatures were associated with intraspecific shifts in phenology that increased synchrony among those taxa. No significant relationships between ΔMAT and the pairwise synchrony of MFDs among co-occurring taxa were detected among the remaining percentile classes (p > 0.11 in all cases; Figure 6c–f).

3.3 | Mean flowering date accumulation rate versus climatic conditions in the absence of intraspecific phenological variation

In the absence of intraspecific variation in MFD among LCRs, significant relationships were still observed between the percentage
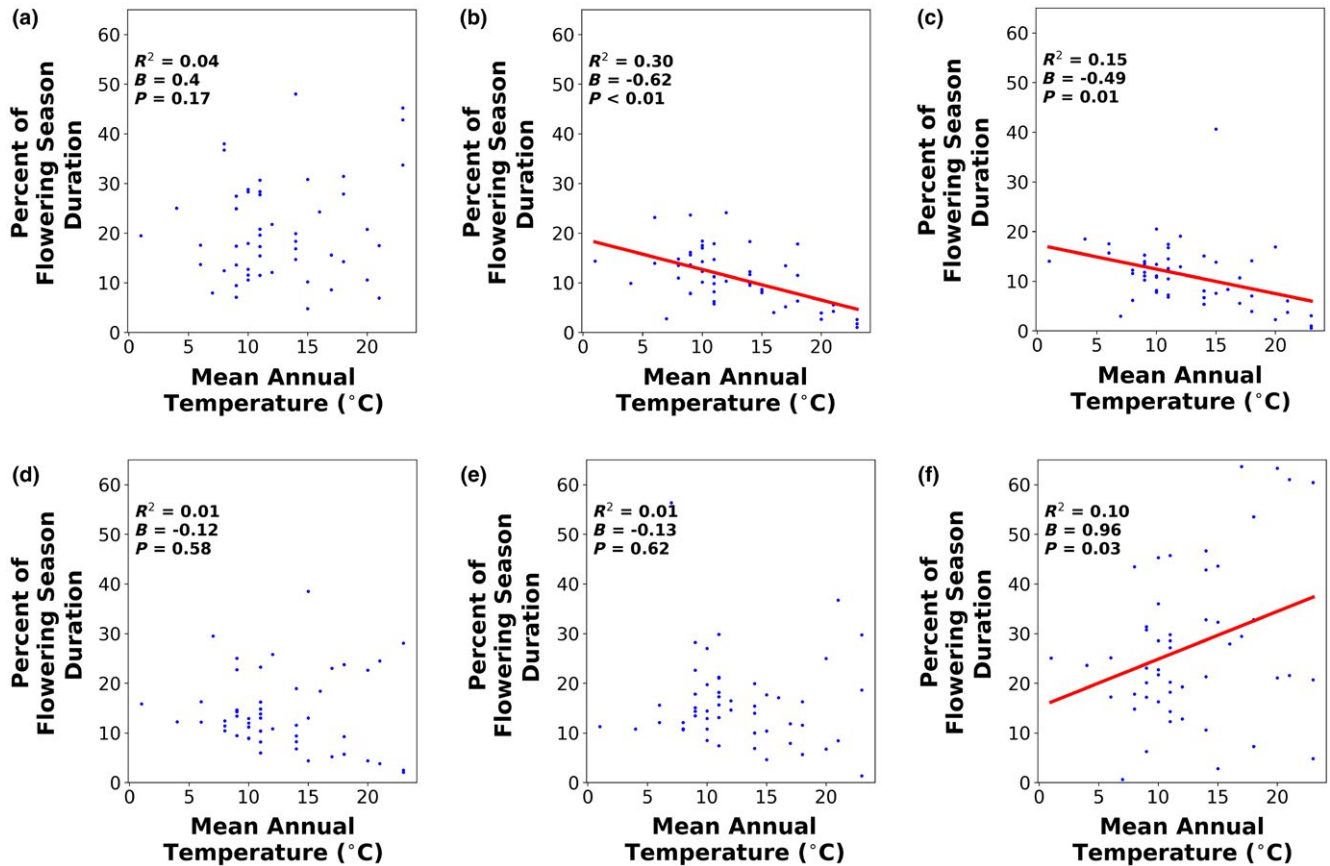
FIGURE 4 Percentage of the flowering season required for each successive 15% of taxa to begin flowering versus mean annual temperature (MAT) among: (a) the first percentile class, representing the 5th–19th percentile; (b) the second percentile class, representing the 20th–34th percentile; (c) the third percentile class, representing the 35th–49th percentile; (d) the fourth percentile class, representing the 50th–64th percentile; (e) the fifth percentile class, representing the 65th–79th percentile; and (f) the sixth percentile class, representing the 80th–94th percentile of species within each local climate region (LCR). Each point represents one LCR. Lines indicate significant linear trends among LCRs. *B* indicates the slope of the linear relationship between the duration of MFD accumulation and MAT within each percentile class

of the flowering season required for all taxa in a given percentile class to reach flowering and MAT among LCRs for the first, second, fifth and sixth percentile classes (Figure 7). Increased synchrony of MFDs was observed in response to higher MAT in both the first (R^2 = 0.19, p < 0.01; Figure 7a) and second percentile classes (R^2 = 0.35, p < 0.01; Figure 7b). In contrast, we observed decreased synchrony of MFDs in response to higher MAT in the fourth (R^2 = 0.10, p = 0.02; Figure 7e) and sixth (R^2 = 0.11, p = 0.02; Figure 7f) percentile classes. Controlling for intraspecific variation in MFD, we detected no significant relationship between the percentage of the flowering season required for all taxa in a given percentile class to reach flowering and MAT among the third or fourth percentile classes (p > 0.14 in both cases; Figure 7c,d).

4 | DISCUSSION

The rate at which taxa flower (estimated as MFD accumulation rate) changes substantially among LCRS with MAT and as the flowering season progresses.

4.1 | Rate of MFD accumulation versus temperature

Among the second and third percentile classes, the MFD accumulation rate increases with MAT. It is therefore likely that flowering synchrony also increases with MAT during the early to mid-portions of the flowering season, unless the flowering durations of these taxa decline sufficiently to reduce or prevent their overlap. Conversely, the MFD accumulation rate among the latest (i.e., sixth) percentile class declines with higher MAT, indicating that the synchrony of MFDs among late-flowering taxa is likely to decrease in warmer environments.

4.2 | Seasonal patterns of MFD accumulation

Collectively, our results indicate that among the earliest-flowering taxa (i.e., the first percentile class), the rate at which sequentially flowering species come into flower is low. This is followed by a short period during which a large proportion of local taxa begin to flower in rapid succession (representing the second and third percentile classes). The rate of MFD accumulation then remains relatively
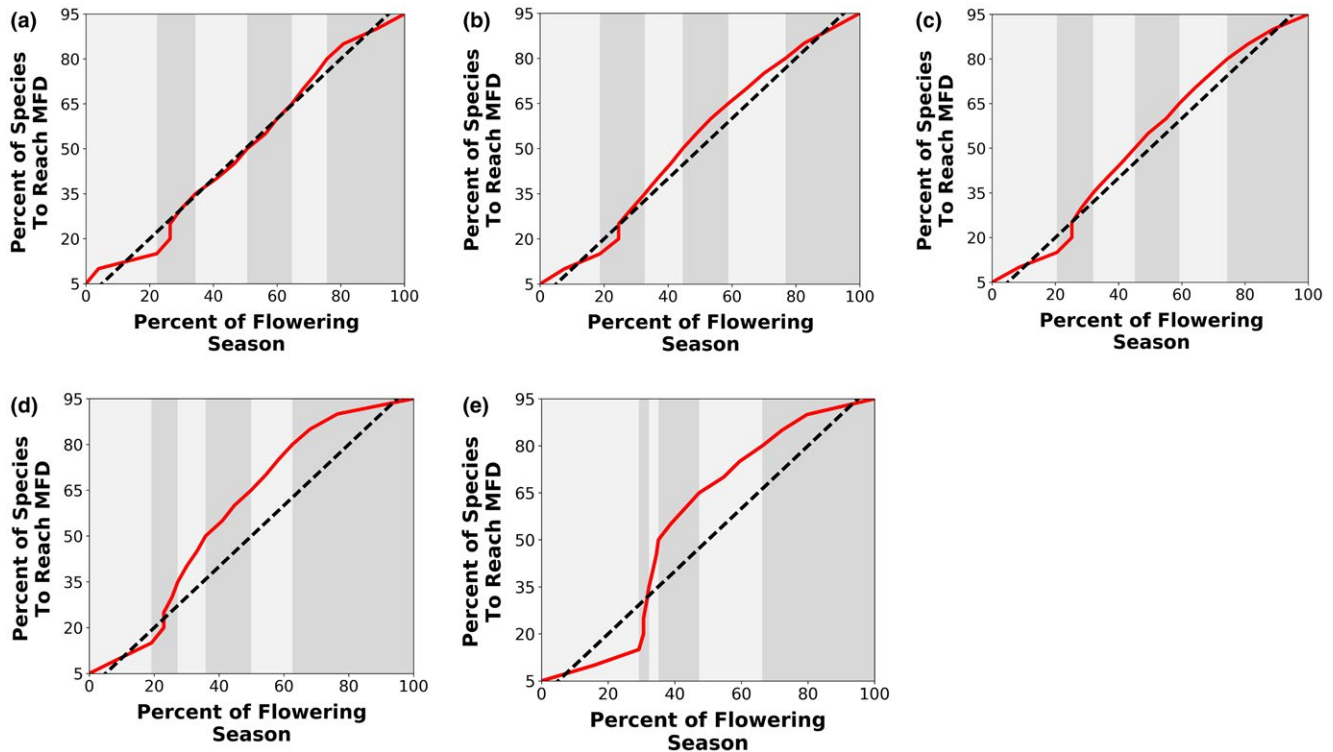
FIGURE 5 Standardized mean flowering date (MFD) accumulation curves. Continuous lines indicate the mean percentage of species observed to have begun flowering as the flowering season progresses among all local climate regions (LCRs) characterized by mean annual temperature: (a) <5°C; (b) from 5 to 9.9°C; (c) from 10 to 14.9°C; (d) from 15 to 19.9°C; and (e) ≥20°C. Dashed lines indicate theoretical constant accumulation rates. In relatively warm regions, the percentage of species that initiate flowering between the 25th and 90th percentage of the flowering season is higher than expected assuming a constant rate of MFD accumulation. Alternating grey bars indicate the proportional duration of each percentile class (as a percentage of the flowering season) within each set of LCRs

steady throughout the fourth and fifth percentile classes and declines in the sixth percentile class. Although this pattern applies to all LCRs regardless of local MAT, the observed deviations from a constant MFD accumulation rate are greater in warmer LCRs.

The magnitude of positive deviations from a constant rate of MFD accumulation also increases sharply with MAT among the second and third percentile classes. Such an increase in the rate of MFD accumulation would inherently be associated with corresponding increases in the number of synchronously flowering species, unless it coincides with systematic decreases in flowering duration among taxa that flower during this period.

4.3 | Disentangling the effects of intraspecific variation versus floristic composition on rates of MFD accumulation

We detected significant relationships between MAT and the MFD accumulation rate that could be attributed solely to intraspecific phenological responses to local climate. However, we also detected significant relationships between MAT and the MFD accumulation rate after eliminating intraspecific phenological variation; these relationships can therefore be attributed to differences in the composition of floras experiencing high or low MAT.

These results support the interpretation that, as with the mean flowering times of regional floras (Park, 2014), two independent mechanisms contribute to the observed relationship between MAT and the MFD accumulation rate: intraspecific changes in phenology in response to differing local temperature (Bradshaw, 1965; Olsson & Ågren, 2002; Vitasse, Delzon, Bresson, Michalet, & Kremer, 2009); and spatial variation in the taxonomic composition of local floras (i.e., species turnover; Craine, Wolkovich, & Towne, 2012; Park, 2014). Furthermore, it appears that although spatial changes in the composition of local floras were sufficient to produce significant relationships between MFD accumulation rates and local MAT throughout both the early and late portions of the flowering season (e.g., the first, second, fifth and sixth percentile classes), intraspecific phenological responses to local MAT affected the synchrony of MFDs only during the early portion of the flowering season (e.g., the first and second cohorts). This finding corroborates a previous study in which intraspecific phenological responses to local climate also exhibited their strongest effect on community-level flowering times during the early portion of the growing season (Park, 2014). Furthermore, the present study represents a significant advance over Park (2014) by demonstrating that intraspecific phenological responses contribute to the rate of MFD accumulation among local floras that differ in MAT and to
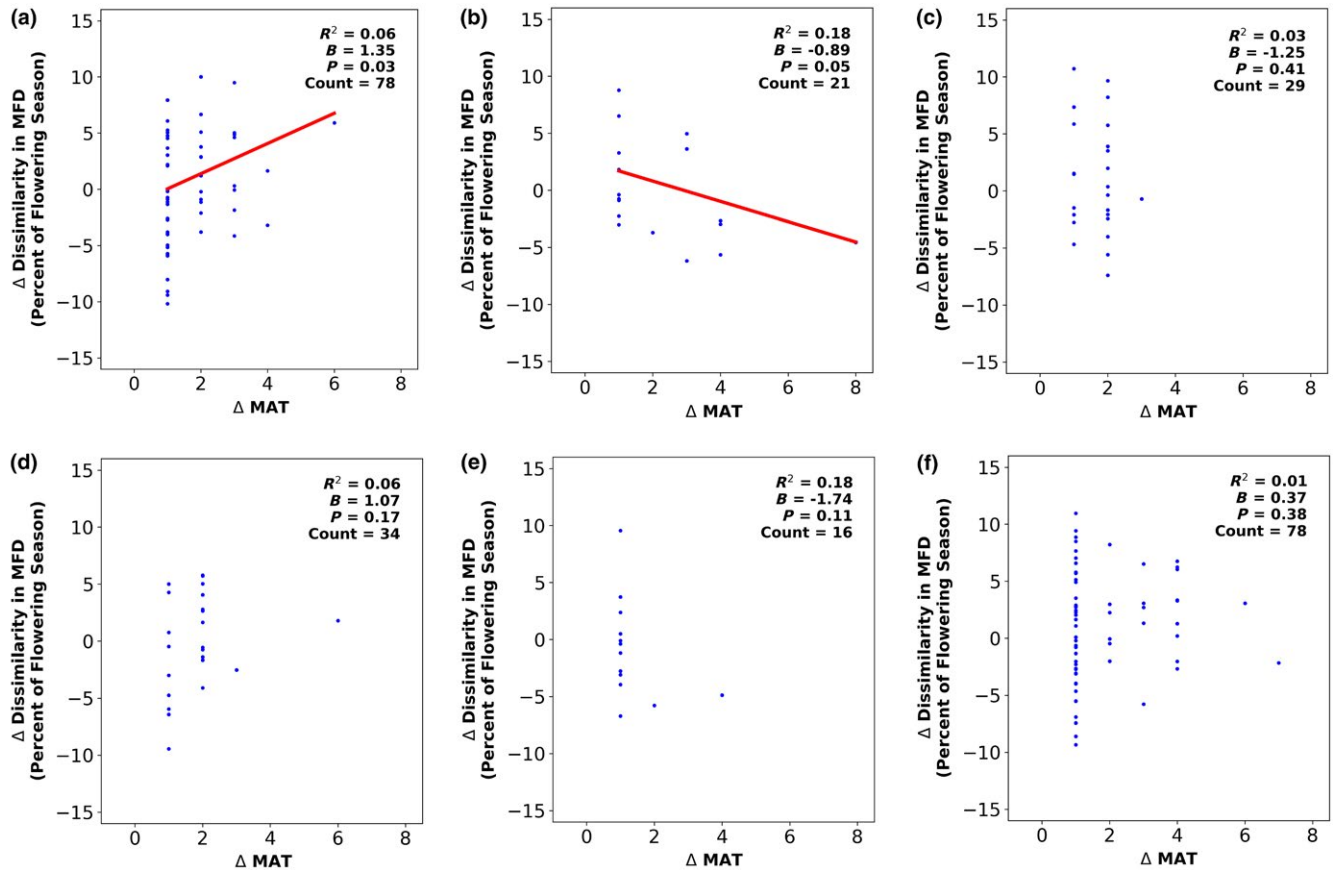
FIGURE 6 Relationship between the difference in pairwise dissimilarities in mean flowering date (MFD) between co-occurring species (ΔDissimilarity) and change in mean annual temperature (ΔMAT) among: (a) the first percentile class, representing the 5th–19.9th percentile; (b) the second percentile class, representing the 20th–34.9th percentile; (c) the third percentile class, representing the 35th–49.9th percentile; (d) the fourth percentile class, representing the 50th–64.9th percentile; (e) the fifth percentile class, representing the 65.9th–79th percentile; and (f) the sixth percentile class, representing the 80th–94.9th percentile of species within each local climate region (LCR). Each point represents the change in the proportional amount of time elapsed between the MFDs of one pair of co-occurring species shared by two LCRs that experience different MAT. *B* indicates the slope of the linear relationship between ΔDissimilarity in MFD and ΔMAT within each percentile class. Within each percentile class, *N* equals the number of estimates of the difference in ΔDissimilarities in MFD

differences in the timing of mean flowering. Unlike the effects of differences in the composition of local floras on the rate of MFD accumulation, however, intraspecific phenological responses to differences in MAT among local floras were found to contribute to shifts in the rate of MFD accumulation during only the early portion of the flowering season. Thus, although both intraspecific phenological shifts and geographical changes in the composition of local floras contribute to geographical variation in the pattern of MFD accumulation throughout the bloom season, they do not contribute equally to the observed relationships between MAT and MFD accumulation throughout the flowering season.

4.4 | Implications for rates of MFD accumulation under future warming

Multiple previous studies have indicated that many spring-flowering species have advanced their flowering times in response to recent warming (Bertin, 2015; Cook et al., 2012; Mazer et al.,

2013; Szabó et al., 2016; Wolkovich et al., 2012). It is also well documented that individual taxa may differ in both the magnitude and the direction of their responses to increasing temperatures (Abu-Asab, Peterson, Shetler, & Orli, 2001; Aldridge et al., 2011; CaraDonna et al., 2014; Du et al., 2017; Gerst, Rossington, & Mazer, 2017; Marchin, Salk, Hoffmann, & Dunn, 2015). The present study demonstrates that these diverse species-specific phenological responses collectively contribute to a systematic shift in the rate of MFD accumulation during the early portion of the flowering season (i.e., the first and second cohorts) among local floras distributed across a spatial temperature gradient. Furthermore, this pattern emerges only early in the flowering season; the observed phenological responses of summer or autumn-flowering species produce no such collective pattern in the rate of MFD accumulation.

In addition, the observed effects of these intraspecific phenological shifts on the synchrony of MFDs in response to MAT can be used to forecast the effects of projected warming on future
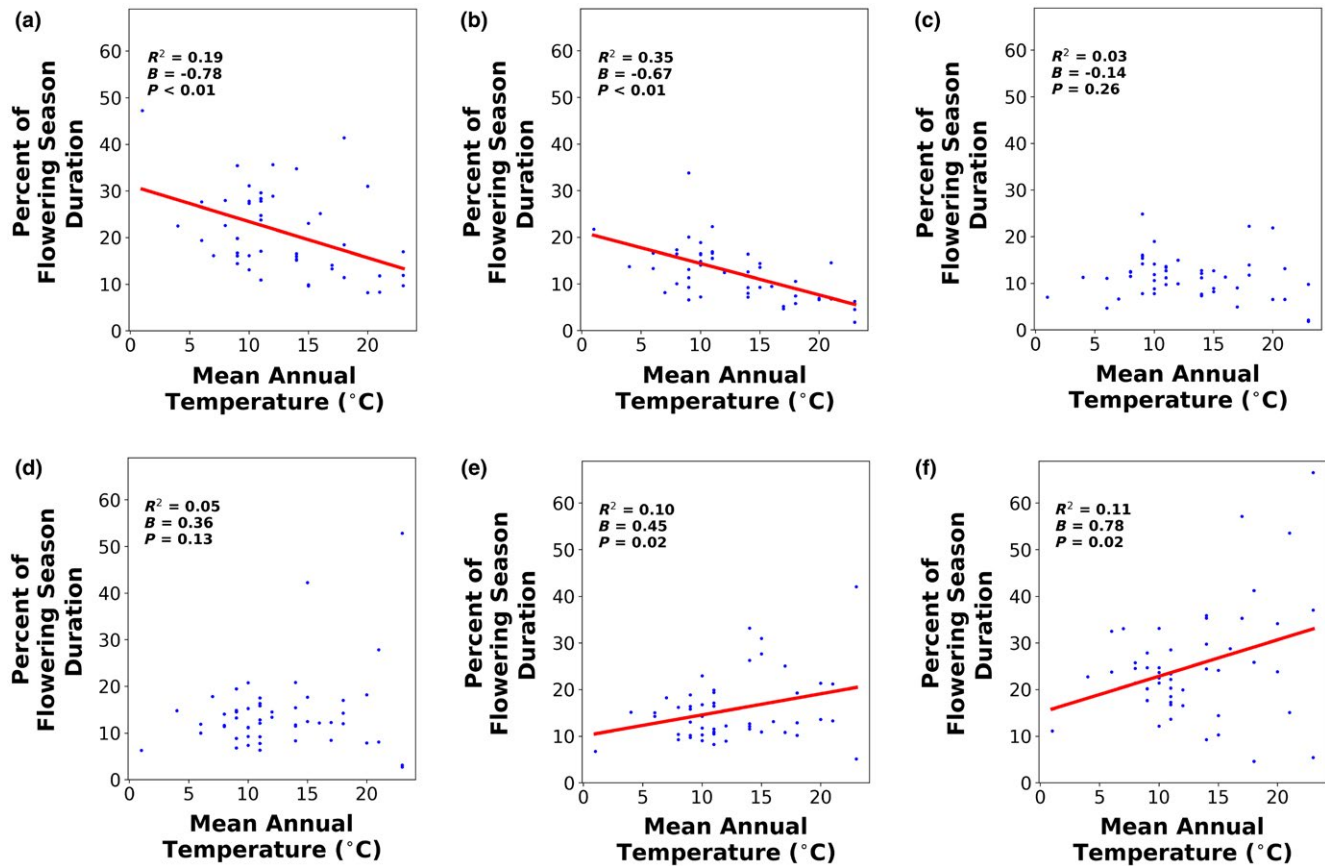
FIGURE 7 Percentage of the flowering season required for each successive 15% of species to begin flowering. The mean flowering dates (MFDs) used for each percentile class are the nationwide mean MFDs for each taxon based on all herbarium specimens, thus eliminating the effects of local temperature on the MFD of each taxon. In this case, any change in the duration of each percentile class across local climate regions (LCRs) in response to increasing temperature is attributable to species composition alone: (a) the first percentile class, representing the fifth–19th percentile; (b) the second percentile class, representing the 20th–34th percentile; (c) the third percentile class, representing the 35th–49th percentile; (d) the fourth percentile class, representing the 50th–64th percentile; (e) the fifth percentile class, representing the 65th–79th percentile; and (f) the sixth percentile class, representing the 80th–94th percentile of species within each LCR. Each point represents one LCR. Lines indicate significant linear trends among LCRs. *B* indicates the slope of the linear relationship between the duration of MFD accumulation and mean annual temperature within each percentile class

rates of floral accumulation. Unlike the taxonomic composition of an LCR, which is unlikely to change rapidly in the face of short-term climate variation, individual plants may change the timing of their flowering in response to inter-annual changes in temperature (Bradley, Leopold, Ross, & Huffaker, 1999; Miller-Rushing, Primack, Primack, & Mukunda, 2006; Walker, Ingersoll, & Webber, 1995). Thus, the magnitude and direction of intraspecific phenological shifts that occur in response to inter-annual variation in MAT, and their corresponding effects on the MFD accumulation rate within a local flora, can be expected to parallel that of intraspecific phenological shifts that accompany spatial temperature gradients.

The results of the present study indicate that many regional floras may experience slower rates of floral accumulation during the earliest portion of the growing season (i.e., the first cohort) in response to warming conditions but more rapid rates of floral accumulation during mid-spring (i.e., the second cohort). Given that intraspecific phenological shifts were not sufficient to generate significant increases or reductions in synchrony among species flowering in the third to sixth cohorts, we also predict that short-term increases in local MAT will produce minimal effects on the synchrony of MFDs among summer- and autumn-flowering taxa. Thus, these results indicate that in the temperate zone, future warming will be likely to produce systematic changes in rates of MFD accumulation during the early portion of the flowering season (represented by the first and second percentile classes). It should be noted, however, that these results primarily represent the western USA. The central and southeastern USA, where sufficient sampling was largely unavailable, might exhibit different trends.

4.5 | Ecological implications

The ecological ramifications of this projected change in the rate of floral accumulation among early-flowering taxa under a warming climate might be substantial. In temperate climates, early to mid-spring

is a period in which many plant communities transition rapidly from a comparatively sparse flowering display to a highly synchronous period, in which large numbers of taxa begin to flower. If future warming produces intraspecific phenological shifts that are analogous to those observed along the spatial temperature gradients observed here, then the resulting phenological shifts are likely to amplify the magnitude of this transition, leading to more extreme periods of floral drought at the onset of the growing season, followed by periods of extreme floral diversity. Taxa that fail to shift their MFD or that alter the timing of their flowering from a period of low synchrony to a period of high synchrony (or vice versa) could experience significant changes in the intensity of competition for pollinators. Likewise, we predict that if conditions warm, then the availability of floral resources will become more uneven, with fewer floral resources available early in the growing season followed by a potential over-abundance of floral resources in mid-spring.

The ecological impacts of such changes on individual species will be complex, however, and will depend not only on the extent to which they share pollinators with co-occurring taxa (with wind-pollinated species probably being largely unaffected), but also on the relative abundances of the plant and pollinator species in question (Ghazoul, 2006; Ye et al., 2014) and the degree to which an increase in the abundance or diversity of co-flowering species increases or decreases pollinator visitation (Feldman et al., 2004).

Although specific predictions of the ecological impacts of climate warming on any particular plant or animal taxon are beyond the scope of this paper, this study does indicate that systematic differences in the sequential structure of the annual bloom display do exist among floras that inhabit regions characterized by differing temperature regimes. Furthermore, our observations of intraspecific responses to higher MAT indicate that future climate warming is likely to disrupt the historical rates of floral accumulation, leading to periods of reduced floral diversity during the earliest portion of the growing season, followed by periods of elevated floral diversity shortly thereafter.

4.6 | Conclusions

The present study reinforces the power of herbarium records for the detection of community-level responses to climatic conditions, distinct from species- and population-level metrics, such as MFD. As a result, herbarium records have the potential to characterize emergent properties of community, ecosystem or regional phenology, to link these properties to spatial variation in climate and to predict responses of these attributes to future climate change. Given that intraspecific phenological variation appears to contribute to the observed changes in synchrony of MFDs along a temperature gradient among the first and second cohorts, it is likely that future climate warming will produce significant changes in the number of synchronously flowering taxa during the first third of the growing season. Although additional research is needed to determine how the synchrony of flowering, which is an emergent property of plant communities and of regional floras, affects

interspecific interactions that influence fruit and seed production, the present study highlights the utility of herbarium records not only to estimate species-level changes in the dates of peak flowering or flowering onset (Davis et al., 2015; Diskin, Proctor, Jebb, Sparks, & Donnelly, 2012; Gallagher, Hughes, & Leishman, 2009), but also to detect collective, community-level responses to climatic conditions and to forecast the potential impacts of future warming on the distribution of floral resources throughout the flowering season.

the University of Arizona herbarium, the Desert Botanical Garden, the Deaver Herbarium, the Navajo Nation Department of Fish and Wildlife, the Grand Canyon National Park herbarium, the University of New Mexico herbarium, the Western New Mexico University herbarium, the Museum of Northern Arizona, the Gil National Forest herbarium, the Arizona Western College herbarium, and the Natural History Institute. All data used in this study were drawn from participants of the Consortium of California Herbaria (ucjeps.berkeley.edu/consortium/), SEINet (http://swbiodiversity.org/seinet/), the SERNEC Data Portal (www.sernecportal.org), the Consortium of Midwest Herbaria (http://midwestherbaria.org/), the Intermountain Regional Herbarium Network, (http://intermountainbiota.org), the North American Network of Small Herbaria (http://nansh.org/), the Northern Great Plains Regional Herbarium Network (http://ngpherbaria.org) and the Consortium of Pacific Northwest Herbaria (http://pnwherbaria.org/), which were accessed on 14 March 2017.

DATA ACCESSIBILITY

Data files and code used to conduct the analyses presented in this study are available online at 10.6084/m9.figshare.5471752

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REFERENCES

Abu-Asab, M. S., Peterson, P. M., Shetler, S. G., & Orli, S. S. (2001). Earlier plant flowering in spring as a response to global warming in the Washington, DC, area. *Biodiversity and Conservation*, 10, 597–612. https://doi.org/10.1023/A:1016667125469

Aldridge, G., Inouye, D. W., Forrest, J. R. K., Barr, W. A., & Miller-Rushing, A. J. (2011). Emergence of a mid-season period of low floral resources in a montane meadow ecosystem associated with climate change. *Journal of Ecology*, 99, 905–913. https://doi.org/10.1111/j.1365-2745.2011.01826.x

Bertin, R. I. (2015). Climate change and flowering phenology in Worcester county, Massachusetts. *International Journal of Plant Sciences*, 176, 107–119. https://doi.org/10.1086/679619

Bock, A., Sparks, T. H., Estrella, N., Jee, N., Casebow, A., Schunk, C., ... Menzel, A. (2014). Changes in first flowering dates and flowering duration of 232 plant species on the island of Guernsey. *Global Change Biology*, 20, 3508–3519. https://doi.org/10.1111/gcb.12579

Borchert, R., Robertson, K., Schwartz, M. D., & Williams-Linera, G. (2005). Phenology of temperate trees in tropical climates. *International Journal of Biometeorology*, 50, 57–65. https://doi.org/10.1007/s00484-005-0261-7

Boyle, B., Hopkins, N., Lu, Z., Raygoza Garay, J. A., Mozzherin, D., Rees, T., ... Enquist, B. J. (2013). The taxonomic name resolution service: An online tool for automated standardization of plant names. *BMC Bioinformatics*, 14(1), 16. https://doi.org/10.1186/1471-2105-14-16

Bradley, N. L., Leopold, A. C., Ross, J., & Huffaker, W. (1999). Phenological changes reflect climate change in Wisconsin. *Proceedings of the National Academy of Sciences USA*, 96, 9701–9704. https://doi.org/10.1073/pnas.96.17.9701

Bradshaw, A. D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, 13, 115–155.

Callinger, K. M., Queenborough, S., & Curtis, P. S. (2013). Herbarium specimens reveal the footprint of climate change on flowering trends across north-central North America. *Ecology Letters*, 16, 1037–1044. https://doi.org/10.1111/ele.12135

CaraDonna, P. J., Iler, A. M., & Inouye, D. W. (2014). Shifts in flowering phenology shape a subalpine plant community. *Proceedings of the National Academy of Sciences USA*, 111, 4916–4921.

Cook, B. I., Wolkovich, E. M., & Parmesan, C. (2012). Divergent responses to spring and winter warming drive community level flowering trends. *Proceedings of the National Academy of Sciences USA*, 109, 9000–9005. https://doi.org/10.1073/pnas.1118364109

Craine, J. M., Wolkovich, E. M., & Towne, G. (2012). The roles of shifting and filtering in generating community-level flowering phenology. *Ecography*, 35, 1033–1038. https://doi.org/10.1111/j.1600-0587.2012.07625.x

Daru, B. H., Park, D. S., Primack, R. B., Willis, C. G., Barrington, D. S., Whitfeld, T. J. S., ... Davis, C. C. (2017). Widespread sampling biases in herbaria revealed from large-scale digitization. *New Phytologist*, 217, 939–955. https://doi.org/10.1111/nph.14855

Davis, C. C., Willis, C. G., Connolly, B., Kelly, C., & Ellison, A. M. (2015). Herbarium records are reliable sources of phenological change driven by climate and provide novel insights into species' phenological cueing mechanisms. *American Journal of Botany*, 102, 1599–1609. https://doi.org/10.3732/ajb.1500237

Diez, J. M., Ibáñez, I., Miller-Rushing, A. J., Mazer, S. J., Crimmins, T. M., Crimmins, M. A., ... Inouye, D. W. (2012). Forecasting phenology: From species variability to community patterns. *Ecology Letters*, 15, 545–553. https://doi.org/10.1111/j.1461-0248.2012.01765.x

Diskin, E., Proctor, H., Jebb, M., Sparks, T., & Donnelly, A. (2012). The phenology of *Rubus fructicosus* in Ireland: Herbarium specimens provide evidence for the response of phenophases to temperature, with implications for climate warming. *International Journal of Biometeorology*, 56, 1103–1111.

Du, Y., Mao, L., Queenborough, S. A., Freckleton, R. P., Chen, B., & Ma, K. (2017). Phylogenetic constraints and trait correlates of flowering phenology in the angiosperm flora of China. *Global Ecology and Biogeography*, 24, 928–938. https://doi.org/10.1111/geb.12303

Feldman, T. S., Morris, W. F., & Wilson, W. G. (2004). When can two plant species facilitate each other's pollination? *Oikos*, 105, 197–207.

Fitter, A. H., Fitter, R. S. R., Harris, I. T. B., & Williamson, M. H. (1995). Relationship between first flowering date and temperature in the flora of a locality in central England. *Functional Ecology*, 9, 55–60.

Gallagher, R. V., Hughes, L., & Leishman, M. R. (2009). Phenological trends among Australian alpine species: Using herbarium records to identify climate-change indicators. *Australian Journal of Botany*, 57, 1–9. https://doi.org/10.1071/BT08051

Gerst, K. L., Rossington, N. L., & Mazer, S. J. (2017). Phenological responsiveness to climate differs among four species of *Quercus* in North America. *Journal of Ecology*, 105, 1610–1622.

Ghazoul, J. (2006). Floral diversity and the facilitation of pollination. *Journal of Ecology*, 94, 295–304. https://doi.org/10.1111/j.1365-2745.2006.01098.x

Heinrich, B. (1976). Flowering phenologies: Bog, woodland, and disturbed habitats. *Ecology*, 57, 890–899. https://doi.org/10.2307/1941055

Homer, C. G., Dewitz, J. A., Yang, L., Jin, S., Danielson, P., Xian, G., ... Megown, K. (2015). Completion of the 2011 national land cover database for the conterminous United States—representing a decade of land cover change information. *Photogrammetric Engineering & Remote Sensing*, 81, 345–354.

Jones, C. A., & Daehler, C. C. (2018). Herbarium specimens can reveal impacts of climate change on plant phenology: A review of methods and applications. *PeerJ*, 6, e4576. https://doi.org/10.7717/peerj.4576

Lacerda, D. M. A., de Araújo Barros, J.-B.-H., de Almeida, E. B., & Rossatto, D. R. (2017). Do conspecific populations exhibit divergent phenological patterns? A study case of widespread savanna species. *Flora*, *236–237*, 100–106. https://doi.org/10.1016/j.flora.2017.10.001

Laverty, T. M. (1992). Plant interactions for pollinator visits: A test of the magnet species effect. *Oecologia*, *89*, 502–508. https://doi.org/10.1007/BF00317156

Lavoie, C., & Lachance, D. (2006). A new herbarium-based method for reconstructing the phenology of plant species across large areas. *American Journal of Botany*, *93*, 512–516. https://doi.org/10.3732/ajb.93.4.512

Marchin, R. M., Salk, C. F., Hoffmann, W. A., & Dunn, R. R. (2015). Temperature alone does not explain phenological variation of diverse temperate plants under experimental warming. *Global Change Biology*, *21*, 3138–3151. https://doi.org/10.1111/gcb.12919

Mazer, S. J., Travers, S. E., Cook, B. I., Davies, T. J., Bolmgren, K., Kraft, N. J. B., … Inouye, D. W. (2013). Flowering date of taxonomic families predicts phenological sensitivity to temperature: Implications for forecasting the effects of climate change on unstudied taxa. *American Journal of Botany*, *100*, 1–17. https://doi.org/10.3732/ajb.1200455

Menzel, A., Estrella, N., & Fabian, P. (2001). Spatial and temporal variability of the phenological seasons in Germany from 1951 to 1996. *Global Change Biology*, *7*, 657–666. https://doi.org/10.1046/j.1365-2486.2001.00430.x

Miller-Rushing, A. J., Primack, R. B., Primack, D., & Mukunda, S. (2006). Photographs and herbarium specimens as tools to document phenological changes in response to global warming. *American Journal of Botany*, *93*, 1667–1674. https://doi.org/10.3732/ajb.93.11.1667

Mitchell, R. J., Flanagan, R. J., Brown, B. J., Waser, N. M., & Karron, J. D. (2009). New frontiers in competition for pollination. *Annals of Botany*, *103*, 1403–1413. https://doi.org/10.1093/aob/mcp062

Olsson, K., & Ågren, J. (2002). Latitudinal population differentiation in phenology, life history, and flower morphology in the perennial herb *Lythrum salicaria*. *Journal of Evolutionary Biology*, *15*, 983–996.

Panchen, Z. A., & Gorelick, R. (2016). Canadian arctic archipelago conspecifics flower earlier in the high arctic than the mid-arctic. *International Journal of Plant Sciences*, *177*, 661–670. https://doi.org/10.1086/687984

Park, I. (2014). Impacts of differing community composition on flowering phenology throughout warm temperate, cool temperate and xeric environments. *Global Ecology and Biogeography*, *23*, 789–801. https://doi.org/10.1111/geb.12163

Park, I. (2016). Timing the bloom season: A novel approach to evaluating reproductive phenology across distinct regional flora. *Landscape Ecology*, *31*, 1567–1579. https://doi.org/10.1007/s10980-016-0339-0

Pau, S., Wolkovich, E. M., Cook, B. I., Davies, T. J., Kraft, N. J. B., Bolmgren, K., … Cleland, E. E. (2011). Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology*, *17*, 3633–3643. https://doi.org/10.1111/j.1365-2486.2011.02515.x

Post, E. S., Pedersen, C., Wilmers, C. C., & Forchhammer, M. C. (2008). Phenological sequences reveal aggregate life history response to climatic warming. *Ecology*, *89*, 363–370. https://doi.org/10.1890/06-2138.1

Prevéy, J., Vellend, M., Rüger, N., Hollister, R. D., Bjorkman, A. D., Myers-Smith, I. H., … Rixen, C. (2017). Greater temperature sensitivity of plant phenology at colder sites: Implications for convergence across northern latitudes. *Global Change Biology*, *23*, 2660–2671. https://doi.org/10.1111/gcb.13619

Primack, D., Imbres, C., Primack, R. B., Miller-Rushing, A. J., & Del Tredici, P. (2004). Herbarium specimens demonstrate earlier flowering times in response to warming in Boston. *American Journal of Botany*, *91*, 1260–1264. https://doi.org/10.3732/ajb.91.8.1260

Rathcke, B. (1988a). Flowering phenologies in a shrub community: Competition and constraints. *Journal of Ecology*, *76*, 975–994.

Rathcke, B. (1988b). Interactions for pollination among coflowering shrubs. *Ecology*, *69*, 446–457.

Reader, R. J. (1975). Competitive relationships of some bog ericads for major insect pollinators. *Canadian Journal of Botany*, *53*, 1300–1305. https://doi.org/10.1139/b75-156

Robbirt, K. M., Davy, A. J., Hutchings, M. J., & Roberts, D. L. (2011). Validation of biological collections as a source of phenological data for use in climate change studies: A case study with the orchid *Ophrys sphegodes*. *Journal of Ecology*, *99*, 235–241. https://doi.org/10.1111/j.1365-2745.2010.01727.x

Staggemeier, V. G., Diniz-Filho, J. A. F., & Morellato, L. P. C. (2010). The shared influence of phylogeny and ecology on the reproductive patterns of *Myrteae* (Myrtaceae). *Journal of Ecology*, *98*, 1409–1421. https://doi.org/10.1111/j.1365-2745.2010.01717.x

Stiles, F. G. (1975). Ecology, flowering phenology, and hummingbird pollination of some Costa Rican *Heliconia* species. *Ecology*, *56*, 285–301. https://doi.org/10.2307/1934961

Stone, G. N., Willmer, P., & Rowe, J. A. (1998). Partitioning of pollinators during flowering in an African acacia community. *Ecology*, *79*, 2808–2827. https://doi.org/10.2307/176518

Szabó, B., Vincze, E., & Czúcz, B. (2016). Flowering phenological changes in relation to climate change in Hungary. *International Journal of Biometeorology*, *60*, 1347–1356. https://doi.org/10.1007/s00484-015-1128-1

Tachiki, Y., Iwasa, Y., & Satake, A. (2010). Pollinator coupling can induce synchronized flowering in different plant species. *Journal of Theoretical Biology*, *267*, 153–163. https://doi.org/10.1016/j.jtbi.2010.08.023

Vitasse, Y., Delzon, S., Bresson, C. C., Michalet, R., & Kremer, A. (2009). Altitudinal differences in growth and phenology among populations of temperate-zone tree species growing in a common garden. *Canadian Journal of Forest Research*, *39*, 1259–1269.

Walker, M. D., Ingersoll, R. C., & Webber, P. J. (1995). Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology*, *76*, 1067–1083. https://doi.org/10.2307/1940916

Wang, C., Tang, Y., & Chen, J. (2016). Plant phenological synchrony increases under rapid within-spring warming. *Scientific Reports*, *6*, 25460. https://doi.org/10.1038/srep25460

Waser, N. M. (1978). Competition for hummingbird pollination and sequential flowering in two Colorado wildflowers. *Ecology*, *59*, 934–944. https://doi.org/10.2307/1938545

Whalen, M. D. (1978). Reproductive character displacement and floral diversity in *Solanum* section *Androceras*. *Systematic Botany*, *3*, 77–86. https://doi.org/10.2307/2418533

Willis, C. G., Ellwood, E. R., Primack, R. B., Davis, C. C., Pearson, K. D., Gallinat, A. S., … Soltis, P. S. (2017). Old plants, new tricks: Phenological research using herbarium specimens. *Trends in Ecology and Evolution*, *32*, 531–546. https://doi.org/10.1016/j.tree.2017.03.015

Wolkovich, E. M., Cook, B. I., Allen, J. M., Crimmins, T. M., Betancourt, J. l., Travers, S. E., … Cleland, E. E. (2012). Warming experiments underpredict plant phenological responses to climate change. *Nature*, *2*, 494–497. https://doi.org/10.1038/nature11014

Ye, Z.-M., Dai, W.-K., Jin, X.-F., Gituru, R. W., Wang, Q.-F., & Yang, C.-F. (2014). Competition and facilitation among plants for pollination: Can pollinator abundance shift the plant–plant interactions? *Plant Ecology*, *215*, 3–13.

Yost, J. M., Sweeney, P. W., Gilbert, E., Nelson, G., Guralnick, R., Gallinat, A. S., … Mazer, S. J. (2018). Digitization protocol for scoring reproductive phenology from herbarium specimens of seed plants. *Applications in Plant Sciences*, *6*, e1022. https://doi.org/10.1002/aps3.1022

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.