

Phenological displacement is uncommon among sympatric angiosperms

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Summary

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- Interactions between species can influence successful reproduction, resulting in reproductive character displacement, where the similarity of reproductive traits – such as flowering time – among close relatives growing together differ from when growing apart. Evidence for the overall prevalence and direction of this phenomenon, and its stability under environmental change, remains untested across large scales.
- Using the power of crowdsourcing, we gathered phenological information from over 40 000 herbarium specimens, and investigated displacement in flowering time across 110 animal-pollinated species in the eastern USA.
- Overall, flowering time displacement is not common across large scales. However, displacement is generally greater among species pairs that flower close in time, regardless of direction. Furthermore, with climate change, the flowering times of closely related species are predicted, on average, to shift further apart by the mid-21st century.
- We demonstrate that the degree and direction of phenological displacement among co-occurring closely related species pairs varies tremendously. However, future climate change may alter the differences in reproductive timing among many of these species pairs, which may have significant consequences for species interactions and gene flow. Our study provides one promising path towards understanding how the phenological landscape is structured and may respond to future environmental change.

Introduction

Interactions between species can affect access to resources and successful reproduction. The outcome of such interactions may result in character displacement, in which the phenotypic similarity of species differs depending on whether they are co-occurring (sympatric) or not (Brown & Wilson, 1956; Grant, 1972; Connell, 1980). Numerous instances of character displacement have been identified across the tree of life (Dayan & Simberloff, 2005; Pfennig & Pfennig, 2009). However, evidence for the overall prevalence and direction of this phenomenon or the stability of such differences under future environmental change is lacking (Levin, 2006; Hopkins, 2013).

Reproductive character displacement – the modification of reproductive traits in sympatric populations of closely related or similar species – is widely considered to be a key mechanism facilitating co-occurrence, reproductive isolation, and ecological and evolutionary divergence (Mayr, 1947; Coyne & Orr, 2004; Grant & Grant, 2011). This is especially true for the timing (phenology) of flowering, which is strongly linked to fitness and often highly variable even among closely related taxa (Galloway,

2002; Stinson, 2004; Briscoe Runquist *et al.*, 2014; Park *et al.*, 2018; Spriggs *et al.*, 2019). Plants often flower and share pollinators with other species across their range, and this community context has been demonstrated to greatly influence reproductive phenology (Stiles, 1975, 1977; Moeller, 2004).

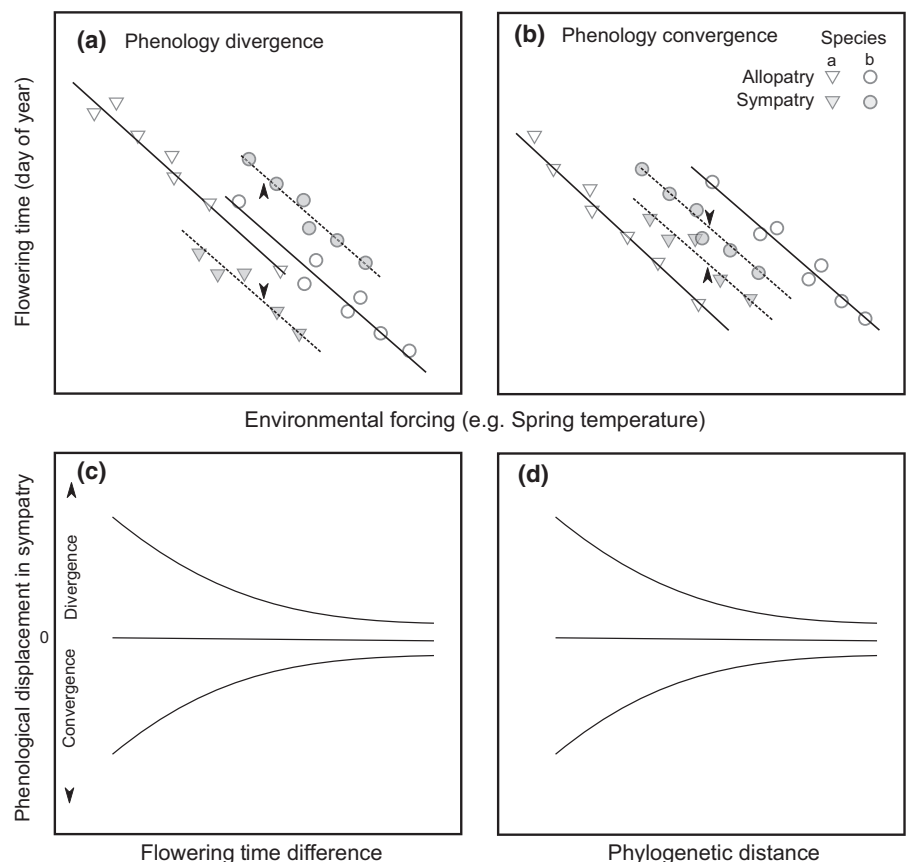
Flowering phenology is a heritable trait on which selection can act rapidly (Allard & Hansche, 1964; Izawa, 2007). Despite its relevance, empirical evidence for phenological character displacement in plants remains limited to a small number of case studies (e.g. Lowry *et al.*, 2008; Briscoe Runquist *et al.*, 2014; Spriggs *et al.*, 2019). This greatly limits our ability to understand the general relevance of phenological displacement governing plant interactions and distributions. Moreover, flowering phenology is highly responsive to climate (Franks *et al.*, 2007; Sherry *et al.*, 2007; Davis *et al.*, 2015), and it remains an open question as to whether current phenological similarities or differences among co-occurring species are likely to remain constant in the face of future climate change.

Phenological character displacement is commonly inferred to imply phenological divergence in sympatry, but it can also manifest as phenological convergence; the nature of interspecific

interactions will determine which applies (Grant, 1972). For example, two species may diverge in flowering time when they co-occur (Fig. 1a), thus reducing competition (Campbell, 1985; Stone *et al.*, 1998; Elzinga *et al.*, 2007). Such asynchronous flowering also can reproductively isolate species and reduce the costs of heterospecific pollen transfer and hybridization (Campbell, 1985; Borchsenius, 2002; Bell *et al.*, 2005; Morales & Traveset, 2008). Alternatively, flowering times of co-occurring species may converge as a result of facilitative interactions or environmental constraints (Fig. 1b). In this case, the presence of other plant species may increase reproductive success via increased pollinator visitation to collectively larger or more diverse floral displays (Johnson *et al.*, 2003; Moeller, 2004; Ghazoul, 2006; Gurung *et al.*, 2018). Synchronous flowering may also decrease the chance of predation on a given species' flowers and seeds by more broadly spreading the risk across the community (Rathcke, 1983; Rathcke & Lacey, 1985). Moreover, phenological character displacement, whether convergent or divergent, is hypothesized to be more likely among closely related species, as more recent ancestry and shared floral morphology make it increasingly likely for taxa to share and experience similar selective pressures from pollinators and predators or experience hybridization and gene flow (Darwin, 1859; Brown & Wilson, 1956; Levin & Anderson, 1970; Pleasants, 1980; Primack, 1985). Finally, we may expect that phenological displacement is more common among species that tend to flower close in time as their interactions in sympatry are likely to be stronger.

Evidence for the general prevalence and direction of flowering time displacement, and its stability under environmental change, remains untested across larger spatial and taxonomic scales. Ideally, flowering time gaps and overlap would be quantified at fine spatiotemporal resolutions, taking into account changes in the number of flowers and individuals that co-occur across the entire reproductive period (Husband & Schemske, 2000; Beans, 2014). However, such high-resolution observational data are lacking for most species and are difficult to generate across wide spatial scales. Along these lines, herbarium specimens comprise phenological information across wide spatiotemporal and taxonomic breadth. Although we cannot always use specimen data to infer exact co-occurrences in space and time, or quantify the number of flowers in bloom, they allow us to assess species' sympatric and allopatric ranges; to model flowering time responses to environmental conditions; and thus to estimate differences in flowering time gaps/overlap across species sympatric and allopatric ranges. Herbarium specimens may not fully represent the flowering season, as they tend to be collected during flowering peaks (Davis *et al.*, 2015). Nonetheless, the timing of flowering peaks have been demonstrated to have significant effects on reproductive interactions even when flowering times overlap among taxa (Husband & Schemske, 2000; Nuismer & Cunningham, 2005), and herbarium specimens should allow us to test for broad patterns of phenological convergence or divergence in peak flowering times.

Fig. 1 Conceptual framework for assessing phenological displacement (convergence or divergence). Interactions between closely related species can cause phenological traits, here flowering time, to differ between related species growing in sympatry vs those growing in allopatry. For example, if interactions between closely related, co-flowering species are shaped by competition for pollinators or reproductive interference, they may undergo reproductive character divergence in flowering time, causing flowering times to diverge in sympatry (dotted lines) relative to expectations derived from climate–phenology relationships in allopatry (solid lines) (a). Alternatively, if interactions are characterized by facilitation or hybridization between species pairs, then flowering times may converge and be closer in sympatry than in allopatry (b). Panels (c) and (d) show expected patterns across closely related species-pairs under the null hypothesis of no displacement (H_0), character divergence (H_1) or character convergence (H_2). Both H_1 and H_2 predict larger deviations for sympatric species pairs that flower at similar times (c) and species pairs that diverged more recently (d).



Here, we examine flowering (a)synchrony and evaluate evidence for phenological character displacement across 110 species in 28 genera across 21 diverse families representing major branches of the angiosperm tree of life. We focus primarily on animal-pollinated species, which have been suggested to have more diverse flowering phenologies than wind- or water-pollinated plants because they may compete for pollinators (Bolmgren *et al.*, 2003). We gathered phenological data by crowdsourcing > 42 000 digitized herbarium specimens collected over 120 yr and 20° of latitude in the eastern United States. Using these data, we test the hypothesis that the flowering times of species in sympatry will differ from expectations derived from underlying climate–phenology relationships, and that these deviations will be greater among species that flower at similar times and are closely related. We further used these data to examine how flowering phenology has changed over time and to predict how flowering (a)synchrony among closely related taxa may shift with future climatic change.

Materials and Methods

Selection of species and data collection

We used digitized specimens from two of the most comprehensive digitized regional floras in the world, the Consortium of Northeastern Herbaria (CNH; <http://portal.neherbaria.org/portal/>) and Southeast Regional Network of Expertise and Collections (SERNEC; <http://sernecportal.org/portal/index.php>). We selected animal-pollinated species from across the eastern United States that satisfied the following criteria: included collection dates and at least county-level locality data; comprised at least 50 unique collections across space and time; had reproductive structures (i.e. buds, flowers and fruit) that were easily identifiable and quantifiable by crowdworkers; and had at least one other congeneric species with a partially overlapping geographic range in our study area. Our final dataset comprised 110 species in 28 genera across 21 angiosperm families (Supporting Information Table S1). As our specimen data alone gave an incomplete picture of species county-level distributions, we determined co-occurrence among congener groups based on combining county-level distributions from our specimen data with county checklist data from the United States Department of Agriculture PLANTS Database (<https://plants.usda.gov/>).

We used estimates of historic (1895–2017) average monthly air temperature and precipitation data at 2.5 arcminute resolution from PRISM (product AN81m; <http://prism.oregonstate.edu/>). Accurate locality data were not available for the majority of historic specimen records, so we used county as our geographical unit of analysis (Park & Davis, 2017). For each county and year, we estimated the mean monthly temperature, precipitation and elevation, and assigned these values to each specimen. Although counties can vary in size and climate, counties in states along the east coast of the United States are generally small in size and geographically homogeneous, and within-county variation in climate does not significantly affect estimations of phenological response in this area (Park *et al.*, 2018).

Phenological data extraction

Civilian-scientists hired through Amazon's Mechanical Turk service (MTURK; <https://www.mturk.com/>) counted the number of buds, flowers, and fruits using crowdsourcing science platform CROWDCURIO (Willis *et al.*, 2017) to assess peak flowering time. Each specimen was independently examined by three people on average (see Park *et al.*, 2018 for detailed crowdsourcing methods). Phenological information was thus gathered from a total of 42 777 digitized herbarium specimens. The expansive spatial, temporal and phylogenetic sampling offered by herbarium collections has become increasingly accessible with widespread digitization (Hedrick *et al.*, 2020), and crowdsourcing has been demonstrated to be an effective, reliable method for assessing phenological traits from natural history collections (Willis *et al.*, 2017). The flowering patterns derived from specimens have been shown to reflect those assessed from field surveys (Borchert *et al.*, 2004; Davis *et al.*, 2015). Further, specimens allow us to assess phenological community patterns at macroecological scales essential to obtain a generalizable understanding of the phenological responses of species and communities (Doi *et al.*, 2017). From the multiple CROWDCURIO-derived observations for each specimen, we first computed the median number of buds, flowers and fruits. For phenological analysis, we used specimens that met the following criteria: (1) contained at least one open flower, (2) contained more flowers than the combined number of buds and fruits, (3) contained a number of flowers representing at least 5% of the maximum (95th quantile) number of flowers observed on a given species, and (4) had collection dates $\geq$ the 5th quantile and $\leq$ the 95th quantile of flowering dates. These filters ensured that the specimens used for analysis were in full flower and excluded outlier specimens collected outside of the main flowering period of each species. Of the 42 777 specimens that were originally phenotyped, we used 19 524 across 110 species in our hierarchical model of flowering time. Although our filtering strategy was quite aggressive, we verified that including less aggressive filters (i.e. removing filters 2–4) did not qualitatively alter our results.

Statistical modeling

Bayesian hierarchical models can help to overcome common biases inherent in herbarium data (Park *et al.*, 2018). For example, specimen data are spatiotemporally sparse, phenological traits are highly plastic, and estimates of displacement among species pairs within a given clade are not independent of one another (Theobald *et al.*, 2017; Daru *et al.*, 2018; Park *et al.*, 2021). Relatively few specimens in our dataset were collected at the same locality and in the same year as their congeners. Flowering time for many of our focal species is highly sensitive to environmental forcing (warmer spring temperatures generally inducing earlier flowering) and flowering times sometimes differed across species' ranges because of climatic differences unrelated to interspecific interactions.

Model overview Our Bayesian model first involved applying a single hierarchical linear model to the filtered specimen dataset to

predict the mean flowering date of each species from climate and co-occurring congeners. We then used posterior samples from this model to generate predictions of flowering time with and without terms representing the influence of congeneric species on flowering time. These predictions allowed us to estimate differences in mean flowering time in sympatry for each species pair that was associated with the presence or absence of particular congeners and separate them from differences in flowering time resulting from underlying species-specific relationships between phenology and climate. Generating estimates from each posterior sample of the model allowed us to propagate uncertainty in estimates of species-specific climate and congener effects to our pairwise estimates of phenological divergence and overall estimates across all species pairs and relationships between divergence, mean flowering time and phylogenetic distance.

Statistical model of flowering time

To estimate species-specific flowering times, and the effects of climate and congeners on the phenology of each focal species, we fitted a hierarchical Bayesian linear regression model. The model treated the day of year (DOY) recorded on each flowering specimen as a normally distributed random variable with mean μ_{DOY} and standard deviation σ_{DOY} . Mean flowering date was related to spring (March–May) total precipitation (P) and average air temperature (T) in the county (c) and year (y) that the specimen was collected using a linear function with species-specific intercepts (β_{0j}) and slopes (β_{1j} , β_{2j}). The model also includes separate categorical intercept terms for each county (β_{3c}), genus (β_{4g}) and the group of congeners present (β_{5u}):

$$\mu_{\text{DOY}} = \beta_{0j} + \beta_{1j}T_{cy} + \beta_{2j}P_{cy} + \beta_{3c} + \beta_{4g} + \beta_{5u}$$

All beta parameters were drawn from normal distributions with hyperparameters:

$$\beta_{0j} \sim N(0, \sigma_{\beta_0})$$

$$\beta_{1j} \sim N(1, \sigma_{\beta_1})$$

$$\beta_{2j} \sim N(1, \sigma_{\beta_2}) \quad \beta_{3c} \sim N(0, \sigma_{\beta_3})$$

$$\beta_{4g} \sim N(0, \sigma_{\beta_4})$$

$$\beta_{5u} \sim N(0, \sigma_{\beta_5})$$

To set the priors for the standard deviations σ_{β_0} through σ_{β_5} in the statistical model of flowering time, we used the default covariance matrix (`decov()`) in the `stan_lmer()` function. This default covariance matrix has diagonal entries equal to the values for $\sigma^2_{\beta_j}$. The vector of variances can be represented as the product of the scalar trace $J\tau^2\pi$, where J is the dimension of the covariance matrix, τ^2 is a scale parameter, and π is a simplex vector summing to 1 whose elements π_j are the proportion of the total variance attributable to each variance $\sigma^2_{\beta_j}$. The default prior for π is a symmetric Dirichlet prior with concentration parameter $\gamma = 1$, and

the default prior for is a gamma distribution with shape and scale parameters equal to 1 ($\Gamma(1,1)$). The result is an essentially uniform (flat) prior on each of the standard deviations σ_{β_0} through σ_{β_5} .

Air temperature estimates were derived from the PRISM 2.5 arc-minute gridded data as listed earlier. Terms for genus (g) were included to account for the potential nonindependence of phenology within genera. Congener group (u) was a categorical variable with unique values indexing different combinations of congeneric species that occur in different parts of a species range. For example, if species A co-occurred with only congener B in county 1 and county 2 but congeners B and C in county 3, then the indices for u would be 1, 1 and 2, respectively. The estimates of the associated parameters β_4 and β_5 should capture the combined influence of co-occurring congeneric species on flowering time.

We fitted our model using Hamiltonian Monte Carlo sampling techniques implemented using the RSTANARM package v.2.19.3 (Goodrich *et al.*, 2020) in R v.3.6.3. The model was fitted using four sampling chains of 8000 iterations each, with the last 1000 iterations retained. We verified model convergence and desirable sampler behavior by visually assessing the model fit using functions implemented in the BAYESPLOT package v.1.7.1 (Gabry & Mahr, 2019), as well as the Gelman–Rubin statistic (Gelman & Rubin, 1992). The effective sample size for all parameters was > 1000 . To assess model fit and ensure that samples from the posterior predictive distribution of the model closely resembled the real data, we used the built-in predictive checks in RSTANARM.

Estimating flowering displacement in sympatry We processed posterior samples from our model to generate estimates of differences in mean flowering time in sympatry across all congeneric species pairs where we had observations of co-occurrence (sympatry) and nonco-occurrence (allopatry) across at least three different counties each (106 species across 26 genera in 20 families). For each sympatric congener pair, we used the complete fit model described earlier to generate estimates of flowering time for each focal species and each congener in each county and year where we had specimens of the focal species and we had either specimens or checklist records of the presence of its congener (in any year). These estimates of flowering time in sympatry (co-occurrence estimates) incorporate model terms representing species-specific flowering times (β_{0j} , β_{4g}), climate-phenology relationships (β_{1j} , β_{2j}), and, critically, the effects of co-occurring congeners (β_{5u}). We then subtracted the predicted flowering times for focal species from flowering time estimates of their congener pair and took the absolute value to generate an estimate of the difference in flowering time for each congener pair in each sympatric county in each year where we had specimens of the focal species. Finally, to represent a typical difference in flowering time in sympatry, we computed the median difference in flowering time across all sympatric counties for each congener pair. To estimate uncertainty in flowering times in our co-flowering estimates, we generated 4000 estimates of each pairwise median, one from each posterior sample of our model.

To isolate the influence of sympatry itself on differences in flowering time, we also generated flowering time estimates for

congener pairs that exclude terms representing the influence of co-occurrence estimates (null expectation). To accomplish this, we used an approach identical to the one we describe above (to generate the co-occurrence estimates) with one key difference: predictions did not include the model's co-occurrence terms (β_{5u}) for either species. Subtracting differences in flowering time of the co-occurrence estimate from the null estimate allows us to measure how much co-occurrence with congeners might affect differences in flowering time, which we define as phenological displacement in sympatry. This was done for each iteration of our Bayesian model, which properly propagated uncertainty from the original data to our final estimates of phenological displacement, both for overall estimates across all species pairs at the genus level and individual pairwise comparisons.

Testing predictions of phenological character displacement

Our two alternative hypotheses, that reproductive interference and pollinator competition drive phenological character displacement (Fig. 1) or that facilitative interactions or environmental constraints drive phenological convergence (Fig. 1) make several testable predictions regarding patterns of co-flowering among species pairs. Both hypotheses lead to the prediction that gaps in flowering time of species pairs in sympatry will differ from expectations derived from underlying climate–phenology relationships (i.e. divergences in sympatry credibly different from zero), and these deviations will be larger for species pairs that flower at similar times and species pairs that are closely related. We tested these predictions by comparing our estimates of phenological displacement in sympatry with differences in mean flowering time and phylogenetic distances. Phylogenetic distances were calculated from a set of published time-calibrated phylogenies of the North American flora based on 12 commonly used molecular loci (Park *et al.*, 2020). Of the 110 species examined, 85 were represented on the phylogeny, and we were able to calculate phylogenetic distance between 48 of the 65 co-occurring congener pairs. Differences in mean flowering time for each species pair were taken from the null estimates described earlier. For each of 1000 posterior samples of our model, we recorded how many showed a negative slope in the linear relationship between (log-transformed) flowering time differences and estimates of phenological displacement in sympatry across all species pairs. Although we did not have posterior samples for phylogenetic distances, we used 100 dated bootstrap replicates in a similar fashion, comparing them with posterior samples of phenological displacement and recording how many posterior samples out of 1000 showed the expected negative relationship between phenological displacement and phylogenetic distance.

To examine how gaps in peak flowering time will shift with climatic change in the near future, we compared the expected timing of peak flowering under climatic conditions of the late 20th century with those expected in the mid-21st century. Predictions for 1985 used mean environmental conditions (1970–1999 spring temperature and precipitation) as estimated from PRISM. Mid-21st century (2055) predictions used county-level temperature and precipitation change estimates (2040–2069) from a set of 18 Coupled Model Inter-comparison Project 5 (CMIP5) global circulation

models downscaled and summarized to the county level using the Multivariate Adaptive Constructed Analogs (MACA) algorithm (Elias *et al.*, 2018). Although these predictions are for a high-emissions scenario (RCP 8.5), predictions for different emissions scenarios do not diverge substantially until the late 21st century.

Results

Phenological trends in eastern United States

Our analysis of herbarium specimens collected in the eastern United States showed substantial variability in mean flowering times and phenological responses to climate, both within and between genera, for our 110 focal species (Fig. 2). Mean flowering dates in average climatic conditions of the late 20th to early 21st century (1977–2017) varied between 86 and 263 in terms of DOY, with a standard deviation of 20 d across species. Using a hierarchical Bayesian linear model (see the Materials and Methods section) we estimated that the mean flowering date of most species (106/110) were responsive to spring (March–May) average air temperatures with > 90% posterior probability: species flowered an average of 2.5 ± 1.61 (SD) days earlier for every degree of temperature increase. Some species (16 of 110) were also sensitive to spring precipitation, but the average response across all species did not differ from zero (1.7 ± 4.00 d per 100 mm of spring precipitation). We found some evidence of phylogenetic signal in peak flowering time (Pagel's $\lambda = 0.80$, $P < 0.001$) and its sensitivity to spring temperature (Pagel's $\lambda = 0.54$, $P < 0.05$), but not precipitation (Pagel's $\lambda = 0$, $P = 1$; Fig. S1). After accounting for temperature and precipitation, a subset of species (18/110) also showed credible residual trends over time (i.e. after accounting for shifts in spring temperature or precipitation), flowering on average 0.23 d earlier per decade across all species. Adding additional climatic variables such as summer temperature or vapor pressure deficit failed to improve the overall performance of the model.

Assessing flowering time displacement among close relatives

Predictions from our hierarchical model additionally allowed us to examine differences in mean flowering dates and to assess flowering time convergence or divergence between 74 congener pairs growing in sympatry. On average, species pairs in 24 of 26 genera were not phenologically divergent or convergent relative to null expectations derived from overall climate–phenology relationships (Fig. 3). This was also true overall, with the observed median difference in flowering time across all congener pairs (25 d) virtually identical to the null expectation (24.2 d; Fig. 3, inset). In general, there was no credible phylogenetic signal in patterns of median phenological convergence or divergence between genera, suggesting that patterns of displacement in flowering phenology were not obviously subject to strong evolutionary constraints (Table S2).

Most individual co-occurring species pairs did not show large degrees of phenological displacement (Fig. 4). However, we

identified highly credible log-linear relationships between the difference in peak flowering time of species pairs and the degree of estimated phenological displacement in sympatry. Species pairs that tended to flower closer in time displayed greater degrees of displacement in their sympatric ranges relative to the expected gap in their flowering times. On average, peak flowering times for species pairs that exhibited phenological convergence were estimated to shift closer by 4.7 ± 0.07 d ($22.5 \pm 0.67\%$); pairs that exhibited phenological divergence were estimated to shift 6.1 ± 0.06 d ($24.7 \pm 0.68\%$) apart.

As character displacement may be expected to be strongest between more closely related (and thus possibly more ecologically similar) species, we also compared patterns of phenological displacement with phylogenetic distances in a subset of pairs for which we had phylogenetic information. We did not find a credible relationship between pairwise phylogenetic distance and phenological displacement, or for gaps in peak flowering time (Fig. S2).

Future projections of flowering phenology among close relatives

To examine how these temporal patterns could change in the near future, we compared the expected timing of peak flowering under climatic conditions of the late 20th century to those expected in the mid-21st century. The flowering season, as defined by the number of days between when 10% and 90% of species pass their peak flower date, was predicted to increase with climatic change by the mid-21st century (Fig. 5a,b). This coincided with an overall expected increase in the temporal gap between peak flowering dates of congeneric species currently growing in sympatry (Fig. 5c,d). Larger changes in temporal gaps were predicted in areas expected to experience larger degrees of climate change. For instance, congeneric species in New England and the Atlantic Coastal Plain were projected to flower 2–4 d further apart, on average. In particular, several sympatric species pairs that exhibited convergence in peak flowering time were predicted to experience increased temporal separation in the face of future climate change (Fig. 6).

Discussion

Patterns of flowering time across the landscape result from the dynamic ecological and evolutionary interplay between the phenology of individual taxa and the biotic and abiotic milieu in which they persist (Ackerly, 2003). It has been hypothesized that phenological patterns contributing to the synchronization of reproductive activity with the availability of (a)biotic resources are adaptive (Brody, 1997; Bolmgren *et al.*, 2003; Elzinga *et al.*, 2007) and may be phylogenetically conserved (Kochmer & Handel, 1986). Along these lines, the peak flowering phenology of nearly all the species we examined were sensitive to spring temperatures and we found evidence of phylogenetic signal in both flowering time and its sensitivity to temperature. However, patterns of phenological displacement among closely related, co-occurring species were complex.

Flowering time displacement in sympatry is not common

On the one hand, sympatric plant species that share pollinators and flower concurrently may reduce each other's fitness if reproductive success is limited by pollination (Robertson, 1895; Levin & Anderson, 1970). Further, overlapping flowering times between closely related species can result in wasted mating effort or hybrids of reduced fitness (Coyne & Orr, 2004). Either of these processes should select for the evolution of staggered, minimally overlapping flowering schedules, especially between closely related taxa. Indeed, divergence in flowering time among sympatric plants has been documented in several studies (e.g. Stiles, 1977; Stinson, 2004; Levin, 2006; Spriggs *et al.*, 2019). On the other hand, phenological convergence can occur if the presence of one species facilitates the reproductive success of another species, or if (a)biotic resources are more temporally constrained in sympatry (Rathcke, 1983; Ghazoul, 2006).

In contrast to either of these expectations, estimated differences in flowering time varied little for most of the co-occurring congeneric species pairs we examined, regardless of whether they were broadly in sympatry or allopatry (Figs 3, 4). Other taxon-specific studies have also demonstrated a lack of flowering time displacement (usually divergence) at smaller spatial scales (Murray *et al.*, 1987; Boulter *et al.*, 2006). This lack of observed displacement could be the result of at least five factors. First, many congeneric species pairs we examined were effectively isolated in time from each other in terms of peak flowering across their ranges regardless of co-occurrence (Fig. 2a). In such cases, small shifts in phenology would probably have negligible effects on competitive or facilitative interactions among co-occurring taxa. Second, in many systems, pollinators are not as limiting as other essential resources (Rathcke & Lacey, 1985; Horvitz & Schemske, 1988). Third, the direction, intensity and outcome of reproductive interactions may vary at smaller spatial scales, mitigated by the abundance and density of interacting species, none of which our large-scale analyses could detect. Fourth, it is possible that some of the species pairs we examined may not have been in sympatry long enough for adaptive phenological displacement to have occurred. Although phenological displacement has been demonstrated to occur even within species and over relatively short timescales (Nuismer & Cunningham, 2005; Silvertown *et al.*, 2005; Hall & Willis, 2006; Spriggs *et al.*, 2019), we do not know for certain how long the focal species pairs in our study have existed in sympatry. Fifth, and finally, flowering time displacement is but one of several mechanisms that can either reduce interspecific competition and gene flow or facilitate net reproductive gains (Levin, 1971; Moeller, 2004; Elzinga *et al.*, 2007).

Phenological displacement is proportionately greater among species that flower close in time

Among species pairs for which we did observe phenological displacement, there was a highly credible log-linear relationship between the difference in peak flowering time of species pairs and the degree of estimated phenological displacement in sympatry. However, even seemingly large changes in flowering time gaps

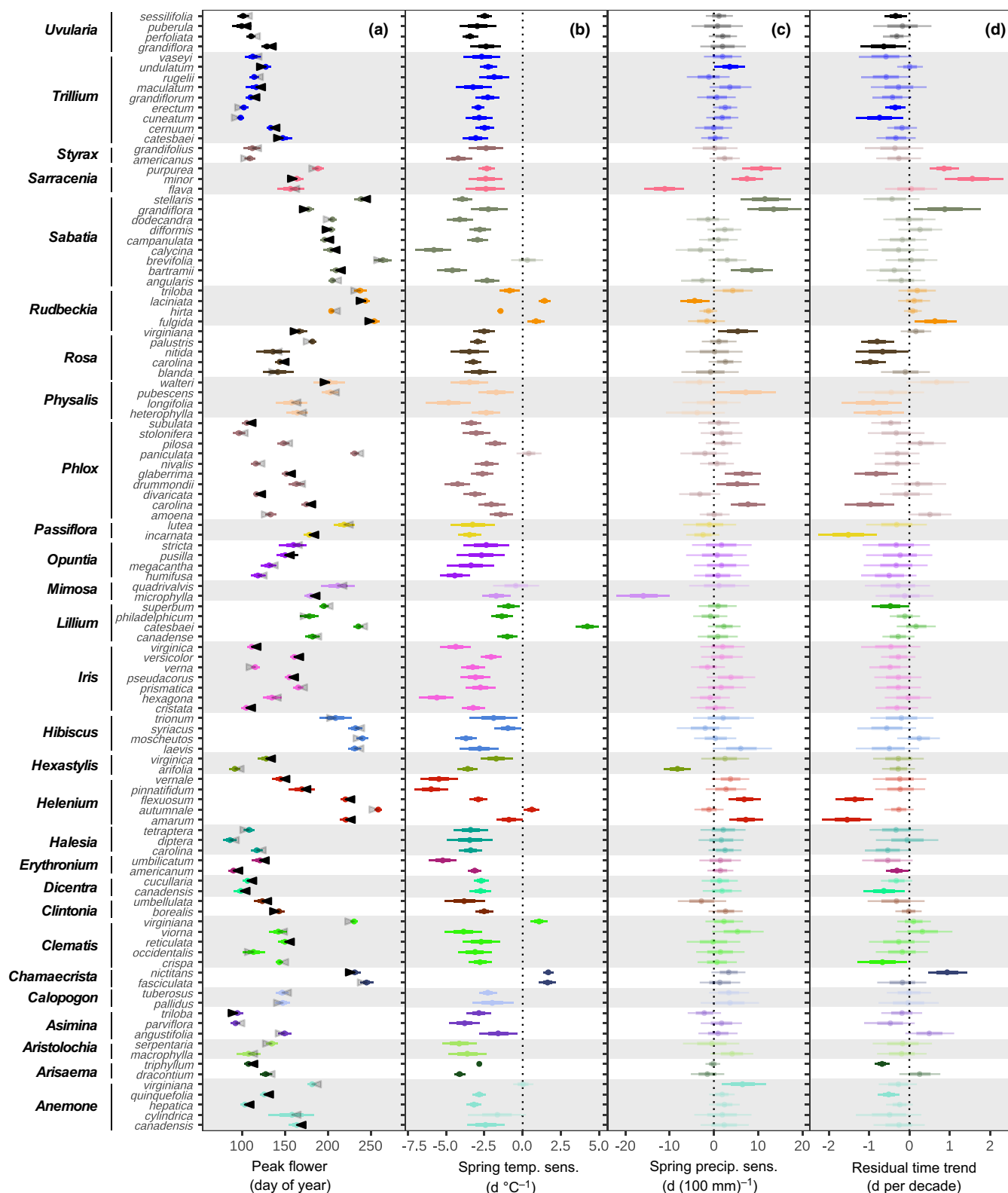


Fig. 2 Phenological response summary of 110 angiosperm species. The first column (a) shows estimated mean flowering dates of species spanning 28 genera and 21 plant families during recent climatic conditions (1987–2017), derived from a hierarchical Bayesian linear mixed model. Black arrows indicate significant directional shifts (posterior probability > 90%) in estimated flowering time under median climatic conditions before and after 1977. Gray arrows indicate nonsignificant directional shifts (posterior probability ≤ 90%). Columns (b)–(d) show estimated climatic sensitivities and residual time trends from the best-performing Bayesian hierarchical model of the effects of climate on flowering time. Thick and thin bars represent 50% and 80% credible intervals on the estimates, respectively.

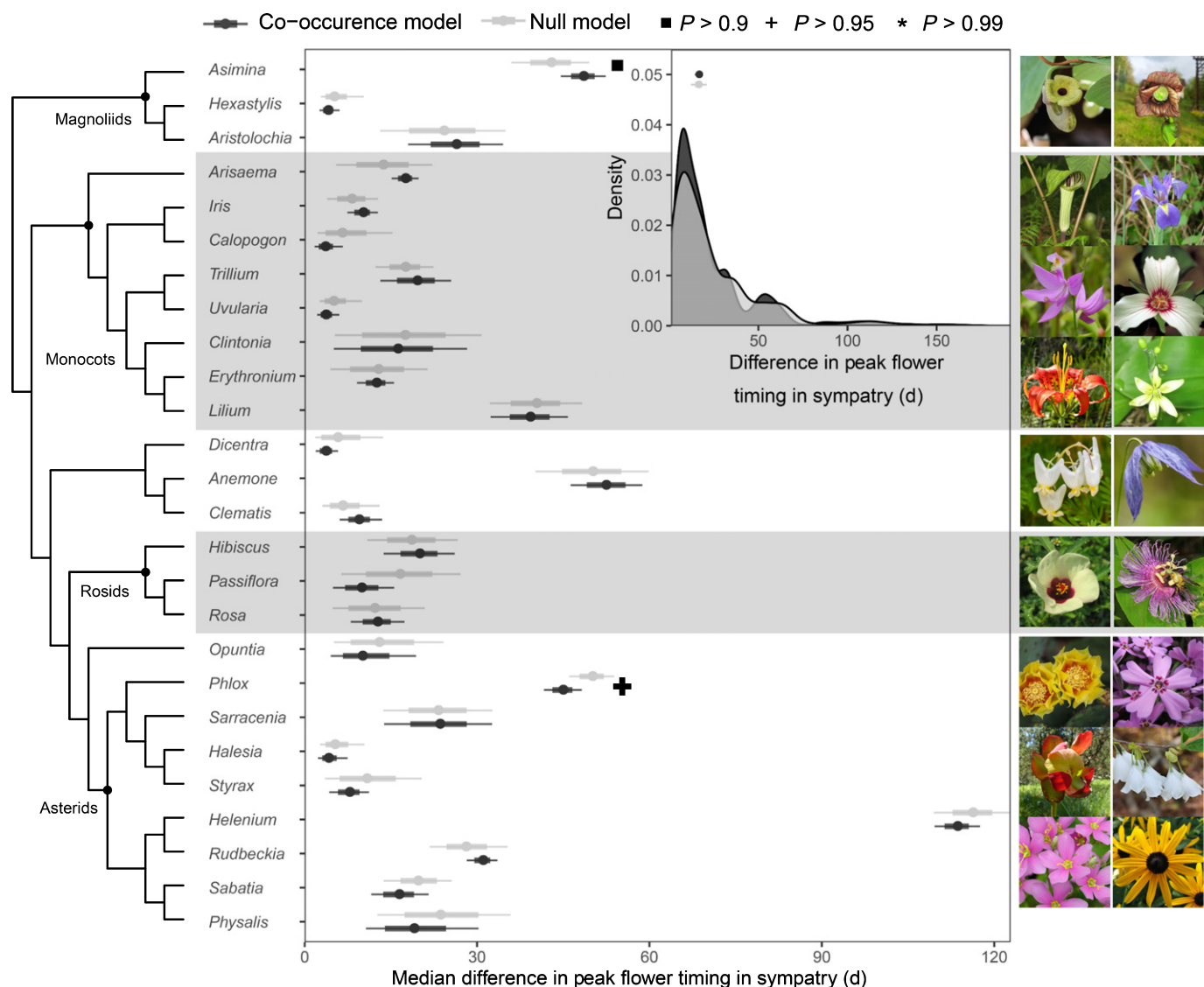


Fig. 3 Phenological displacement across genera. Median differences in estimated peak flowering time in sympatry between congener pairs (dark gray) are compared with null expectations that remove the potential influence of species co-occurrence on flowering time (light gray). Differences among species pairs were averaged within each genus. Density plots (inset) show the distribution of estimates across all congener pairs. Circles and lines at the top left represent estimates and 95% credible intervals, respectively, for the median absolute difference in flowering time across all congener pairs. Genera with median estimates for convergence or divergence that are credibly different from zero are indicated with symbols (■, $\Pr(x \neq 0) > 0.9$; +, $\Pr(x \neq 0) > 0.95$; *, $\Pr(x \neq 0) > 0.99$). Major clades are labeled on the phylogeny with black dots. Photographs depicting representative species from each clade are shown to the right. Photographs are from Wikimedia Commons (<https://commons.wikimedia.org/>) under a Creative Commons 2.0 generic license. Estimates are derived from a hierarchical Bayesian linear model of flowering time (see the Materials and Methods section).

between species may have little effect on reproductive competition or facilitation. For instance, a convergence of 10 d for a pair of *Helenium* species that tend to flower 3 months apart is unlikely to greatly alter the nature of their interactions (Fig. S3). Along these lines, when we quantified the relationship between proportional phenological displacement and estimated gaps in flowering time, we found that the amount of displacement was greater among species pairs that tended to flower closer in time. In particular, closely related species with similar peak flowering times tended to exhibit even more convergent flowering times when they co-occurred. This observation supports hypotheses that aggregated flowering of species during a relatively narrow window of time can be advantageous in certain conditions

(Thomson, 1978; Rathcke & Lacey, 1985). Flowering phenology can be influenced by other selective pressures as well. For instance, selection to avoid herbivores can conflict with pollinator-mediated selection on flowering time (Elzinga *et al.*, 2007; Sletvold *et al.*, 2015). In certain regions, climatic conditions suitable for growth and flowering may be short-lived, resulting in phenological convergence among lineages (Levin, 2006). Understory species can be temporally constrained by a limited window of high light availability before canopy closure (Kudo *et al.*, 2008). Edaphic conditions can also mediate phenological responses (Brady *et al.*, 2005; Sambatti & Rice, 2007). Flowering time can also be constrained indirectly by selection effects on the timing of germination or dispersal (Primack, 1987).

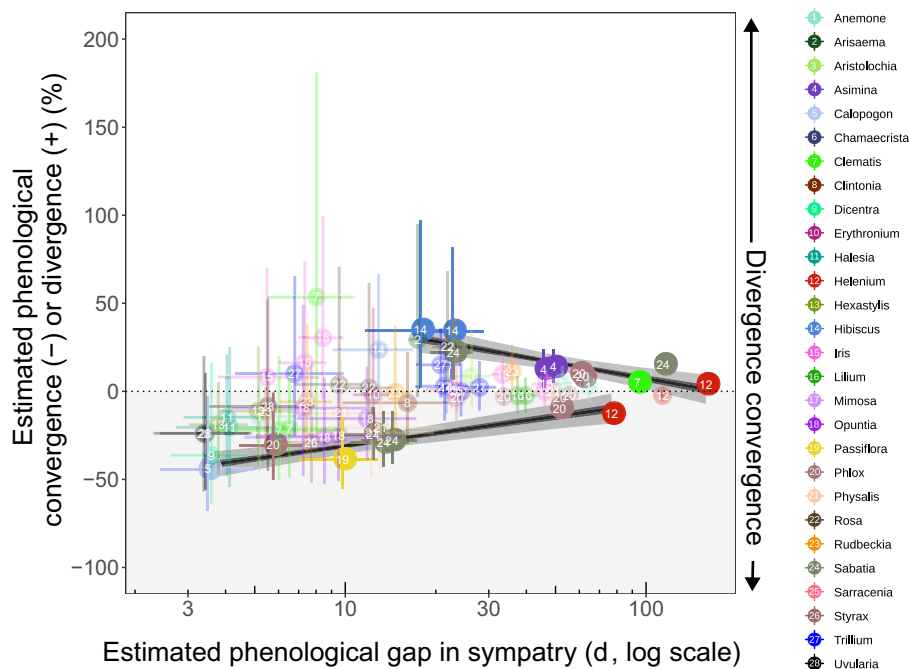


Fig. 4 Phenological displacement in sympatry compared with differences in peak flowering time between congener pairs. Estimates of phenological displacement (y-axis) are differences in flowering time in sympatry compared with null expectations of flowering time assuming no species interactions, and are depicted as percentage change relative to expected gaps in flowering time among congeners. Genera appear in different colors and are numbered alphabetically. Circles represent median estimates, and bars represent 25% and 75% posterior quantiles for each species pair. Estimates not credibly different from zero are faded. Dark shading and light shading represent 50% and 95% credible intervals, respectively, for the linear relationships indicated by the black lines.

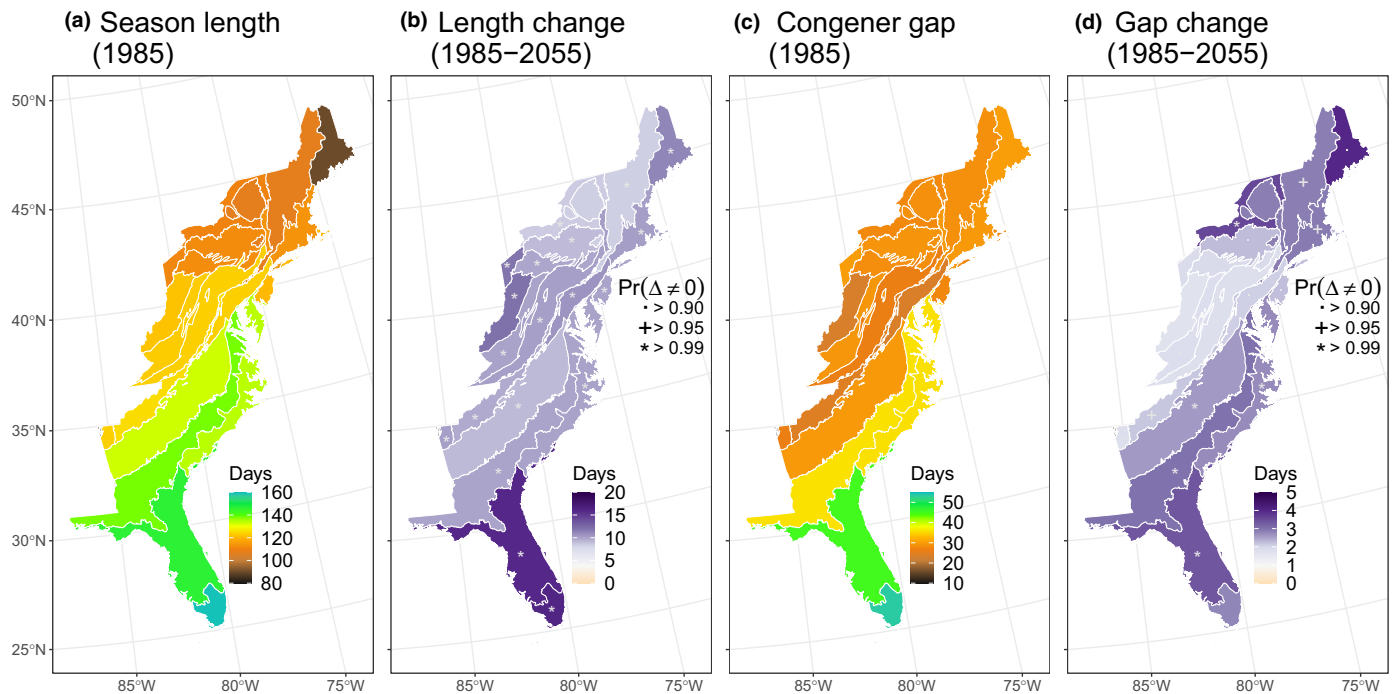
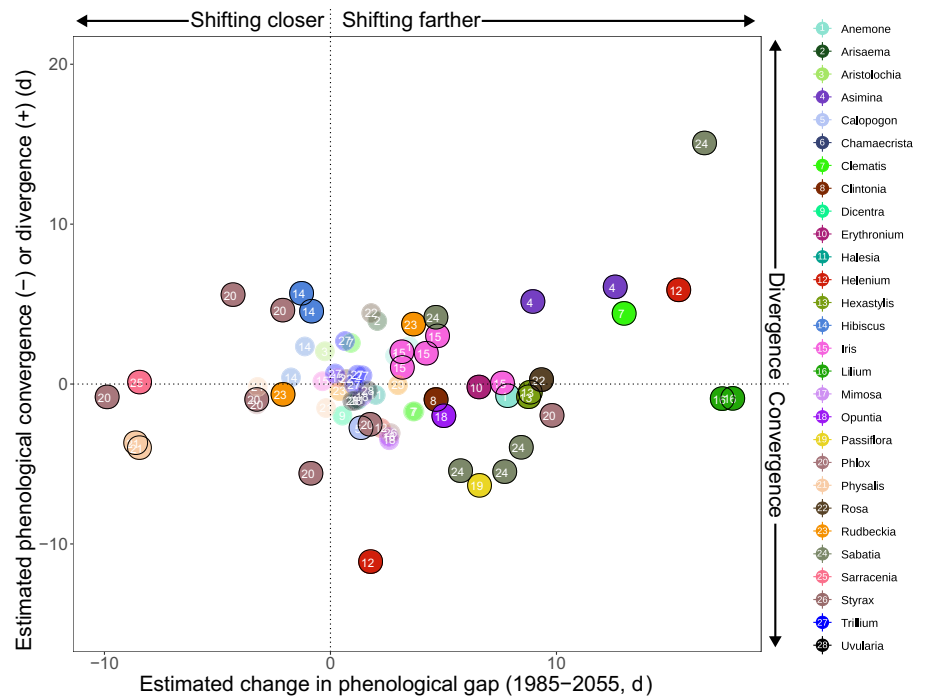


Fig. 5 Predicted changes in flowering gaps and season length. Variation in climate–phenology relationships between species and assemblages give rise to large-scale geographic gradients in flowering season length (a) and predicted expansion of the flowering season under anthropogenic climate change (b). Similar patterns appear in median differences in flowering time between sympatric congeneric pairs (c), which are predicted to diverge from each other across much of New England, the Southeastern Coastal Plain, and Peninsular Florida by the mid-21st century (d). Maps show county-level predictions from a Bayesian linear mixed model of flowering time summarized by EPA Level III ecoregions (see the Materials and Methods section). Posterior probabilities of changes in growing season length and flowering time for ecoregions in maps (b) and (d), represented by symbols in each region, are derived from summarizing posterior samples of the Bayesian model.

Although in most cases the degree of phenological displacement was less than 1 wk, even such small changes in the temporal separation between different taxa can have significant impacts.

For instance, Kudo & Ida (2013) demonstrated that a 5 d increase in the gap between *Corydalis ambigua* flowering and the emergence of its pollinator *Bombus hypocrita* can reduce seed set

Fig. 6 Comparison of expected mid-21st century shifts in flowering synchrony between congener pairs and their degree of phenological displacement in sympatry. Pairs that display credible phenological displacement or changes in phenological gaps in synchrony are circled in black and pairs that do not (with lower than 50% posterior probability) are faded. Circles represent individual species pairs and (as in Fig. 4) colors and numbers within circles represent different genera.



by 20%. Also, Heberling *et al.* (2019) found that a 2 d reduction in the gap between wildflower leaf-out and canopy closure could result in a 4–8.7% reduction in carbon budget for wildflowers and a 6.5 d reduction up to 26%. Further, a week's difference in flowering between two cytotypes of *Chamerion angustifolium* has been shown to reduce opportunities for inter-cytotype mating to 2% from 49% expected under random mating, through the cumulative effects of phenology and associated impacts on insect visitation patterns (Husband & Schemske, 2000). Although these examples do not directly pertain to convergences or divergences in flowering date among closely related species, they nonetheless demonstrate that small shifts in the gap between phenological events of co-occurring species on the scale we observe here can have significant ecological consequences.

In summary, our results suggest that while the direction and degree of displacement vary greatly among taxa, displacement is typically stronger among species that flower closer in time. However, we did not detect any relationship between displacement and phylogenetic distance, suggesting that the strength of interspecific interactions do not scale predictably with evolutionary relatedness. Relatedness is not always a good predictor of the strength of interspecific interactions (Cahill *et al.*, 2008; Bennett *et al.*, 2013), but future studies incorporating a more comprehensive phylogenetic framework are necessary to elucidate whether this is indeed the case for phenological displacement (Davis *et al.*, 2010).

Climate change will alter temporal interactions among closely related species

Climate is not predicted to change evenly across space, and even closely related species in our study region can vary significantly in their phenological sensitivity to climate (Fig. 2). Thus, as the

climate continues to change, its effect on flowering time gaps will vary across the landscape and the diverse competitive or facilitative outcomes among species will be driven in part by idiosyncratic shifts in phenology. For instance, if the lack of flowering time divergence among closely related sympatric species is at least partially the result of facilitative interactions among taxa, there may be negative consequences of future divergence driven by differences in phenological sensitivity to changes in temperature. Less diverse, smaller floral displays may reduce pollinator visitation, whereas increased asynchrony in flowering can concentrate the chance of predation on a given species' reproductive organs (Rathcke, 1983; Feldman *et al.*, 2004; Moeller, 2004; Ghazoul, 2006; Gurung *et al.*, 2018). Phenological divergence can also create new reproductive niches, which may be conducive to invasion by nonnative species (Sherry *et al.*, 2007; Wolkovich & Cleland, 2014; Reeb *et al.*, 2020). Finally, changes in climate can directly modify selective pressures on flowering phenology and alter associated biotic interactions across trophic levels (Filchak *et al.*, 2000; Forkner *et al.*, 2008; Renner & Zohner, 2018). Although it is difficult to predict the outcome of increased divergence of flowering times between co-occurring closely related species, climate-induced changes in phenology will lead to new temporal patterns of reproductive overlap, potentially affecting species interactions and resulting in altered species compositions across space and time (Post *et al.*, 2001; Sherry *et al.*, 2007; Pau *et al.*, 2011).

Recognizing that some cases of true phenological character displacement do exist, future assessments should seek to understand how flowering time interacts with other ecological and evolutionary constraints, such as pollinator availability and postzygotic reproductive barriers. For instance, although the congeneric species pairs we examine display similar floral morphologies and often share the same pollinators (e.g. *Dicentra* sp.), it would be

necessary to determine the number of pollinators available during the reproductive period of a plant population of a given size and distribution to demonstrate competitive exclusion or facilitation (Macior, 1978). Also, while many of the species pairs we examined are known or suspected to be able to hybridize, the full extent of hybridization and the viability of their hybrid offspring are largely unknown (Table S3). Along these lines, although we assume the species we examine interact across broad spatial scales, with many of them having also been directly observed to occur in close proximity, the nature of their interactions at finer scales remains to be determined for many taxa. Finally, meeting the numerous criteria to ascertain the occurrence of character displacement is difficult in any system, particularly more so at larger scales (Schluter & McPhail, 1992; Beans, 2014). However, although our study design may not allow us to conclusively prove the existence of phenological displacement, it does allow us to demonstrate that the majority of taxa examined definitely do not meet the criteria for displacement; that flowering time displacement is more likely to occur among close relatives that flower close in time; and that the differences in flowering times among close relatives are likely to shift with future climate change.

Although our study focused on temperate, insect-pollinated plants, we included a wide array of species from across the angiosperm phylogeny, ranging from trees to understory herbs. The same methods could be used to test whether similar patterns are found for wind-pollinated plants, among which it has been suggested that flowering time displacement could be more common (McNeilly & Antonovics, 1968; Hopkins, 2013). The methods and results presented here provide one promising path towards understanding how the phenological landscape is structured and may respond to future environmental change.

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Author contributions

CCD conceived the initial idea for the study and supervised the work; DSP, CCD, AME and IKB designed the study; DSP and GML collected the data; IKB, AME and DSP analyzed the data; DSP and IKB drafted the first version of the manuscript and all authors contributed significantly to subsequent revisions.

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Data availability

All data, (permanent links to) imagery, and model code are available from the Harvard Forest Data Archive (<https://harvardforest.fas.harvard.edu/data-archive>), number HF335 (doi: 10.6073/pasta/7250b11b09301501d4e9087c718f8548), and from the Environmental Data Initiative (doi: 10.6073/pasta/c17fcc2ba0f9212938b2b5f6161615d8).

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Supporting Information

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

Fig. S1 Phylogenetic signal in peak flowering phenology and its sensitivity to environmental forcings.

Fig. S2 Estimated phenological gap and displacement in sympatry compared with phylogenetic distances between congener pairs.

Fig. S3 Phenological displacement in sympatry compared with differences in peak flowering time between congener pairs.

Table S1 List of species pairs examine in study.

Table S2 Phylogenetic signal in patterns of median phenological displacement between genera.

Table S3 Species co-occurrence and hybridization.

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