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ARTICLE

Climate Ecology

Scaling flowering onset and duration responses among species predicts phenological community reassembly under warming

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Abstract

Global warming has caused widespread shifts in plant phenology among species in the temperate zone, but it is unclear how population-level responses will scale to alter the structure of the flowering season at the community level. This knowledge gap exists largely because—while the climatic sensitivity of first flowering within populations has been studied extensively—little is known about the responsiveness of the duration of a population's flowering period. This limits our ability to anticipate how the entire flowering periods of co-occurring species may continue to change under warming. Nonetheless, flowering sensitivity to temperature often varies predictably among species between and within communities, which may help forecast temperature-related changes to a community's flowering season. However, no studies—empirical or theoretical—have assessed how patterns of variation in flowering sensitivity among species could scale to alter community-level flowering changes under warming. Here, we provide a conceptual overview of how variation in the sensitivity of flowering onset and duration among species can mediate changes to a community's flowering season due to warming trends. Specifically, we focus on the effects of differences in (1) the mean sensitivity of flowering onset and duration among communities and (2) the sensitivity of flowering onsets and durations among species flowering sequentially through the season within a community. We evaluated the manner and degree in which these forms of between-species variation in sensitivity might affect the structure of the flowering season—both independently and interactively—using simulations, which covered a wide but empirically informed range of parameter values and combinations representing distinct community-level patterns. Our findings predict that communities across the temperate zone will exhibit varied and often contrasting flowering responses to warming across biomes, underscoring that accounting for the temperature sensitivity of both

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phenological onset and duration among species is essential for understanding community-level flowering dynamics in a warming world.

KEYWORDS
community-level phenology, ecological scale, emergent properties, flowering duration, flowering onset, flowering termination, global change, interspecific trait variation, intraspecific trait variation, phenological sensitivity

INTRODUCTION

Community-level flowering responses to warming are ecologically critical but poorly understood

The flowering season (the portion of the year during which the flowering of most co-occurring species within communities in the temperate zone occurs) is an ecologically critical period that mediates the fitness of plants and of the diverse organisms that depend on floral resources for survival and reproduction. The flowering season is the cumulative product (and an emergent property) of the blooming period of co-occurring plant species, and its structure determines the temporal distribution of floral diversity and abundance within a community. This temporal flowering structure mediates several ecological processes. For example, the local abundance of floral resources determines pollinator flight distances and the amount of pollen or nectar they collect (Pope & Jha, 2018; Zurbuchen et al., 2010). Accordingly, floral resource availability can mediate population growth rates among pollinator species (Roulston & Goodell, 2011). For plants, the density of co-flowering species can mediate various ecological processes, including attraction and competition for pollen and seed dispersers, herbivory, flower and fruit predation, or gene flow among and within populations (Aide, 1988; Devaux & Lande, 2009; Gavini et al., 2021; Jones & Comita, 2010). Consequently, the seasonal diversity, distribution, and abundance of floral resources influence a suite of ecological outcomes that can shape the evolution of life-history strategies (Elzinga et al., 2007). Importantly, many wild plants also support important crop pollinators (Morandin & Kremen, 2013; Reilly et al., 2020), or produce pollen that is allergenic to humans (Oh, 2022; Stinson et al., 2018). Accordingly, changes to the structure of the flowering season could have important implications for agriculture and human health.

In recent decades, warming trends have resulted in widespread shifts in flowering time across the temperate zone that could profoundly alter the network of ecological interactions within communities (Renner & Zohner, 2018) and the overall structure of their flowering seasons (CaraDonna et al., 2014; Diez et al., 2012; Theobald et al., 2017). Although the potential effects of warming on species interactions are well appreciated, it is unclear how the flowering responses of populations from different species will scale to jointly alter the flowering season at the community level. Few studies have assessed community-level changes to the flowering season (e.g., Jabis et al., 2020; Zhou et al., 2022), and they have largely focused on simple directional changes to season length. Consequently, existing studies encompass few regional floras, and the responses to temperature of more granular (and ecologically critical) characteristics of the season—such as the temporal distribution of the diversity and abundance of species in flower throughout the season—remain unexamined aside from select study systems (e.g., CaraDonna et al., 2014). Addressing these knowledge gaps is difficult because long-term phenological datasets representing enough species to characterize the flowering season of a community, or to measure floral resources throughout the season, are exceedingly rare (CaraDonna et al., 2014; Willis et al., 2017). In turn, although remotely sensed spectral data can capture the onset and duration of the growing season across much of the temperate zone, a community's flowering season generates a much weaker spectral signal that is typically undetectable through satellite imagery despite successes in a few systems (e.g., Chen et al., 2019; Dixon et al., 2021).

In principle, changes to community-level flowering patterns caused by warming could be inferred by aggregating the flowering responses of co-occurring species. However, our ability to do so is severely limited by an incomplete understanding of how warming affects the blooming periods of populations within species. To date, most phenological research has focused on the sensitivity to temperature of the onset of the flowering period (i.e., first flowering date, or "FFD"), with most studies measuring the effects of temperature on the emergence of the first flowering individuals within a population or site (hereafter "S_{FFD}"; Figure 1) (Fitter & Fitter, 2002; Miller-Rushing & Primack, 2008; Prevéy et al., 2019; Wolkovich et al., 2012). In contrast, comparatively little

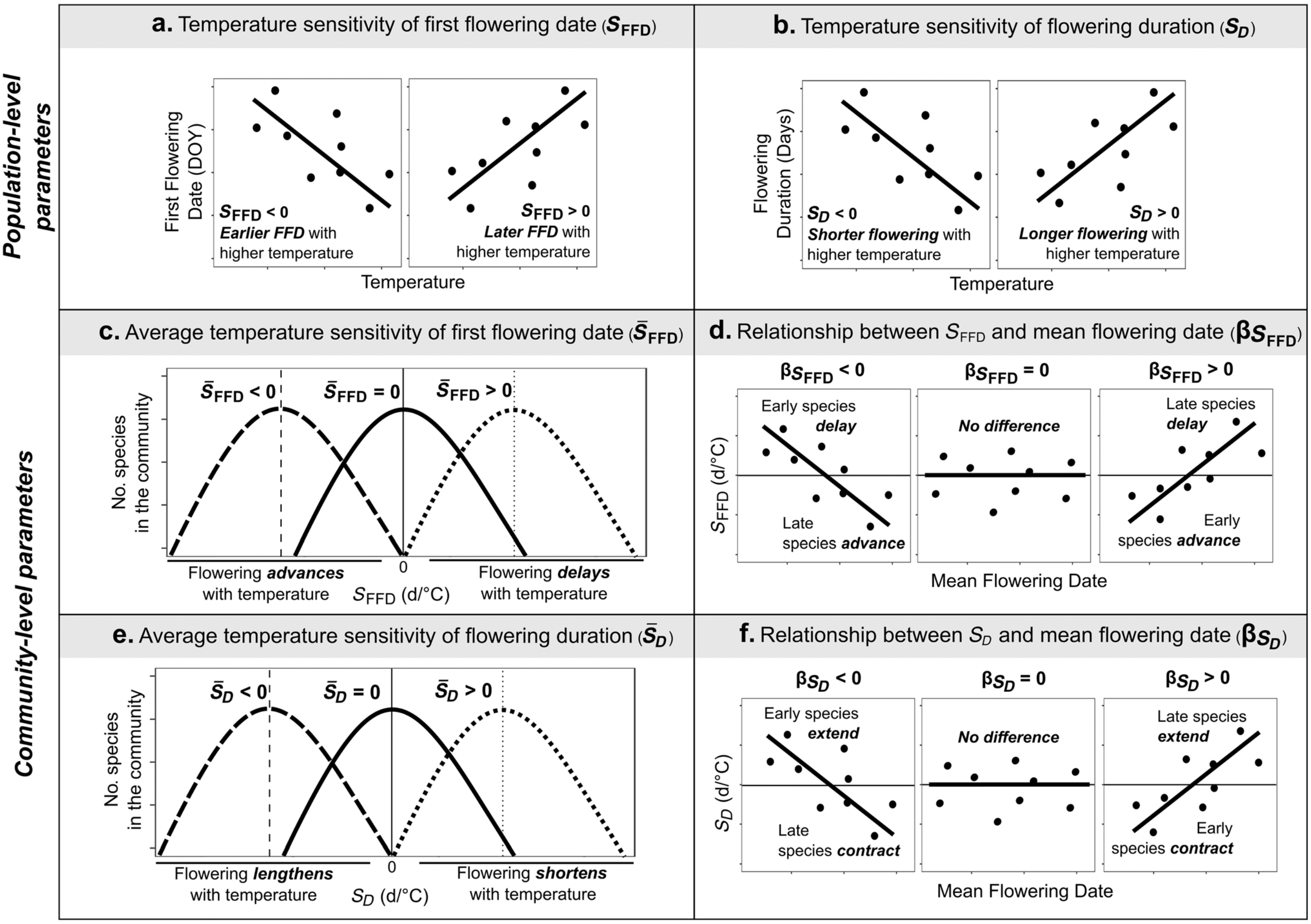

FIGURE 1 (a, b) Population-level sensitivities and (c–f) patterns of variation in sensitivity among co-occurring species that determine the responses of a community's flowering season to temperature. (a, b) The manner in which a population's first flowering date ("FFD") and the duration of its flowering period change with temperature, with points respectively representing FFDs and durations of a single population across years with different temperatures in the season leading up to flowering. The temperature sensitivity of first flowering dates ("S_{FFD}") is defined as (a) the slope of the relationship between FFD and temperature, with negative values indicating earlier FFD under higher temperatures, and positive values indicating later FFD under higher temperatures. Similarly, (b) the temperature sensitivity of flowering duration ("S_D") is measured as the slope of the relationship between duration and temperature, with negative values indicating shorter flowering periods under higher temperature, and positive values indicating longer flowering under higher temperatures. As population-level sensitivity metrics, S_{FFD} and S_D are mediated by factors affecting the mean and variability of plastic phenological responses among individuals, such as genetic or microsite differences. In turn, (c–f) show patterns of among-species variation in S_{FFD} and S_D. (c, e) Variation among communities in average S_{FFD} and S_D among species ("$\overline{S}_{\mathrm{FFD}}$" and "$\overline{S}_D$"), with each curve representing the among-species distribution of sensitivities within communities with different means. Negative values of $\overline{S}_{\mathrm{FFD}}$ or $\overline{S}_{\mathrm{FFD}}$, respectively, indicate that species tend to advance or contract their flowering under warming, whereas positive values respectively indicate that species tend to delay or extend their flowering. Values of 0 for these parameters indicate that, on average, first flowering dates and flowering durations do not tend to change under warming. (d, f) Variation among communities in the relationship between the mean flowering date and both S_{FFD} ($\beta_{S_{\mathrm{FFD}}}$) and S_D (β_{S_D}) for species flowering successively throughout the season. Accordingly, points in (d) and (f) represent species within a community. Negative values of $\beta_{S_{\mathrm{FFD}}}$ indicate that S_{FFD} decreases among species as the season progresses. Depending on the community's mean S_{FFD}, these patterns may respectively correspond to a transition from delays to advances between early and late flowering species (i.e., S_{FFD} switches sign), a decrease in the degree of delay under higher temperatures (i.e., S_{FFD} closer to 0), or increases in the degree of advancement under higher temperatures (i.e., S_{FFD} further from 0 in the negative direction). In turn, positive $\beta_{S_{\mathrm{FFD}}}$ indicate that S_{FFD} increases among species as the season progresses (with an interpretation opposite to that of $\beta_{S_{\mathrm{FFD}}} < 0$). Similarly, negative values of β_{S_D} indicate that S_D decreases among species as the season progresses, which can correspond to a transition from flowering extensions to contractions among species throughout the season (i.e., S_D switches sign), decreases in the degree of flowering extension (i.e., S_D becomes less positive), or increases in the degree of flowering contraction (i.e., S_D becomes more negative). Positive $\beta_{S_{\mathrm{FFD}}}$ then indicate increases in S_D as the season progresses. $\beta_{S_{\mathrm{FFD}}}$ or β_{S_D} equal to 0 respectively indicate no difference in average S_{FFD} and S_D among early- and late-flowering species. For simplicity, (d) and (f), respectively, depict scenarios in which $\overline{S}_{\mathrm{FFD}}$ and $\overline{S}_D$ equal 0.

is known about the effects of temperature on the duration of the period over which individuals are observed in flower (i.e., the temperature sensitivity of population-level flowering duration, hereafter "S_D") (Figure 1b). At the individual level, the termination of flowering—whose timing relative to flowering onset determines flowering duration—can be induced by different endogenous and environmental factors than those triggering its onset (González-Suárez et al., 2020; Nagahama et al., 2018). Consequently, S_{FFD} might not predict the temperature sensitivity of flowering termination (and by extension, S_D), which has been measured directly in a relatively narrow range of species and biomes (Li et al., 2021; Zhou et al., 2022). Moreover, population-level flowering duration is also driven by variation in flowering onset and duration among individuals, and the drivers of such variation (e.g., microenvironmental differences, genetic variation in flowering plasticity, resources status) are largely unresolved across regions and taxa. These limitations—compounded by a scarcity of long-term observational records of flowering duration of individual populations—preclude inferences of the way in which blooming period responses to temperature among co-occurring species will scale to alter a community's flowering season (Park et al., 2024).

Community-level flowering responses to warming can be predicted from nonrandom variation in sensitivity among co-occurring species

A recent surge of phenological research has established that flowering sensitivity typically varies nonrandomly among species within and among communities, which can be leveraged to predict how flowering at the community level will change under ongoing warming trends (Figure 1c–f). For example, due to species turnover across regions or variation in sensitivity within species ranges, the mean S_{FFD} observed among co-occurring species (hereafter "$\overline{S}_{\text{FFD}}$") often differs between communities (Park et al., 2019; Prevéy et al., 2017; Zhang et al., 2015) (Figure 1c). Moreover, many studies have established that co-occurring species that flower at different times within a season tend to show marked differences in the climate sensitivity of their first (and peak) flowering dates (i.e., in S_{FFD}) (e.g., Mazer et al., 2013; Ramirez-Parada et al., 2024; Wolkovich et al., 2012). In relatively mesic communities, such directional variation in S_{FFD} among species throughout the season (hereafter "$\beta_{S_{\text{FFD}}}$"; Figure 1d) typically consists of greater advances under warming among early-flowering species than among late-flowering species (Cook et al., 2012). In turn, high-latitude and high-elevation communities show more variable patterns that include greater advances among late-flowering species (Prevéy et al., 2019). Meanwhile—and although still rare compared to research on flowering onset—studies of population-level flowering duration have reported substantial variation in mean S_D among species in different communities (hereafter "$\overline{S}_D$"; Figure 1e), with some communities showing average increases and others average decreases in flowering duration among species in response to warming (Chen et al., 2020; Hu et al., 2020; Huang et al., 2020; Jabis et al., 2020; Nagahama et al., 2018; Nam & Kim, 2020). Some communities also exhibit variation in S_D among species that flower at different times throughout the season (hereafter "β_{S_D}"; Figure 1f), with some exhibiting greater sensitivity among early-flowering and others among late-flowering species (Chen et al., 2022; Li et al., 2021).

Such forms of nonrandom variation in S_{FFD} and S_D among species should have distinct impacts on the structure of a community's flowering season under warming (depicted in simplified hypothetical scenarios in Figure 2). For example, for communities with an identical flowering structure before warming (Figure 2a)—and assuming no other forms of variation in S_{FFD} and S_D among species (i.e., $\overline{S}_D$, $\beta_{S_{\text{FFD}}}$, and β_{S_D} all equal 0)—$\overline{S}_{\text{FFD}}$ should determine whether the FFDs of co-occurring species tend to advance or delay under higher temperatures. In such cases, warming would significantly alter the start and end of the season but not the relative distribution of the flowering periods of different species (Figure 2b). In contrast, directional variation in S_{FFD} as the season progresses ($\beta_{S_{\text{FFD}}}$) should mediate the degree to which the blooming periods of species tend to converge or diverge within the season (Figure 2c). For example, $\beta_{S_{\text{FFD}}} > 0$ would tend to spread the flowering periods of co-occurring species, advancing the start and delaying the end of the season (thus lengthening it), decreasing flowering overlap among species, and therefore the mean richness of flowering species throughout the season. In turn, greater advances among late-flowering species would concentrate the blooming periods of different species, shortening the season and increasing both the degree of flowering overlap and the average richness of co-flowering species throughout the season. Among-species variation in S_D should have distinct effects from those generated by among-species variation in S_{FFD}. A community's $\overline{S}_D$ would affect the timing of flowering termination among species, predominantly altering their degree of flowering overlap, the richness of co-flowering species (or the cumulative flowering intensity of the community), and the duration of the season (Figure 2d). In turn, directional variation in S_D

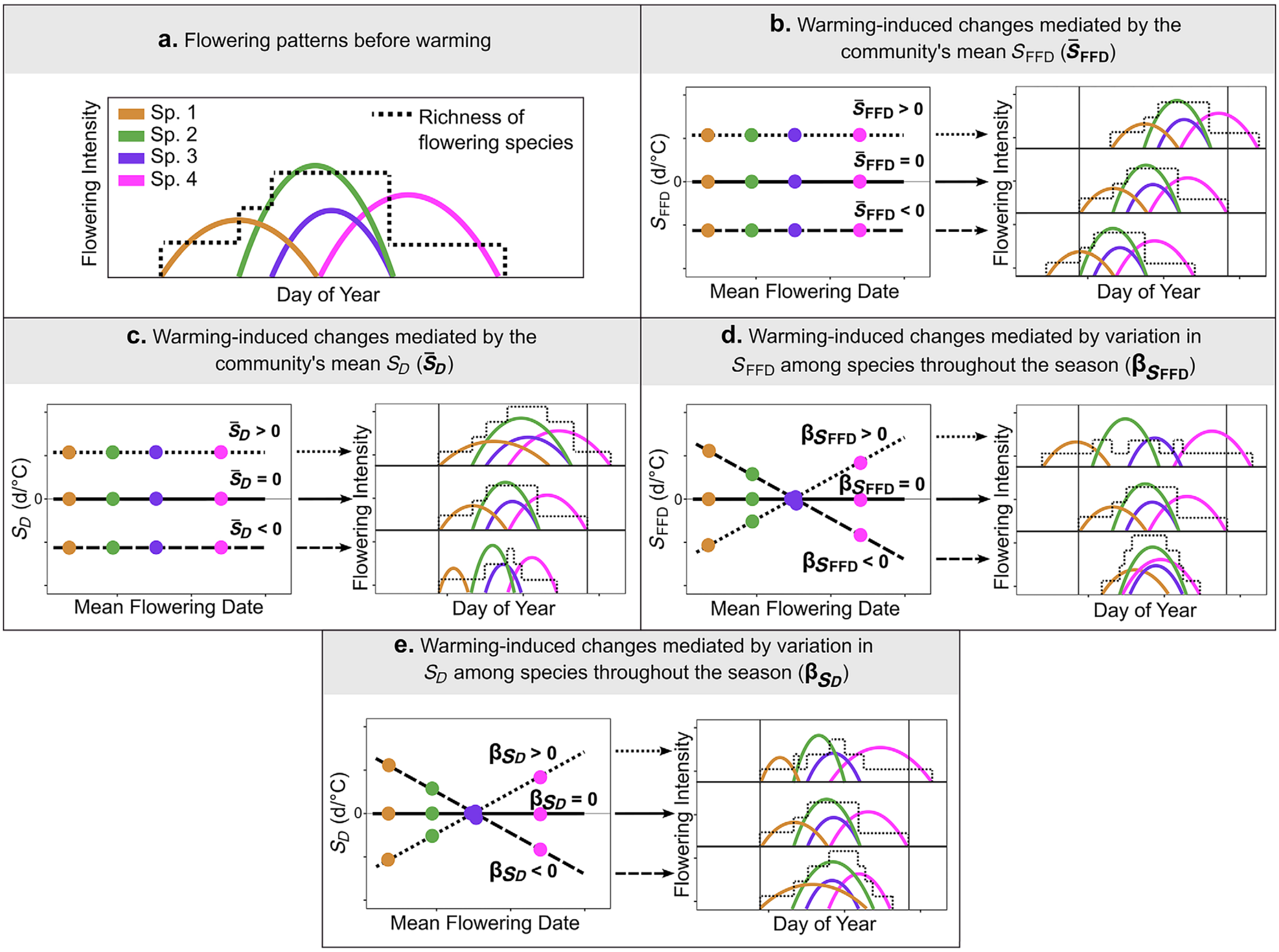

FIGURE 2 Community-level flowering responses to warming mediated by different forms of nonrandom variation in S_{FFD} and S_D among co-occurring species. (a) A hypothetical community of four species, with each colored line representing the flowering intensity (interpretable as the number of individuals flowering or the cumulative flowering output of the population) each day of the season. (b–e) Various forms of nonrandom variation in S_{FFD} or S_D among species, and the responses to warming that they would generate for the community depicted in (a). Arrows between panels in (b–e) connect each form of among-species variation in S_{FFD} and S_D to the community-level flowering pattern that would emerge under warming. In each scenario, the community is assumed to exhibit only the focal form of among-species variation in S_{FFD} and S_D (i.e., other parameters describing nonrandom variation among species are assumed to equal 0). The vertical, solid lines in the right-hand panels of (b–e) indicate the start and end of the flowering season for the community before warming (for reference). FFD, first flowering date.

throughout the season (β_{S_D}) would most strongly impact the degree of flowering overlap among species and the richness of co-flowering species within it (Figure 2e).

These forms of interspecific variation in sensitivity can generate nonanalog flowering events in response to warming, with previously asynchronous species now overlapping (e.g., spp. 1 and 4; Figure 2c–e), previously synchronous species no longer overlapping (e.g., spp. 1 and 3; Figure 2c–e), and species flowering partially outside of (or no longer in) the community's historical flowering season (Figure 2b–e). Such nonanalogous synchrony patterns may therefore reassemble the network of interactions mediated by flowering (e.g., pollinator attraction or competition) among species within a community (Theobald et al., 2017).

While predicting community-level responses is simple when considering these patterns of variation in isolation, realized changes to the structure of the flowering season will depend on how these community-level attributes jointly mediate variation in S_D and S_{FFD} within communities. Moreover, the direction and magnitude of such changes are not intuitively obvious. For example, if late-flowering species advance their flowering but delay flowering termination, it is unclear whether the end of the season would delay or advance. Moreover, directional changes in season length or flowering peaks do not necessarily indicate whether floral diversity and abundance—or the network of flowering overlap among species—might increase or decrease during different parts of the season. It is also difficult to anticipate how these types of nonrandom variation in sensitivity among species might operate in more complex communities (e.g., temperate communities can harbor hundreds of species) or what their impact would be for more granular attributes of the flowering season (such as the community's cumulative flowering output each day of the season). To our knowledge, no studies—empirical or theoretical—have assessed whether and how nonrandom variation in S_{FFD} and S_D determines temperature-related changes to the structure of the flowering season at the community level. This is largely because few datasets document the duration of the flowering period of plant populations across multiple years—which is needed for measuring the sensitivity of flowering duration to interannual temperature variation—and to our knowledge, none have done so comprehensively among co-occurring species within a community.

Simulations enable scaling of flowering responses from species to communities

Studies examining community-level flowering responses to climate are rare and have predominantly measured simple attributes of the season (e.g., season length), limiting our understanding of how the seasonal distribution of floral diversity and abundance will change in response to ongoing warming across regions. Assessing this knowledge gap empirically is difficult due to a scarcity of long-term datasets on the phenological sensitivity of both flowering onset and termination that also include enough species to reconstruct community-level patterns.

To circumvent these limitations, we used computer simulations to evaluate how patterns of nonrandom variation in S_{FFD} and S_D among species—some of which have been extensively reported in the literature—independently and jointly mediate the seasonal distribution of flowering species and the structure of flowering overlaps among species within a community. We modeled three forms of among-species variation in sensitivity that have been documented in the literature: (1) the degree and direction in which S_{FFD} varies among species flowering successively throughout the season (i.e., $\beta_{S_{\mathrm{FFD}}}$), (2) the degree to which co-occurring species tend to shorten or extend their flowering periods under warming (i.e., mean S_D among species or $\overline{S}_D$), and (3) the degree and direction of variation in S_D among species flowering successively throughout the season (i.e., β_{S_D}) (Figure 1). We excluded $\overline{S}_{\mathrm{FFD}}$ from the simulations because, although it affects the overall timing of the flowering season within the year, it does not alter the timing of each species' flowering period relative to the rest of the community, nor the emergent community structure (Figure 2b; Appendix S1: Figure S1). By simulating communities under a range of values for $\beta_{S_{\mathrm{FFD}}}$, $\overline{S}_D$, and β_{S_D}, we explored three general scenarios: one in which S_{FFD} and S_D vary independently among species (Scenario 1; Figure 3a), and two others in which S_D and S_{FFD} are correlated either positively (Scenario 2; Figure 3b) or negatively (Scenario 3) due to their shared covariation with the timing of flowering of a species within the season (Figure 3c).

Our goals in using simulations were multifold. First, we evaluated how species-level responses scale to alter community-level attributes beyond simple directional responses to season length. Such attributes included changes to the diversity and abundance of flowering each day of the flowering season and to the network of flowering overlaps within the community (which mediates the potential for flowering-mediated species interactions). Second, we were able to concurrently assess the effects of flowering onset and duration sensitivities, identifying their distinct impacts during different portions of the season and on specific types of community-level flowering responses. Finally, simulating empirically documented forms of among-species variation in sensitivity for a wide range of parameter combinations enabled us to explore a much wider range of scenarios—or types of communities—than that captured by the few empirical studies conducted to date.

Overall, our simulations demonstrate that nonrandom variation in S_{FFD} and in S_D among species (modeled by $\beta_{S_{\mathrm{FFD}}}$, $\overline{S}_D$, and β_{S_D}) is likely to have profound and predictable impacts on the structure of the flowering season, underscoring (i) the importance of measuring the climatic responsiveness of phenological onsets and durations and (ii) that characterizing patterns of among-species variation will help predict changes in community-level flowering patterns and their potential ecological consequences under a changing climate. Importantly, recent research suggests that directional variation in temperature sensitivity among species active at different times throughout the season—such as that described in this paper—might be common among producers, primary and secondary consumers, and saprotrophs (Roslin et al., 2021). Therefore, the modes of change described here might have implications for

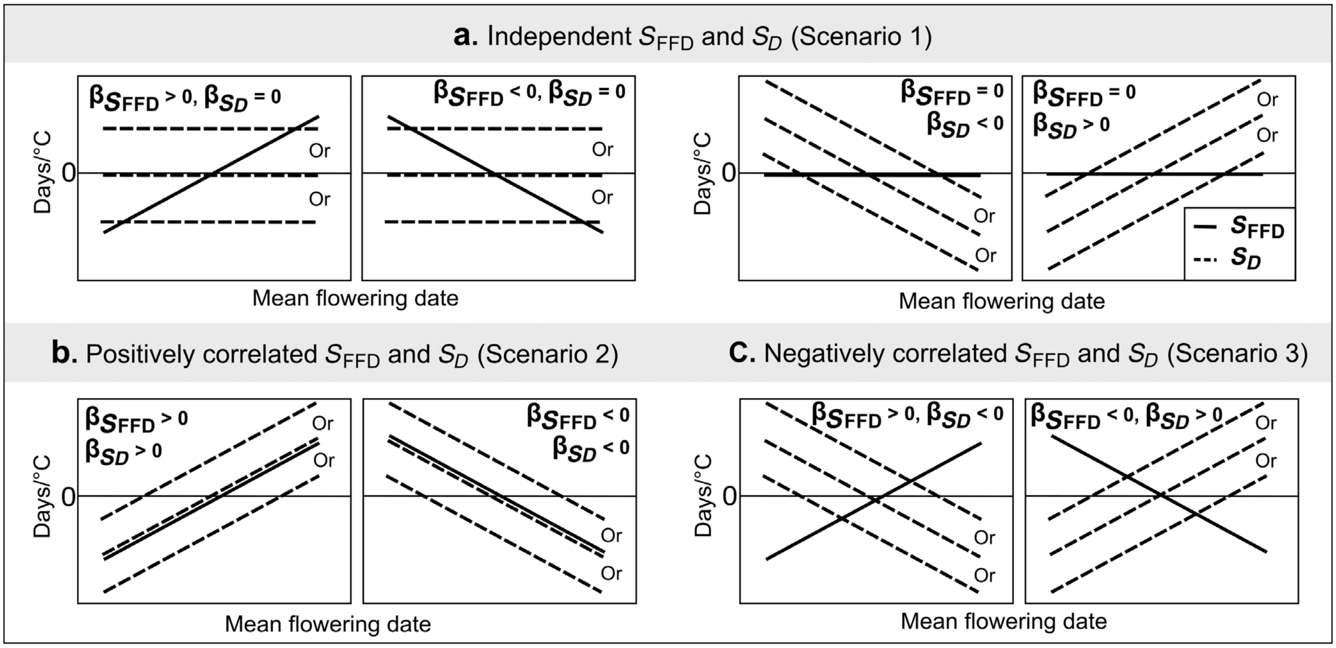

FIGURE 3 Combinations of $\beta_{S_{FFD}}$ and β_{S_D} values generating scenarios in which S_{FFD} and S_D are (a) independent (Scenario 1), (b) positively correlated (Scenario 2), or (c) negatively correlated (Scenario 3) across species. Across panels, multiple dashed lines depicting the relationship between S_D and mean flowering date are shown because communities may differ in the mean sensitivity of S_D observed among species (i.e., $\overline{S}_D$), which changes the *y*-intercept of the relationship without altering its slope. FFD, first flowering date.

understanding community-level phenological changes beyond plants and flowering phenology.

METHODS

Assigning community-level parameters

The simulations assessed changes to the flowering season under warming across communities differing in the structure of among-species variation in S_{FFD} and S_D, which we modeled using three parameters ($\beta_{S_{FFD}}$, $\overline{S}_D$, and β_{S_D}; Figure 1). $\beta_{S_{FFD}}$ modeled the degree and direction in which S_{FFD} (measured in days/°C) varied among species flowering successively throughout the season as a linear relationship between each species-specific S_{FFD} and mean flowering date (Figure 4a). Therefore, a negative $\beta_{S_{FFD}}$ indicates decreasing S_{FFD} as the season progresses, whereas a positive $\beta_{S_{FFD}}$ indicates increasing S_{FFD}. Because mean S_{FFD} was set to 0 for all communities (as it did not affect the structure of the flowering season; Figure 2b; Appendix S1: Figure S1), negative $\beta_{S_{FFD}}$ implies a transition from positive S_{FFD} (i.e., flowering delays under warming) to negative S_{FFD} (i.e., flowering advances under warming) between early- and late-flowering species in a community. Each simulated community (described below) was assigned one of five $\beta_{S_{FFD}}$ values ranging from −0.1 (i.e., S_{FFD} decreases by 1 day/°C for every 10-day increase in mean flowering date among species) to 0.1 (S_{FFD} increases by 1 day/°C for every 10-day increase in mean flowering date) in 0.05 increments. We approximately set the midrange of values for $\beta_{S_{FFD}}$ (−0.05 to 0.05) based on studies that have evaluated the relationship between mean flowering dates and S_{FFD} empirically (e.g., Cook et al., 2012; Fitter & Fitter, 2002; Mazer et al., 2013; Park et al., 2019; Prevéy et al., 2019; Wolkovich et al., 2012). As most studies comparing phenological sensitivities have been conducted within mesic regions of North America and Europe, we included more extreme values of $\beta_{S_{FFD}}$ (−0.1 and 0.1) to account for the possibility of more extreme relationships between S_{FFD} and mean flowering date in unstudied systems.

We modeled variation among communities in both the mean S_D observed among species (i.e., $\overline{S}_D$) and in the degree to which S_D varied among species flowering successively throughout the season. $\overline{S}_D$ indicates whether (and to what degree) a community shows average decreases or increases in flowering duration under warming (Figure 4b). Each community was assigned one of five $\overline{S}_D$ values ranging from −5 days/°C (i.e., mean decreases in the duration of the flowering period of 5 days/°C among species) to 5 days/°C (i.e., mean duration increases of 5 days/°C) in 2.5 days/°C increments. In this scenario, S_{FFD} and S_D are assumed to be uncorrelated among species. In turn, we modeled $\beta_{S_{FFD}}$ as a linear

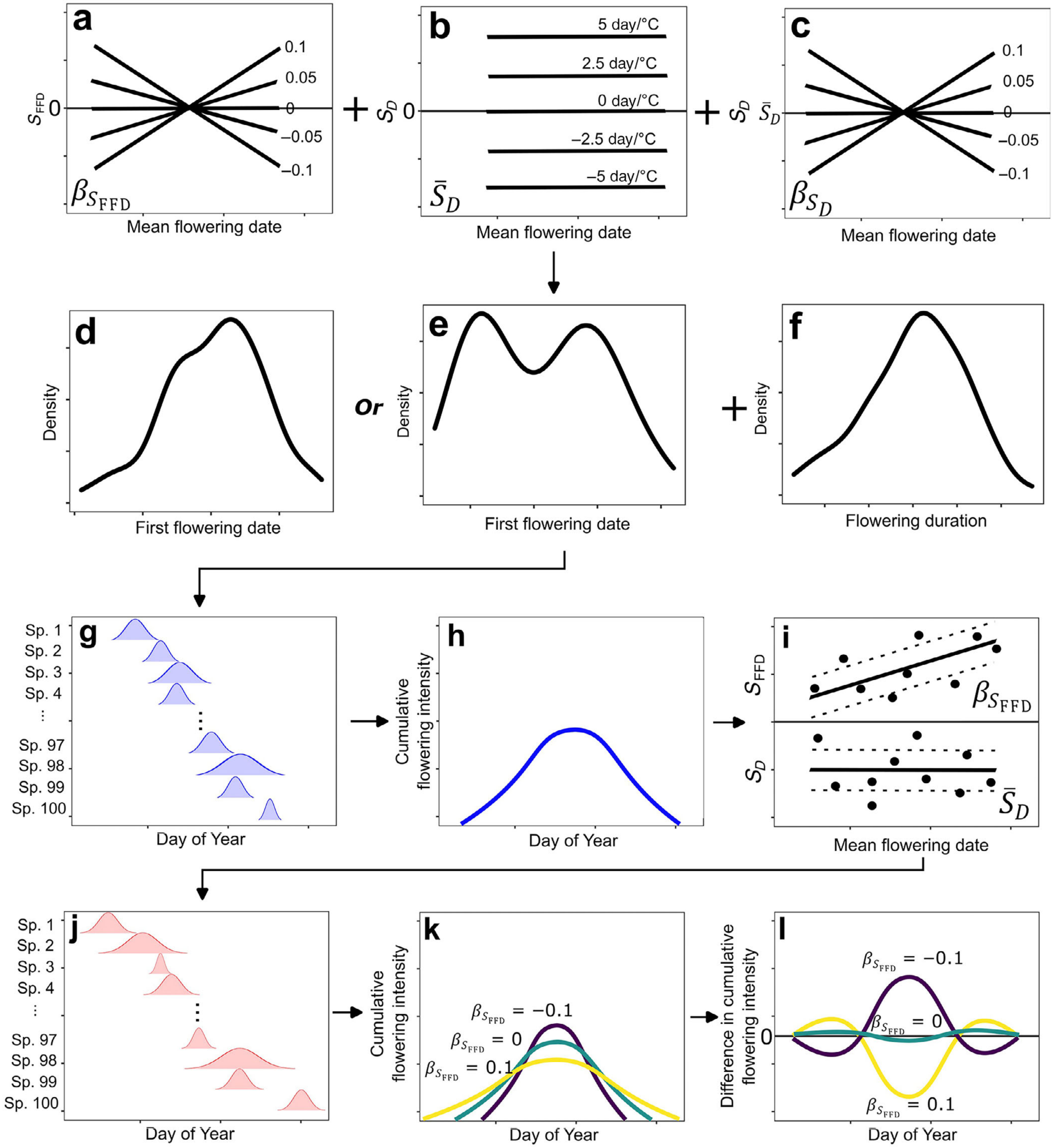

FIGURE 4 Diagram of the simulation design. For each combination of community-level parameter values describing variation in (a) the sensitivity of first flowering dates (FFDs) among successively flowering species ($\beta_{S_{FFD}}$), (b) the mean sensitivity of flowering duration among species ($\bar{S}_D$), and (c) the sensitivity of flowering duration among successively flowering species (β_{S_D}), 200 communities were simulated: half showing a single seasonal peak of FFDs among species, and half showing two peaks. For each community, 100 species were simulated by combining (d, e) random first flowering dates (drawn from either unimodal or bimodal distributions) and (f) flowering durations. For each species, (g) population-level flowering time series were generated from their FFDs and durations assuming a bell-shaped flowering curve, and (h) the flowering season attributes before were calculated for each community. Then, (i) each species was assigned an S_{FFD} and an S_D based on the relationship between these sensitivities and mean flowering date determined by its community's $\beta_{S_{FFD}}$, $\bar{S}_D$, and β_{S_D} values prior to (j) generating new flowering periods predicted by each species' S_{FFD} and S_D under 2°C warming. (k) Flowering season attributes were recalculated for each post-warming community and (l) compared to the preseason baseline.

function of mean flowering date throughout the season, with values ranging from −0.1 (i.e., S_D decreases by 1 day/°C for every 10-day increase in the mean flowering date of a species) to 0.1 (S_D increases by 1 day/°C for every 10-day increase in mean flowering date) in 0.05 increments (Figure 4c). Again, the range of possible values for β_{S_D} was roughly approximated from the few studies that have quantified among-species variation in S_D throughout the season (e.g., Chen et al., 2020; Li et al., 2021), including more extreme values to acknowledge the possibility of stronger relationships (values of −0.1 and 0.1) than those documented to date. As communities differed in both β_{S_D} and $\overline{S}_D$, negative β_{S_D} can indicate a transition between early- and late-flowering species from positive to negative S_D (i.e., flowering lengthening to contraction), decreases in the degree of flowering lengthening (i.e., lower but still positive S_D among late-flowering species), or increases in the degree of contraction among late-flowering species (i.e., more negative S_D). In turn, positive β_{S_D} can indicate the opposite of each of these patterns (i.e., a switch from contractions to lengthening, increases in the degree of lengthening, or decreases in the degree of contraction between early- and late-flowering species).

Different combinations of $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D} generated distinct relationships between S_{FFD} and S_D, with a value of 0 for $\beta_{S_{\mathrm{FFD}}}$ or β_{S_D} generating independent S_{FFD} and S_D (Scenario 1; Figure 3a), nonzero $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D} of the same sign generating positively correlated S_{FFD} and S_D through their congruent relationship with mean flowering date (Scenario 2; Figure 3b), and opposite signs generating negatively correlated S_{FFD} and S_D through their discordant variation throughout the season (Scenario 3; Figure 3c).

Simulating prewarming communities

For each of 125 combinations of parameter values (5 × 5 × 5 combinations of $\beta_{S_{\mathrm{FFD}}}$, $\overline{S}_D$, and β_{S_D} values), we simulated 200 initial prewarming communities for a total of 25,000 simulated communities. In each community, 100 species were simulated by first generating a random sample of "FFDs" drawn from one of two alternative types of community: those with a single flowering peak (i.e., unimodal distribution; 100 communities per parameter value combination; Figure 4d) or those with two weaker flowering peaks (i.e., bimodal distribution; 100 communities per combination; Figure 4e). These community types emulate flowering patterns known to occur in North American plant assemblages; unimodal patterns have been reported in mesic communities, while bimodal patterns have been described in semiarid assemblages experiencing summer monsoons and in subalpine communities (e.g., CaraDonna et al., 2014; Diez et al., 2012). FFDs for the single-peak communities were obtained from a normal distribution centered on May 31, with an SD of 30 days. In turn, FFDs for the bimodal communities were obtained from a joint distribution combining two truncated normal distributions: one bound between January 1 and May 21, with a mean (or peak) on April 30 and an SD of 30 days, and another bound between May 22 and December 31 with mean DOY on Jun 20, and an SD of 30 days. By using normal distributions, we assume that species within each community do not exhibit significant skew in FFD. Although many communities across the temperate zone likely do not conform to this assumption, the degree of skew in the distribution of FFDs among co-occurring species has not been widely characterized across biomes. The choice of normal distributions is agnostic about the prevalence of right- versus left-skewed species-level FFD distributions across communities (or of greater first vs. second flowering peaks in the case of bimodal communities), and we thus consider it an appropriately conservative assumption.

Once FFDs were generated, we randomly assigned a flowering duration (in days) to each species by drawing values from a truncated normal distribution (lower bound = 14 days, mean = 60 days, SD = 10 days; Figure 4f). Parameters for this truncated normal distribution were chosen to generate a plausible range of variation in population-level flowering durations among species, which typically ranged from 14 to 90 days among species within a community. We then calculated flowering termination dates by adding the flowering duration of each species to its FFD (subtracting one). This approach assumes that the duration of the flowering period of a population is independent of its date of onset.

Next, we modeled the intensity of flowering of each species' population throughout its flowering period under the simplifying assumption that the time series of flowering intensity—interpretable either as the proportion of individuals in flower, the mean number of flowers produced per individual, or the floral output of the population each day relative to its peak—was bell-shaped with a peak at the median flowering date of each species (Figure 4g). We implemented this by modeling the amplitude of each species' flowering period using truncated normal distributions bound by the flowering onset and termination dates for each species, with the median date between onset and termination as the mean, and SD equal to a third of the duration of the flowering period. To make the amplitude of the time series interpretable—and to make the range of variation in the amplitude of the flowering period among species comparable—we scaled each time series to a maximum amplitude of 1 at its peak. Consequently, for a given species, each point in the time series indicates the species' proportional flowering intensity relative to its flowering peak. As with the choice of distribution to model among-species variation in FFD, the choice of a bell-shaped distribution of flowering intensity during the flowering period of each species is agnostic about the prevalence of left- versus right-skewed flowering among species, which is poorly documented across biomes.

Flowering season baselines prior to simulated warming

To generate a baseline against which to compare the structure of the flowering season after warming for every simulated community, we calculated (1) the cumulative intensity of flowering across all species on each day throughout the growing season (defined below), (2) the length of the flowering season, (3) the amplitude of the season's flowering peak, and (4) the degree of flowering overlap between each pair of species in a community (Figure 4h).

The cumulative intensity of flowering for each day throughout the season was calculated as the sum of the amplitudes of flowering curves across species. Because the amplitude of the flowering curve of a species ranges from 0 (no flowering) to 1 (its flowering peak), this community-level metric is bounded by 0 (no species flowering on that date) and a theoretical maximum equal to the number of species in the community (100 in all simulations), which would represent a scenario in which all species reach their flowering peaks on the same date. Accordingly, the more synchronous the flowering period of co-occurring species within a community, the greater its expected peak cumulative flowering intensity. Through this method, each species contributes to the cumulative intensity of the season in proportion to the intensity of its flowering on a given date. Consequently, this approach does not account for potential differences in the ecological importance of each species' flowering that may originate, for example, from variation among species in abundance or in the amount and quality of floral resources provided by individuals. Finally, we calculated the length of the season as the uninterrupted period during which at least 10 species were observed flowering, and the amplitude of the flowering peak as the maximum cumulative flowering intensity observed throughout the season.

Within each community, we measured flowering overlap among each pair of species (for 100 species, 4950 unique pairs within each community). To do so, we restandardized the flowering distribution of each species in a community so that it integrated to 1. Doing so ensured that the area under any segment of a population's flowering curve corresponded to the proportion of the total flowering effort that was observed during that period. Then, we measured the area under the intersection of the flowering curves of each pair of species. Therefore, the value of the flowering intersection between two species ranged from 0 (no overlap) to 1 (identical flowering curves).

Flowering season under warming

Prior to generating post-warming flowering distributions, each species was assigned temperature sensitivities for FFD (S_{FFD}) based on its mean flowering date and its community's $\beta_{S_{\mathrm{FFD}}}$, and temperature sensitivities for duration based on its community's $\overline{S}_D$ and β_{S_D} parameters (as well as its mean flowering date) (Figure 4i). S_{FFD} was assigned to each species using a normal distribution whose expected value for each species (i.e., its mean) was equal to the product between the slope parameter $\beta_{S_{\mathrm{FFD}}}$ and the species' mean flowering date. Prior to computing these expected values, we centered mean flowering dates around the median species in each community, which resulted in an among-species distribution of S_{FFD} centered around 0 for all simulated communities. As previously noted, we set mean S_{FFD} to 0 because its value determined the extent to which the entire flowering season advanced or delayed without altering its internal structure (Figure 2; Appendix S1: Figure S1).

Additionally, by doing this, we ensured that prewarming and postwarming flowering seasons for a community were centered around the same date, making it easier to isolate changes to the structure of the flowering season resulting from nonrandom variation in S_{FFD} among species. Once the expected S_{FFD} for each species was calculated, we obtained a randomized value around the predicted mean using a random error (i.e., SD) of 3 days/°C. The magnitude of the random error was selected to approximate the level of scatter observed around the relationship between S_{FFD} and mean flowering date among species reported in empirical studies (e.g., Cook et al., 2012; Mazer et al., 2013; Prevéy et al., 2019; Wolkovich et al., 2012).

When $\beta_{S_D} = 0$ (Figure 1a,b), S_D values were drawn randomly from a normal distribution with mean equal to $\overline{S}_D$ (ranging from −5 to 5 days/°C) and SD equal to

3 days/°C. In turn, for scenarios in which $\beta_{S_D} \neq 0$ (Figure 1c–h), S_D values for each species were obtained from a normal distribution with mean equal to $\overline{S}_D$ plus the product of β_{S_D} and mean flowering date for each species, and a SD of 3 days/°C.

Then, for each species in each community, postwarming FFDs and durations were generated based on (1) their initial FFDs and durations and (2) their S_{FFD} and S_D (Figure 2j) as:

$$\text{FFD}_{\text{post}} = \text{FFD}_{\text{pre}} + S_{\text{FFD}} \times \text{Warming}, \tag{1}$$

$$\text{Duration}_{\text{post}} = \text{Duration}_{\text{pre}} + S_D \times \text{Warming}. \tag{2}$$

We used a warming level of 2°C for all communities because, as many regions in North America have already experienced temperature increases of about 1.5°C, it reflects a scenario already occurring in warm years across the temperate zone (IPCC, 2023, Chapter 14). Moreover, some species have documented decreases in phenological sensitivity to temperature under warmer conditions (Fu et al., 2015), with declines often occurring beyond warming thresholds of 2°C (Guo et al., 2023). Therefore, the assumption that phenology and temperature are linearly related is reasonable when simulating responses under a warming level of 2°C. Nonetheless, we also ran simulations with temperature increases of 4°C to determine whether qualitatively different flowering season responses may emerge with higher temperature increases.

From the postwarming FFDs and durations, we obtained flowering termination and median dates that we used to generate flowering periods for each species through the same procedure described for prewarming communities (Figure 4j). We calculated the same attributes of the flowering season for communities after warming as we did for each prewarming community: cumulative flowering intensity throughout the season, season length, and peak amplitude, and pairwise flowering overlap among species (Figure 4k). Then, we measured warming-induced changes in the composition of flowering overlaps among species in each simulated community using the Bray–Curtis Dissimilarity Index (henceforth “BCI”) (Bray & Curtis, 1957). The BCI is typically used to measure the degree of dissimilarity in species composition between communities or sites, accounting for both differences in the identity of species present and their abundance. More broadly, however, the BCI measures the compositional differences between two sets of observations of categorical entities, and therefore can be broadly used to measure compositional dissimilarity for data other than species surveys. In our data, the categorical entities corresponded to each pair of species within a community (4950 unique pairs from among 100 unique species in each community) weighted by their degree of flowering overlap. Accordingly, the BCI measured compositional dissimilarity in flowering overlaps prewarming and postwarming for each simulated community accounting for changes in the identity and degree of overlap for each unique pair of species, with values of 0 indicating complete similarity prewarming and postwarming for a community (i.e., same identity and degree of overlap among species pairs) to 1 (complete mismatch in the identity of overlapping pairs).

Finally, we summarized how variation in S_{FFD} and S_D among species affected community-level flowering season outcomes under warming by aggregating results from simulated communities generated using each combination of $\beta_{S_{\text{FFD}}}$, $\overline{S}_D$, and β_{S_D} values (Figure 4l). Specifically, we calculated the range of outcomes—for each metric used—for the central 90% and the median of simulated communities for each pair of parameter values. To assess whether the influence of $\beta_{S_{\text{FFD}}}$, $\overline{S}_D$, and β_{S_D} differed depending on the distributions of FFDs among species in a community, changes in season length, peak amplitude, cumulative flowering intensity throughout the season, and turnover in species overlap were conducted separately for single-peak and bimodal simulated communities.

RESULTS

Scenario 1: Independent variation in S_{FFD} and S_D among species

Nonrandom variation among species in S_{FFD} and S_D (represented by $\beta_{S_{\text{FFD}}}$, $\overline{S}_D$, and β_{S_D}) determined the magnitude and direction of changes to the flowering season under warming. As expected (Figure 2), communities in which early species showed advances and late species delays in flowering ($\beta_{S_{\text{FFD}}} > 0$) tended to show season lengthening and less pronounced flowering peaks, whereas those showing the opposite patterns ($\beta_{S_{\text{FFD}}} < 0$) tended to show season contraction and amplified flowering peaks (Appendix S1: Figure S2a,b). Also expectedly, among communities in which S_D varied with species' mean flowering dates (i.e., $\beta_{S_D} \neq 0$), those in which early species tended to contract and late species to extend flowering showed season lengthening (or less shortening, depending on their $\overline{S}_D$) and less pronounced flowering peaks, whereas communities in which late species tended to contract and early species to extend flowering showed the opposite pattern (Appendix S1: Figure S2b,d). The range of variation among communities due to differences

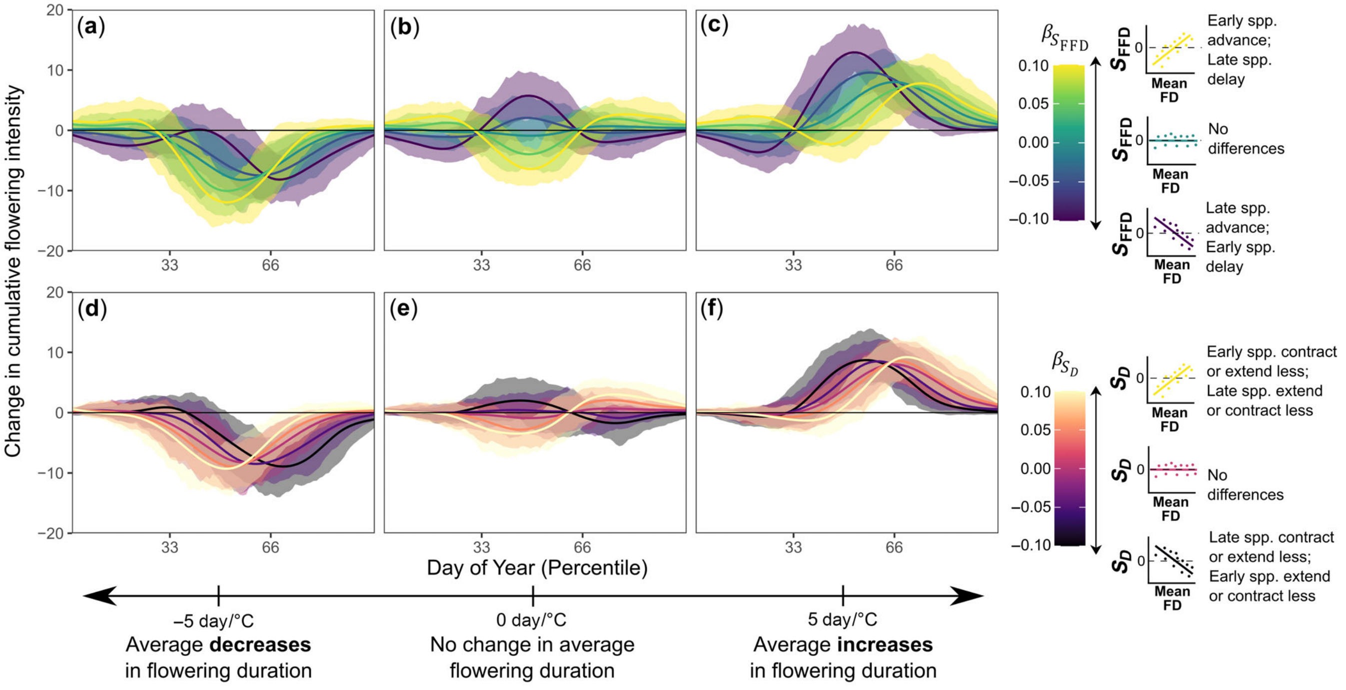

FIGURE 5 Changes in cumulative flowering intensity given uncorrelated variation between S_{FFD} and S_D within communities. The solid-colored lines in (a–c) correspond to the median change in cumulative intensity—across percentiles of the flowering season—due to warming compared to the prewarming baseline among simulated communities with the same combination of $\beta_{S_{\text{FFD}}}$ and $\overline{S}_D$ values (and for which $\beta_{S_D} = 0$; see Figure 1a,b). The solid-colored lines in (d–f) correspond to the median change in cumulative intensity due to warming compared to the prewarming baseline among simulated communities with the same combination of β_{S_D} and $\overline{S}_D$ values (and for which $\beta_{S_D} = 0$; see Figure 1c,d). The shaded regions indicate the 90% range of variation across communities grouped by each combination of parameter values. Scenarios of $\beta_{S_{FFD}} = 0$ or $\beta_{S_{\text{FFD}}} = 0$, respectively, correspond to communities in which S_{FFD} or S_D varied randomly (around the community mean) among species flowering successively throughout the season (middle curves in each panel). FFD, first flowering date.

in β_{S_D}, however, was much narrower than that generated by differences in $\beta_{S_{\text{FFD}}}$ (e.g., Appendix S1: Figure S2b vs. S2d). Ultimately, changes to the amplitude and date of seasonal flowering peaks relative to the prewarming baseline were determined by nonrandom variation in both S_{FFD} and S_D among species (Appendix S1: Figure S3), with both sensitivity types either offsetting or exacerbating the effects of the other.

Changes to the distribution of flowering diversity and abundance throughout the season—which we measured as cumulative flowering intensity, interpretable also as community-wide flowering synchrony—were jointly influenced by $\overline{S}_D$, $\beta_{S_{\text{FFD}}}$, and β_{S_D}, but their precise effects differed among the early, mid, and late seasons (Figure 5). For example, changes due to warming during the early flowering season (percentiles 0–33) differed only among communities with distinct values of $\beta_{S_{\text{FFD}}}$, with early-season flowering intensity increasing among communities in which FFDs advanced with warming among early species and delayed among later flowering species (note yellow line) and declining among communities exhibiting the opposite pattern (dark purple line). In contrast, cumulative changes during mid and late seasons varied widely with $\overline{S}_D$ and β_{S_D} (in addition to $\beta_{S_{\text{FFD}}}$) among communities. Communities showing average decreases in flowering duration among species under warming ($\overline{S}_D < 0$) tended to show decreases in cumulative flowering intensity during the mid and late seasons, with variation in $\beta_{S_{\text{FFD}}}$ mediating their magnitude (Figure 5a). In turn, communities whose species showed average increases in duration ($\overline{S}_D > 0$) showed increases in cumulative flowering intensity across much of the flowering season and whose magnitude was mediated by $\beta_{S_{\text{FFD}}}$ (Figure 5c). Variation in S_D throughout the season (β_{S_D}; Figure 5d–f) primarily impacted the timing of changes in cumulative flowering intensity mediated by $\overline{S}_D$. Among communities with $\overline{S}_D < 0$, those in which early species contracted flowering more than late species ($\beta_{S_D} > 0$) showed decreases in cumulative flowering intensity earlier in the season (yellow line) than communities in which late species contracted more ($\beta_{S_D} < 0$, purple line; Figure 5d). The converse was true among communities with $\overline{S}_D > 0$: those with $\beta_{S_D} > 0$ showed increases in cumulative flowering intensity later in the season (yellow line) than those with $\beta_{S_D} < 0$ (purple line; Figure 5f). Communities with bimodal flowering distributions

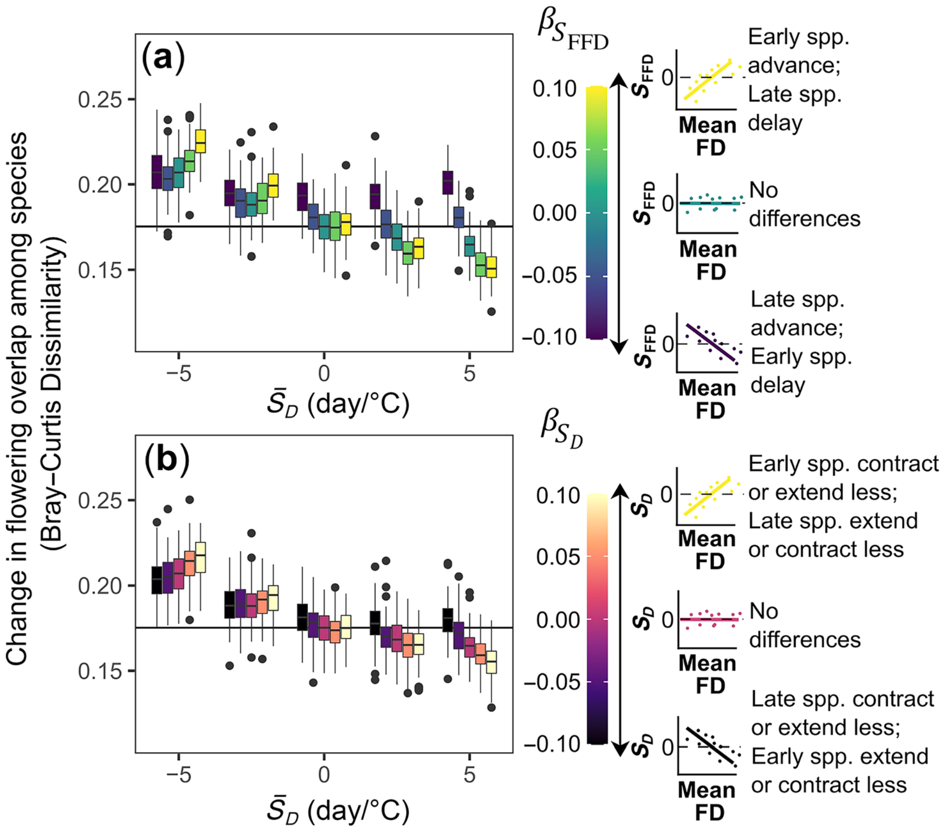

FIGURE 6 Changes in the composition of pairwise flowering overlaps among species due to warming across communities under scenarios of independent variation among species in S_{FFD} and S_D. In each community, change in the composition of flowering overlaps was measured using the Bray–Curtis dissimilarity index, with values of 0 corresponding communities with the same identity and degree of pairwise species overlaps, and values of 1 indicating complete dissimilarity in the identity of its pairwise overlap prewarming and postwarming communities. Colored boxplots in (a) and (b) depict the range of variation in turnover rates for communities varying in $\beta_{S_{\text{FFD}}}$ and β_{S_D}, respectively, with groups across the *x*-axis representing sets of communities with varying $\bar{S}_D$. In each panel, the horizontal solid black line indicates the degree of dissimilarity observed among communities showing no average changes in flowering duration (i.e., $\bar{S}_D = 0$), and random variation in both S_{FFD} and S_D among species throughout the season (i.e., $\beta_{S_{\text{FFD}}} = 0$ and $\beta_{S_D} = 0$). The lower and upper bounds of each box correspond to the 25th and 75th percentiles of the response's distribution for that combination of parameters. The upper and lower whiskers extend from the bounds to the largest or lowest values, respectively, no further than 1.5 times the distance between the 25th and 75th percentiles away from the bounds. Points indicate outlying data beyond this range. The lines in each box correspond to the median.

showed the same pattern of change in cumulative flowering intensity throughout the season as those with a single flowering peak (Appendix S1: Figures S4 and S5). Similarly, simulating flowering seasons under 4°C resulted in intensified but qualitatively identical patterns of change (Appendix S1: Figure S6).

Variation in S_{FFD} and S_D also altered the network of flowering overlaps among species (Figure 6). Communities showing average decreases in flowering duration among species ($\bar{S}_D < 0$) tended to show the greatest changes in the composition of flowering overlaps, with the greatest differences observed among those also showing flowering advances among early-flowering species and delays among late-flowering species (Figure 6a), or also showing flowering contractions among early species and flowering extension among late flowering species (Figure 5b). Nonetheless, the composition of flowering overlaps changed substantially even among communities showing no average changes in flowering duration among species ($\bar{S}_D = 0$) and showing no average differences in S_D and S_{FFD} among early versus late flowering species (i.e., those communities showing random variation in S_D and S_{FFD} among species, or $\beta_{S_{\text{FFD}}} = 0$ and $\beta_{S_D} = 0$; the middle group of Figure 5a,b).

The effects of nonrandom variation in S_{FFD} and S_D among species throughout the season (i.e., of $\beta_{S_{\text{FFD}}}$ and β_{S_D}) reversed for communities showing no average changes in flowering duration or showing average increases (i.e., $\bar{S}_D \geq 0$). For communities with $\bar{S}_D = 0$, flowering overlap dissimilarity was greatest in those showing flowering delays among early-flowering species and advances among late-flowering species, or showing flowering extension among early-flowering species and contraction among late-flowering species. Finally, communities showing averages increases in flowering duration $(\overline{S}_D > 0)$ tended to show the least species compositional changes in flowering overlap. However, as was the case for communities with $\overline{S}_D = 0$, compositional changes were least among those showing advances among early flowering species and delays and among late flowering species (Figure 6a) or showing flowering contractions among early-flowering species and extensions among late-flowering species (Figure 6b). These patterns remained consistent when measuring the degree of change in pairwise flowering overlaps based on turnover of interacting pairs (i.e., sum of new overlaps gained or former overlaps lost relative to the total number of overlapping pairs prewarming and postwarming; Appendix S1: Figure S7).

Scenarios 2 and 3: Correlated variation in S_{FFD} and S_D among species throughout the season

Covariation between S_{FFD} and S_D (mediated by β_{S_D} and $\beta_{S_{\mathrm{FFD}}}$) either attenuated or amplified changes in flowering intensity during the mid and late season relative to scenarios of uncorrelated sensitivities (Figure 7). Communities in which S_{FFD} and S_D were positively correlated throughout the season tended to show changes in cumulative flowering intensity of nearly twice the magnitude as those generated by equivalent scenarios (i.e., those with the same $\beta_{S_{\mathrm{FFD}}}$ and $\overline{S}_D$) but in which S_{FFD} and S_D varied independently among species (Figure 7a–e). In contrast, communities in which S_{FFD} and S_D were negatively correlated tended to show lesser changes in cumulative flowering intensity (of nearly half the magnitude) compared to those observed in scenarios in which S_{FFD} and S_D varied independently (Figure 7f–j) (see

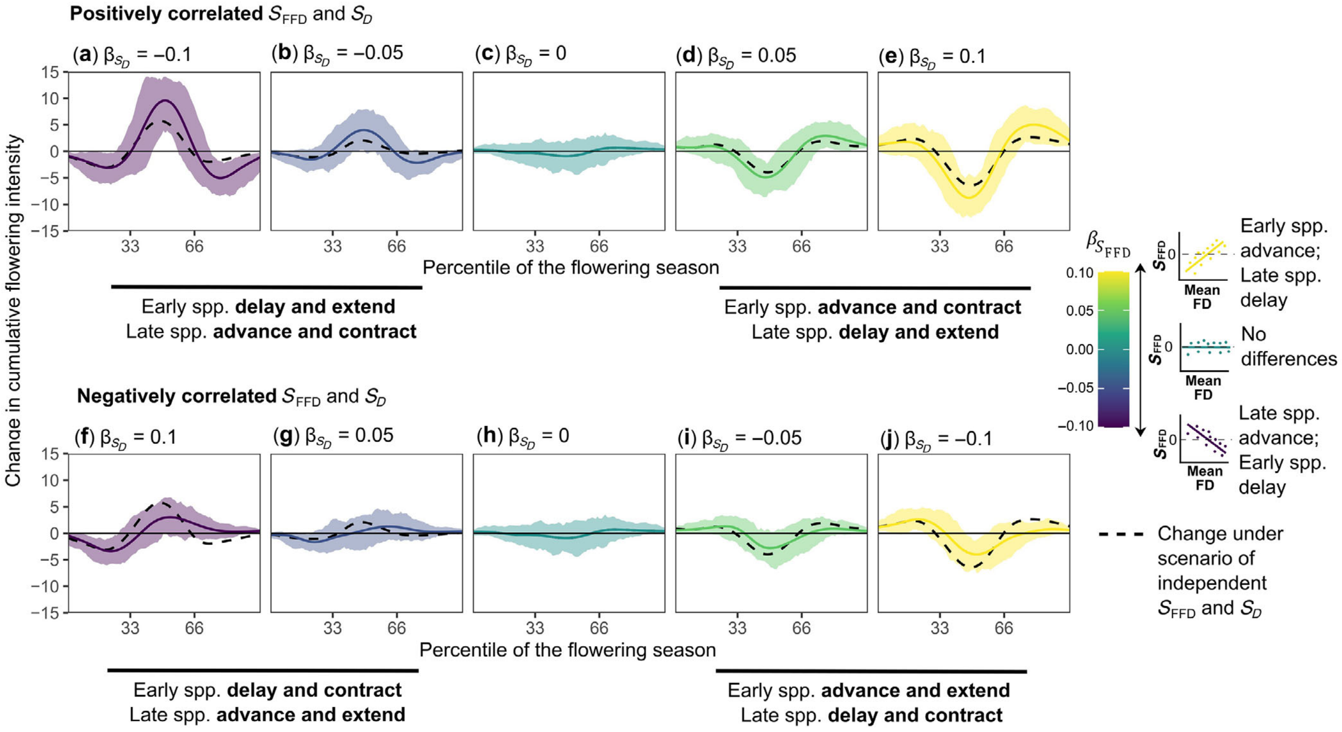

FIGURE 7 Warming-induced changes to cumulative flowering intensity due to correlated variation among species between S_{FFD} and S_D throughout the season (determined by $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D}) across communities with a single flowering peak. In each panel, solid-colored lines and shaded regions depict the median and 95% range of variation in cumulative flowering intensity change observed among communities sharing a combination of values $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D}. The black dashed lines in each panel depict a reference scenario of uncorrelated S_{FFD} and S_D, with $\beta_{S_{\mathrm{FFD}}}$ varying within columns but β_{S_D} coefficient equal to 0 for all panels. (a–e) Scenarios in which S_{FFD} and S_D are positively correlated among species throughout the season (i.e., $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D} have the same magnitude and the same sign). (f–j) Scenario in which S_{FFD} and S_D are negatively correlated among species throughout the season (i.e., $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D} have the same magnitude but opposite sign). $\overline{S}_D$ was set to 0 days/°C. Scenarios of $\beta_{S_{\mathrm{FFD}}} = 0$ or $\beta_{S_{\mathrm{FFD}}} = 0$, respectively, correspond to communities in which S_{FFD} or S_D varied randomly (around the community mean) among species flowering successively throughout the season. FFD, first flowering date.

Appendix S1: Figure S8 for results for all combinations of $\beta_{S_{\mathrm{FFD}}}$ and β_{S_D}). Correlated S_{FFD} and S_D for communities with $\overline{S}_D \neq 0$ also generated amplified or attenuated differences in the degree of change between the mid and late seasons (for positive and negative correlations, respectively) (Appendix S1: Figures S9 and S10).

A positive correlation between S_{FFD} and S_D (i.e., β_{S_D} and $\beta_{S_{\mathrm{FFD}}}$ with the same sign) resulted in greater changes in season length and peak flowering intensity compared to equivalent scenarios in which S_{FFD} and S_D varied independently (i.e., those with the same $\beta_{S_{\mathrm{FFD}}}$ and $\overline{S}_D$ but $\beta_{S_D} = 0$) (Appendix S1: Figure S11a). In contrast, negatively correlated S_{FFD} and S_D (i.e., β_{S_D} and $\beta_{S_{\mathrm{FFD}}}$ with different sign) resulted in lesser changes to season length and peak flowering intensity (Appendix S1: Figure S11b). Correlated S_D and S_{FFD} also impacted the degree of change in the network of flowering overlaps among species within a community (Appendix S1: Figure S12). Specifically, positively correlated S_{FFD} and S_D resulted in greater compositional changes in flowering overlap compared to a scenario of uncorrelated S_D and S_{FFD} (Appendix S1: Figure S12a–e). In turn, negatively correlated S_D and S_{FFD} attenuated rates of composition change under warming relative to those expected under independent sensitivities (Appendix S1: Figure S12f–j).

DISCUSSION

Characterizing among-species variation in the sensitivity of flowering onset and duration is essential for resolving community-level responses to warming

Flowering sensitivity to temperature differs widely among co-occurring species; however, phenological datasets that include flowering duration and that sample sufficient species to characterize flowering dynamics of entire communities are rare (Willis et al., 2017), hindering generalizations of how species variation in temperature responses will scale to alter community-level flowering patterns.

Here, we illustrate the wide range of community-level flowering outcomes that could result from nonrandom variation among species in the temperature sensitivity of both FFDs (S_{FFD}) and flowering duration (S_D). Specifically, using simulations, we show that three empirically documented forms of among-species variation in sensitivity within a community—the magnitude and direction of change in S_{FFD} with the mean flowering date of a species ($\beta_{S_{\mathrm{FFD}}}$), the mean S_D of a community ($\overline{S}_D$), and the magnitude and direction of change in S_D with the mean flowering date of a species (β_{S_D})—may have profound impacts on the postwarming structure of the flowering season both independently and interactively. While variation in S_{FFD} affected the structure of the entire flowering season, variation in S_D predominantly impacted its mid and late portions. This suggests that among-species variation in S_{FFD} and S_D will have distinct impacts on flowering-dependent ecological processes that occur at different times within the season. Moreover, the severity of simulated flowering reassembly depended on whether S_{FFD} and S_D were positively or negatively correlated among sequentially flowering species throughout the season, which respectively amplified or attenuated responses relative to scenarios of independent sensitivities. These results further demonstrate that models that solely evaluate changes in onset or median flowering dates of a population are insufficient to fully capture these dynamics, emphasizing the importance of also accounting for the temperature sensitivity of phenological terminations for understanding community-level flowering responses to climate change.

Changing flowering seasons will likely have profound but uncertain consequences from populations to communities

Redistribution of floral resources within a community—such as that observed in many of our simulation scenarios—might result in cascading ecological consequences within an ecosystem. For example, the availability and variety of floral resources throughout the season within a community strongly mediate the diversity and abundance of its pollinators (Fründ et al., 2010; Potts et al., 2003; Scheper et al., 2015). Studies of specialist bees have demonstrated that individuals typically travel longer distances for lesser pollen and nectar rewards during periods of floral scarcity (Minckley, 1994; Pope & Jha, 2018), and local scarcity of floral resources has been directly linked to decreases in brood provisioning and pollinator population declines in some systems (Schenk et al., 2018; Williams & Kremen, 2007). Although measuring the broad resource base of generalist pollinators is more challenging than for specialists, the population sizes of the former are generally positively correlated over space and time with the local density of floral resources (Potts et al., 2003; Scheper et al., 2015). Therefore, if the flowering intensity of a community decreases, or if pollinators are phenologically mismatched with either their specialized mutualist plants (in the case of specialists), or with overall peaks in floral abundance (in the case of generalists), we might expect significant declines in pollinator abundance or species diversity.

In turn, net decreases in floral abundance or phenological synchrony between plants and their mutualists partners can negatively impact plant fitness through their effects on density-dependent processes such as pollinator attraction, fertilization and genetic recombination, seed dispersal, or predator attraction and satiation (Bergamo et al., 2020; Carlo & Morales, 2008; Elzinga et al., 2007, Jones & Comita, 2010; Nilsson & Wastljung, 1987). Additionally, the pollen of many wind-pollinated tree and grass species across the temperate zone is allergenic to humans (García-Mozo, 2017; Oh, 2022; Songnuan, 2013). Therefore, depending on the degree to which variation in S_{FFD} and S_D among allergenic species matches the broader community-level pattern, the substantial redistribution of flowering periods illustrated in many of our simulation scenarios could significantly alter the length and intensity of the allergy season.

The precise consequences of broad community-level changes, however, are not straightforward to predict. Our simulations describe how the temporal distribution of floral resources might respond to warming, but not their overall abundance. Changes in net pollen and nectar production among species caused by warming might amplify or attenuate the ecological impacts of the changes in the temporal distribution of floral resources. For example, if among-species variation in S_{FFD} and S_D decrease the density of co-flowering species within a given season, then a lower production of floral resources among species that remain active during that period would exacerbate the consequence of phenologically driven reductions in the richness of flowering species (e.g., where changes in cumulative flowering intensity are negative in Figures 5 and 7), whereas increases in floral resource production might attenuate such consequences.

In many taxa, fitness may be most strongly affected by a small number of species interactions. For example, specialist pollinators might rely on one or a few plant species for floral resources. Consequently, the persistence of specialist pollinator populations under warming depends on the degree to which they remain synchronized with a subset of plant species whose flowering shifts might not mirror the community-level pattern. Generalist florivores and pollinators might shift their phenology at different rates than the plant community (Memmott et al., 2007), and depending on initial patterns of synchrony, these changes could result in periods of activity overlapping with a greater or lesser diversity and abundance of floral resources. Moreover, many plant communities are dominated by a handful of species (e.g., Sherry et al., 2007) whose flowering responses could deviate from the broader community pattern. Finally, while flowering synchrony among species can mediate density-dependent ecological processes, whether such processes increase or decrease plant reproductive success can vary among species and ecological contexts (Elzinga et al., 2007), further complicating simple predictions of the ecological consequences of changes to the flowering season.

Considering these complexities, evaluating the effects of warming on the quality and quantity of floral resource productions across species is essential for advancing our ability to predict the consequences of changes to the flowering season. Similarly, to illuminate the broader ecological consequences of their results, studies of flowering responses to climate should consider the local abundance and floral output (or other important attributes such as allergenic potential) of the species under examination.

Warming-induced changes to the flowering season will differ among temperate communities, but critical knowledge gaps remain

In North America, temperate and semiarid plant communities consistently show greater advances in response to warming among species flowering early in the season compared to those flowering later (i.e., $\beta_{S_{\mathrm{FFD}}} > 0$) (e.g., Ramirez-Parada et al., 2024). Therefore, the simulations presented here predict that temperate communities should typically show a longer flowering season under warming, with a greater proportion of floral resources becoming available during its early and late portions, resulting in decreased flowering peaks (Figure 5a–c). In contrast, patterns of variation in S_{FFD} among species throughout the season can vary in direction and magnitude among communities at high latitudes and elevations (Prevéy et al., 2019). Nonetheless, greater advances in FFD among late-flowering than early-flowering species appear to be common in such systems ($\beta_{S_{\mathrm{FFD}}} < 0$) (e.g., Prevéy et al., 2019), which would result in a shorter flowering season with a higher proportion of floral resources becoming available around its median (Figure 5a–c). Therefore, our results imply that such well-documented variation in $\beta_{S_{\mathrm{FFD}}}$ among communities will generate distinct impacts on the structure of the flowering season in different regions.

The warming responses of the mid and late flowering seasons, however, were also highly sensitive to the structure of among-species variation in S_D within a community (i.e., $\overline{S}_D$ or β_{S_D}; Figure 5d–f), for which geographic variation has not been extensively studied. Therefore, although recent research has established that communities often differ in both $\overline{S}_D$ and β_{S_D} (e.g., Nam & Kim, 2020; Zhou et al., 2022), it is unclear whether and how these parameters vary systematically across plant assemblages that occupy different climate zones or that differ in the relative abundance of species across functional groups. Furthermore, flowering onset and termination can be mediated by different abiotic factors. For example, while flowering onset is often controlled by abiotic cues triggering the start or resumption of reproductive development (Amasino, 2010), the termination of flowering may be mediated by constraints on the timing of subsequent phenophases, or by different cues, including the onset of physiologically stressful conditions, resource depletion, or seasonal cooling (Desclaux & Roumet, 1996; Ettinger et al., 2018; Zohner et al., 2023). Therefore, it is likely that S_{FFD} and S_D will show different patterns of variation across regional floras, precluding the categorization of many biomes into the scenarios explored in the simulations presented here, and consequently, general predictions of how the structure of the flowering season will change under warming across regions.

The degree of reassembly of flowering overlaps within a community was mediated interactively by nonrandom variation among species in the sensitivity of flowering onset and duration (Figure 6). Consequently, as geographic differences in patterns of among-species variation in S_D within communities are not well characterized, it is hard to determine a priori which regional floras should show the greatest degree of flowering reassembly under ongoing warming. Moreover, the degree of change in community-level flowering patterns depended on the degree and direction of correlation between S_{FFD} and S_D among species (Figure 7; Appendix S1: Figure S12). As such, determining the ecological contexts in which S_{FFD} and S_D might be negatively correlated, independent, or positively correlated among successively flowering co-occurring species will be key to forecasting community-level phenological reassembly due to ongoing climatic change.

CONCLUSIONS

Despite complexities in predicting the ecological consequences of community-level flowering shifts and limited knowledge of among-species variation in S_D across communities, our simulations demonstrate that $\beta_{S_{\mathrm{FFD}}}$, $\overline{S}_D$, and β_{S_D} might have profound impacts in community-level flowering patterns. To date, among-species variation in S_{FFD} and S_D has been predominantly studied in temperate communities in North America and Europe (Piao et al., 2019), and a disproportionate attention to phenological onset dates has limited assessments of flowering duration to comparatively few species. Expanding the biogeographic scope of empirical studies quantifying patterns of variation in sensitivity among species and a greater research focus on flowering duration are essential steps towards understanding how the structure of the flowering season might continue to change across geographically, ecologically, and climatically distinct plant assemblages. The worldwide abundance, vast temporal and taxonomic scope, and increasing digital availability of herbarium records provide rich data with which to estimate these parameters (Park et al., 2024; Ramirez-Parada et al., 2022; Willis et al., 2017). Additionally, determining the biomes in which advances or delays in flowering among early and late flowering species are typically associated with contractions or extensions in flowering duration would help determine where—and how frequently—we should observe each of the patterns demonstrated in our simulations.

Finally, although we focused solely on temperature and flowering phenology, our simulation design can be extended to examine any phenophase (e.g., leaf out, fruiting), and to account for the independent and interactive effect of multiple climate variables for any hypothesized forms of structural variation in climate sensitivity among species in a community (e.g., nonlinear variation in S_{FFD} and S_D among flowering species). Recent research suggests that differences in sensitivity among species between the early, mid, and late seasons might be common among taxa spanning several trophic levels (Roslin et al., 2021). Therefore, the effects of among-species variation in sensitivity in mediating community-level responses to warming described here might characterize the modes of phenological change due to warming not only for flowering, but for a much wider range of ecological phenomena.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

No data were collected for this study. All novel code used to generate the simulated data for this study (Ramirez-Parada, 2024) is available from Figshare: https://doi.org/10.6084/m9.figshare.24750204.

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SUPPORTING INFORMATION

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

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