



Bee species exhibit different phenological trajectories in communities of annual flowering plants in the genus *Clarkia*

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ABSTRACT

Phenological matching between the timing of flowering and pollinator activity is critically important for the persistence of pollination systems globally. Phenological mismatch between plants and their insect pollinators can occur if flowering and adult insect activity do not occur simultaneously. There is evidence that the phenological trajectories vary among bee species, but little has been done to compare these trajectories with the phenology of the corresponding floral community. In this work, we use daily pan trapping across nine different annual *Clarkia* (Onagraceae) plant communities that vary in *Clarkia* species composition to estimate the phenological trajectory (within-season abundance curve) of the two most abundant bee pollinators - *Lasioglossum incompletum*, a generalist, and *Hesperapis regularis*, a *Clarkia* specialist - over the course of a *Clarkia* flowering season in California USA. *Clarkia* flower at the end of the winter annual growing season when all other winter annual plants have senesced, and therefore are phenologically separate from other flowering plants. We find that *Hesperapis* pollinator abundances follow the same phenological trajectory as *Clarkia* floral abundances in all community types. In contrast, *Lasioglossum* abundances do not track *Clarkia* floral abundance through time. Our results demonstrate that *Clarkia* exhibit closer phenological matching with *Hesperapis* than with *Lasioglossum*. These findings imply that pollinator communities may not respond monolithically to changes in the environment. Future research should study the phenological trajectories of plants and pollinators in different systems to determine if this pattern is common and repeatable.

Introduction

The rise in mean global temperature has been associated with phenological shifts in many species [14,45,50]. For example, phenological advancement has occurred in such life history events as bud burst, insect emergence, and egg laying dates [1,12,34] in association with events brought on by climate change such as earlier snowmelt and extended warm seasons [32,34]. In communities of flowers and their insect pollinators, changes in the timing of species' life history events have the potential to disrupt pollination because plant flowering and pollination must occur simultaneously in order for these interactions to be successful [1,32]. The temporal interruption of species interactions, a phenomenon known as phenological mismatch, may cause local extinctions and failure of key ecological functions [49]. Studies have shown cases in which phenological mismatch in plant-pollinator communities is already occurring due to climate change, and have suggested they are likely to increase in frequency and intensity [13,16,21,31,46,48].

The vast majority of flowering plant communities rely on unique assemblages of pollinators, and bees in particular are responsible for

pollination services of terrestrial plant species worldwide [25]. Previous studies of the impact of climate change on plant and bee phenology have demonstrated shifts in the timing of flowering, adult bee activity, or both, rendering these mutualisms vulnerable to phenological mismatch [1,14,34,39,50]. Bee diversity may act as a buffer against plant community collapse [19,22,30]: in the face of phenological mismatch, if bees exhibit species-specific responses to changing environmental conditions driven by species-specific phenologies, then the likelihood of complete phenological mismatch between a flowering plant and its suite of bee pollinators will be lower than if bees do not exhibit species-specific phenologies [1]. This is because even if some pollinator phenologies shift drastically, others may not, thereby affording plants (and their bee pollinators) continued reproductive assurance.

Recent work from Stemkovski et al. [44] shows that pollinator species do exhibit species-specific phenologies. Less addressed in the literature is that the potential for mismatch may depend on the extent to which suites of plants and pollinators are specialized on each other. For example, there is some evidence that bees specialized on a particular floral resource are on the same phenological 'clock' as that resource,

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whereas more generalist bees may respond to cues to track overall flowering in their region [27]. This aspect of bee and plant ecology is important for understanding how species-specific variation is associated with phenological shifts in the future: if the timing of a bee species' activity consistently matches that of a particular floral resource due to mutual specialization, then they likely respond to similar cues that control their flight/flowering activity, thereby reducing the risk of phenological mismatch [6,13,33,37].

Because bee species can have unique phenologies and be affected by environmental change differently [4,42,44], it is important to now build an understanding of how bee phenologies differ within and across plant-pollinator systems. Little is known about phenological differences among bee species from the same flowering communities, particularly according to how specialized they are on various floral resources [4,20,32,42]. In this study, we use communities of showy, outcrossing annual flowering plants in the genus *Clarkia* (Onagraceae) and two bee pollinators in the Kern River Canyon (Kern County, California) to understand how bee phenologies can differ within the flowering season of a specific floral resource. Importantly, the four *Clarkia* species sympatric in this region co-flower at the end of the winter annual growing season, a time when all other annual plants have senesced and there is no significant perennial floral resource; as such *Clarkia* make up the vast majority of plants in flower when they flower and are generally phenologically isolated. These *Clarkia* rely on a shared suite of bees for pollination services ([24,28], Singh 2014). Some of these bees are oligoleges (specialized on the *Clarkia* genus) and exhibit morphological and behavioral traits that help them collect *Clarkia* pollen [24], whereas other species visiting *Clarkia* are apparent non-specialists that still visit *Clarkia* and carry *Clarkia* pollen [17,28], as it is the dominant genus of flowering plants when in flower. Accordingly, the distinct flowering phenology of *Clarkia* allows us to evaluate if its pollinators' phenological trajectories vary with respect to their level of *Clarkia* specialization.

Due to its flowering phenology in the region and the varied specialization of its pollinators, the unique natural history of this *Clarkia* system allows us to investigate differences among bee species' phenological trajectories through the *Clarkia* flowering season. To do this, we use daily pan trapping in *Clarkia* communities to assess the phenologies of the two most abundant bee species in the system: *Lasioglossum incompletum* (Halictidae) and *Hesperapis regularis* (Melittidae). *Hesperapis regularis* exhibits specialization on *Clarkia*, while *Lasioglossum incompletum* is a known generalist. We hypothesize that *Lasioglossum incompletum* and *Hesperapis regularis* will exhibit different phenological trajectories through time, where the shape of the abundance curve through time and the date of peak abundance should be different between the two taxa. Furthermore, we predict that the abundance curves of *Hesperapis* bees and *Clarkia* flowers should coincide through the season and have similar dates of peak abundance due to the specialization of *Hesperapis regularis* on *Clarkia*, whereas the *Lasioglossum incompletum* and *Clarkia* abundance curves will not match.

Methods

System

There are four common and abundant outcrossing species of *Clarkia* that are sympatric in the Kern River Canyon in Kern County, California: *C. cylindrica* ssp. *clavicarpa* (Jeps.) Lewis & Lewis, *C. speciosa* ssp. *polyantha* Lewis & Lewis, *C. unguiculata* Lindl., *C. xantiana* ssp. *xantiana* A. Gray. The *Clarkia* in this region co-occur in annual plant communities comprising one to four species of *Clarkia*. Both bee species in this study, *Hesperapis regularis* (Melittidae) and *Lasioglossum incompletum* (Halictidae) are highly common in the area of *Clarkia* sympatry and active during *Clarkia* flowering periods (Singh 2014). *Hesperapis regularis* is very specialized on *Clarkia*. It has scopae of thinly distributed hairs that are adapted for accommodating clumps of large *Clarkia* pollen grains con-

nected by viscin threads [24,28]. Furthermore, *Hesperapis* also exhibits a vibratory 'pollen dance' when foraging for pollen on *Clarkia* to harvest pollen from the slow-dehiscing anthers of *Clarkia*, and it is reported to be locally highly adapted to the food resources in *Clarkia* communities [24]. On the other hand, *Lasioglossum incompletum* is not a known *Clarkia* specialist, and does not exhibit morphological or behavioral adaptations to *Clarkia* pollen or anther dehiscence [24]. Irrespective of their specialization on *Clarkia*, both taxa collect and carry *Clarkia* pollen when *Clarkia* is flowering ([28], James unpublished data).

Experimental design

We used daily pan trapping to collect bees at nine *Clarkia* communities in the Kern River Canyon, from 9 May to 13 June 2016 on a nine-day rotation. We sampled one site per day for the duration of the *Clarkia* flowering period, and each site was visited 4 times over the course of the season. Though all four *Clarkia* species overlap in flowering phenology, two of the species (*C. unguiculata* and *C. cylindrica*) begin flowering earlier than the other two (*C. xantiana* and *C. speciosa*; Eisen et al. 2019, [18]). To capture the widest possible phenological variation in communities throughout the entire *Clarkia* flowering season, we sampled three common multi-species community types in the Kern River canyon — those comprising *C. cylindrica* and *C. unguiculata* (CU); *C. speciosa* and *C. xantiana* (SX); and all four species (CUSX; Fig. 1; Table 1). We selected *Clarkia* communities that were discrete spatially and separated from each other by at least a 0.5 km of linear distance (but almost always more; Fig. 1). As both bee species are small-bodied, we were reasonably certain that bees were not flying between sites [53]. In the case of *Hesperapis regularis*, MacSwain et al. [24] reported that bee populations are self-contained within *Clarkia* communities and bees do not venture far from their home communities.

At each site, we placed four 20-meter-long permanent transects through *Clarkia* patches that remained in the same locations through the study. We made an effort to sample across the whole site, and transects were at least 10 m apart, and usually farther apart. Along each transect, we placed four 30 ml (1 ounce, 4.5 cm diameter at the top and 3.2 cm tall) pan traps at five-meter intervals (two yellow and two blue traps). Pan traps of this size are thought to perform as well as larger pan traps and to be less susceptible to evaporation in arid environments [8]. On sampling days, we filled the traps with soapy water between 7:00AM and 8:00AM. We returned in the afternoon to collect the traps' contents between 3:00PM and 4:00PM. We also measured *Clarkia* floral density along the transects in the afternoon by placing a ½ m² quadrat on either side of the transect at four-meter intervals along the transects and recording the number of open flowers of each *Clarkia* species in the quadrats. After collection, bees were washed, pinned, and identified [15,25]. *Lasioglossum* specimens were identified by Joel Gardner (University of Manitoba). After bee identification, we selected the most abundant bee species in our samples for analysis, one a *Clarkia* specialist, and one generalist: *Hesperapis regularis* was the most common *Clarkia* specialist, and *Lasioglossum incompletum* was the most common generalist. We captured ten additional bee species in our samples in 2016, but chose not to include them in the present analysis due to their lower abundances through time.

Table 1
Species composition and site names of locations sampled.

Site Type	Species Present	Site Names
CU	<i>C. unguiculata</i> , <i>C. cylindrica</i>	Mile marker 26.09; BAR 25.91; Little Tree
SX	<i>C. xantiana</i> , <i>C. speciosa</i>	Site 8; Green Rock East; Black Gulch Trail Sign
CUSX	<i>C. unguiculata</i> , <i>C. cylindrica</i> , <i>C. xantiana</i> , <i>C. speciosa</i>	Lower China Gardens; Democrat; Mill Creek

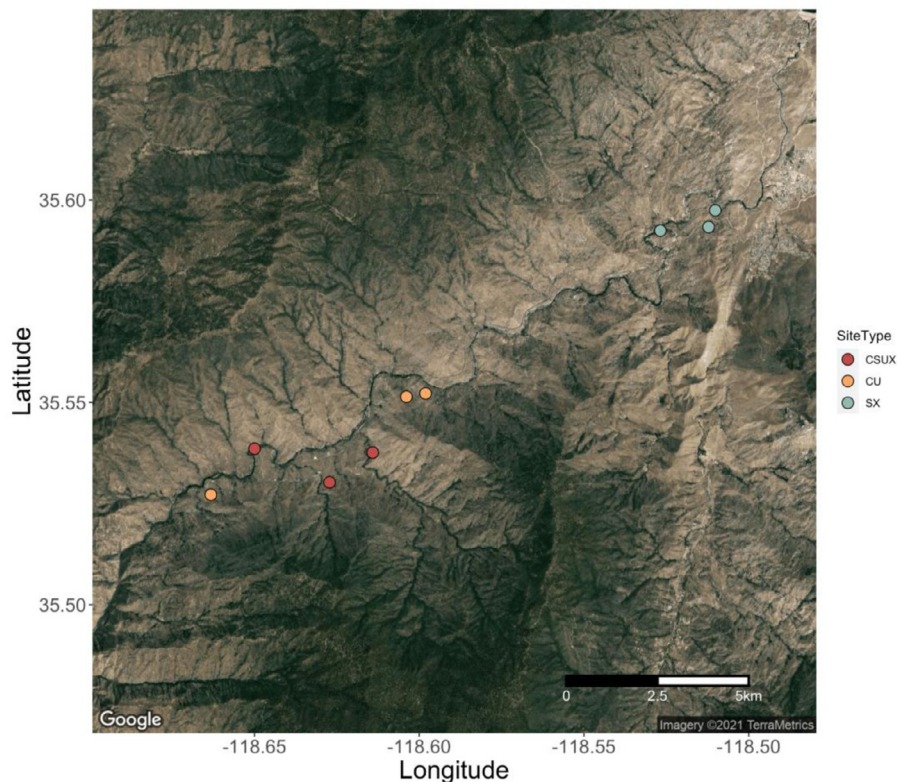


Fig. 1. Map of sampling locations. Point color indicates the phenology and *Clarkia* species composition of the site.

Data and statistical analysis

We analyzed bee and floral abundance through time using generalized linear mixed effects models (GLMMs). The floral abundance response variable was the total number of open flowers in the quadrats placed along the transects (flowers per 4m²), and the bee abundance variables were the total number of each bee species recovered in the 16 pan traps per day. To predict *Clarkia* floral abundance and estimate the phenology curve for each community type, we built two candidate models. The first included an interaction of two fixed effects: community type (CU, CUSX, or SX) and date (days since the start date). The second model included an interaction of community type, date, and the second-order polynomial of date. The polynomial term allowed for a potential increase, peak, and then decrease of abundance in each community type as the season progressed. We used a Poisson error distribution with a log link function and included two random effects: site identity, and an observation level random effect to account for overdispersion in the count data. We used AICc to compare model fit, and used the model with the lower AICc score to generate *Clarkia* abundance predictions.

To predict daily bee abundance for both bee species, we built two candidate models for each dataset: the first included the interacting fixed effects of community type and date, and the second included the interaction of community type, date, and a second-order polynomial of the date to allow for a potential peak. We included models without a second-order effect to determine if the species exhibited a peak or not during the period of time that we were collecting samples. We also included an additive fixed effect of centered and standardized floral abundance (number of flowers counted per day) in these models to account for variation in bee abundance that could be explained by variation in floral abundance rather than date alone. We used a Poisson error distribution with a log link function, and included the site identity as a random effect in all candidate models. As before, we calculated the candidate models' AICc scores. Using the best-fit models (lowest AICc scores), we determined the predicted date of peak abundance for *Clarkia* flowers, *Hesperapis regularis*, and *Lasioglossum incompletum* by (1) find-

ing the maximum predicted abundance values for each taxon, and then (2) extracting the day that corresponds to these values. All predictions were limited to the sampled *Clarkia* flowering period. We also estimated marginal and conditional pseudo R² values to determine how well the models explained variation in abundance data, where marginal pseudo R² is the value for only the fixed effects in the model, and conditional pseudo R² is the value for the model including random effects. All analyses were performed in R version 3.5.3 (R [36]) using the lme4, bootpredictlme4, and MuMIn packages [2,3,10].

Results

In total, we captured 250 bees over the course of 34 sampling days. Of these, 92 bees were *Hesperapis regularis* and 49 were *Lasioglossum incompletum*. We did not sample for the entirety of the fourth round of sampling, stopping two days short (that is, not sampling the two remaining sites in the fourth round) due to the decline to zero *Clarkia* floral abundance in all community types by day 34. The best-fit model of *Clarkia* abundance explained a high amount of variation in the data (Marginal pseudo R²=0.90, Conditional pseudo R²=0.91). Predictions from the best-fit models of *Clarkia* abundance indicate that floral abundance is best explained with a second-order polynomial term in the model, and follows a hump shape throughout the course of the season (Table 2). The *Clarkia* SX community type had significantly lower floral abundances than the CU community ($p<0.001$; Table S1) and the CUSX community (data not shown), but the CU and CUSX communities exhibited similar floral abundances (Table S1).

As in the *Clarkia* model, the best-fit model of *Hesperapis regularis* abundance explained a high amount of variation in the data (Marginal pseudo R²=0.79, Conditional pseudo R²=0.91). This model included a second-order polynomial term (Table 2), indicating a nonlinear relationship between abundance and date. As with floral abundance, predictions from the best-fit *Hesperapis regularis* models indicate that the nonlinear relationship is hump-shaped through the season (Table 2, Fig. 2). The best-fit model of *Lasioglossum incompletum* did not include a polyno-

Table 2

Model comparisons for predicting *Clarkia*, *Hesperapis regularis*, and *Lasioglossum incompletum* abundance. All models were GLMM with Poisson error distributions. Best-fit models have a dAICc score of zero.

Model	dAICc	Degrees of Freedom	Weight	Residual Degrees of Freedom
<i>Clarkia</i> Floral Abundance ~ Day * Site Type + Day ² * Site Type + (1 Sample ID) + (1 Site ID)	0.0	11.0	1.0	26
<i>Clarkia</i> Floral Abundance ~ Day * Site Type + (1 Sample ID) + (1 Site ID)	27.7	8.0	<0.001	23
<i>Hesperapis regularis</i> Abundance ~ Day * Site Type + Day ² * Site Type + Floral Abundance + (1 Site ID)	0.0	11.0	1.0	23
<i>Hesperapis regularis</i> Abundance ~ Day * Site Type + Day ² * Site Type + Floral Abundance + (1 Site ID)	10.5	8.0	0.0	26
<i>Lasioglossum incompletum</i> Abundance ~ Day * Site Type + Floral Abundance + (1 Site ID)	0.0	8.0	0.8	23
<i>Lasioglossum incompletum</i> Abundance ~ Day * Site Type + Day ² * Site Type + Floral Abundance + (1 Site ID)	3.0	11.0	0.2	26

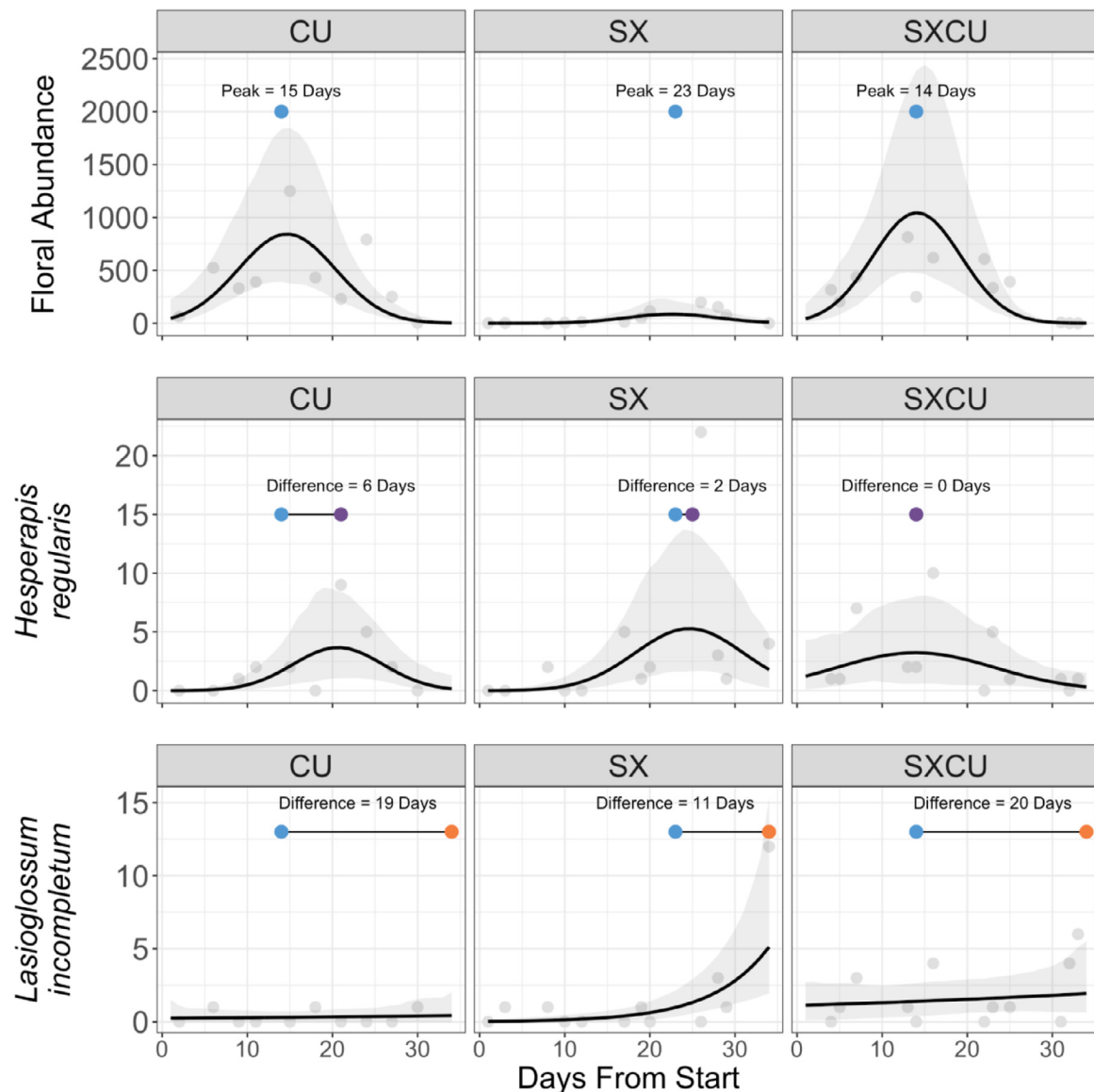


Fig. 2. Predicted phenological trajectories of *Clarkia* abundance (top row), *Hesperapis regularis* abundance (middle row), and *Lasioglossum incompletum* abundance (bottom row) in each site type: CU (left column), SX (middle column) and CUSX (right column). Predicted abundance values all represent back-transformed model-predicted daily abundance. Blue points in all panels indicate the best-fit model predictions for peak *Clarkia* floral abundance. Purple points in the middle row indicate the best-fit model predictions for peak *Hesperapis regularis* abundance, and orange in the bottom row are the best-fit model predictions for peak *Lasioglossum incompletum* abundance. Line segments between the points show the difference between the predicted peak of floral abundance and predicted peaks of bee abundance. Curved lines are the model predictions for abundance through the season, or what we call phenological trajectories. Gray ribbons are 95% confidence intervals, and gray points are actual counts.

mial, and instead described a linear relationship between *Lasioglossum incompletum* abundance and date in all site types. This model explained a moderate amount of variation in the *Lasioglossum incompletum* abundance (Marginal pseudo $R^2=0.59$, Conditional pseudo $R^2=0.67$). In all site types, the relationship between *Lasioglossum incompletum* abundance and floral abundance increased with date (Table 2, Fig. 2, Table S1).

The predicted days of peak floral abundance varied among site types, where CU and CUSX community types exhibited peak abundances at 15 days and 14 days, respectively, while floral abundance peaked at 23 days in SX communities (days are reported as days from the start of the sampling period). The predicted peak for *Hesperapis regularis* pollinator abundance occurred 6 days after peak floral abundance in the CU sites, 2 days after in the SX sites, and on the same day in CUSX sites. By contrast, the predicted peak of *Lasioglossum incompletum* was on the final census day in all site types (19, 11, and 20 days later than peak *Clarkia*, respectively).

Discussion

Although phenological shifts are being reported in plant-pollinator communities, we are currently unable to predict the occurrence or magnitude of these shifts [5,7,49,51]. Recent research shows that bee phenology responds to environmental changes based on species' functional traits [44], but we still do not know which species are most at risk for phenological mismatch, or the impact this will have on pollinator assemblages and their host plants' survival [21,44,51]. One reason for our lack of knowledge is that there is little information on differences in phenology among pollinator species from the same communities. In our study of *Clarkia* plant-pollinator communities, we focused on a group of plants that flower at the end of the winter annual growing season in California, providing the abundant food resource to bees before seasonal dry down. We found that the phenology of *Hesperapis regularis*, a *Clarkia* specialist, closely matches *Clarkia* flowering phenology, while the phenology of *Lasioglossum incompletum*, a generalist *Clarkia* pollinator, does not. Our work corroborates and adds to findings in other systems [38]. We propose that because pollinators exhibit different phenological trajectories in this system, they may differ in the extent to which their phenologies shift in response to climate change.

Previous studies have suggested that bee phenologies might differ due to bee species' unique foraging and reproductive needs [13,29,40,47,52]. In our study, we addressed this by comparing *Clarkia* abundance curves over a growing season to those of the two most abundant bee pollinators. Predictions from the best-fit models for *Hesperapis regularis* show that peak *Hesperapis regularis* abundance occurs in the middle of the *Clarkia* flowering season, and that *Hesperapis regularis* peaked at each site type very close to the peak *Clarkia* abundance at those site types. Such a pattern indicates that *Hesperapis regularis* populations are very closely phenologically matched to local *Clarkia* abundance. Future studies based on more frequent sampling at all sites are needed to confirm the close matching between *Hesperapis regularis* and *Clarkia*. In contrast to *Hesperapis regularis*, the best-fit model for *Lasioglossum incompletum* did not exhibit a hump-shaped abundance peak during *Clarkia* flowering. In fact, *Lasioglossum incompletum* abundance increased over time, suggesting that we captured only a portion of its abundance curve. Specifically, we may have only captured a portion of this species' phenological trajectory: this particular species is not known to specialize on any particular floral resources (including *Clarkia*), and therefore may peak at a different time in the year.

Our study constitutes evidence that bee species from the same flowering communities differ in their within-season abundance curves through time. The next step is to understand the mechanisms that cause such differences in bee species' phenological trajectories, which will help determine the link between variation in bee species' intra-annual phenological trajectories and variation in their inter-annual responses to climate change. This is because the drivers or mechanisms explaining species-level differences in abundance curves within a year may also

be what drive changes in phenologies between years as climate change progresses. For example, environmental cues such as temperature and soil humidity affect the timing of adult emergence of different bee species and therefore cause variation in bee species' abundance through time within growing seasons [13,27,35,47]. Studies have suggested that species-specific differences in emergence cues will cause species phenologies to differentially respond to climate change- in particular, specialist pollinators might not experience phenological mismatch to the same extent that generalists do [26,41]. Therefore, though our study shows that different pollinators have species-specific phenological trajectories that may be related to their level of specialization on *Clarkia*, more research is needed on the emergence biology of *Hesperapis regularis* and other *Clarkia* specialist pollinators (e.g. *Diadasia angusticeps*, a *Clarkia speciosa* specialist), especially in contrast to other more generalist species such as *Lasioglossum incompletum*. In addition, multi-year studies of *Clarkia* flowering phenology, which can shift inter-annually based on rainfall and temperature (*pers. obs.*), and of pollinator flight phenology would help pin down the degree of matching for specialist vs. generalist pollinators. If *Hesperapis regularis* and other specialists exhibit phenological matching with *Clarkia* by responding to the same cues for emergence (as in other systems; [27]), while generalists such as *Lasioglossum incompletum* do not, this would suggest that specialists will be less vulnerable to phenological mismatch with *Clarkia*. Whether a phenological mismatch with *Clarkia* affects generalist pollinators would depend on the role of *Clarkia* in supporting their populations.

Finally, evidence of species-specific phenological trajectories has implications for how pollinator communities might phenologically fracture as the environment changes. The community-level ramifications of phenological mismatch are unclear for most plant-pollinator communities, but changes in pollinator assemblages will likely result in a long-term fitness decline of both host plants and pollinators due to declines in pollination efficiency and redundancy [9]. In the *Clarkia* system, we know *Hesperapis regularis* is a more effective *Clarkia* pollinator than *Lasioglossum incompletum* due to its morphological and behavioral specialization on *Clarkia* [11,24]. Thus, if *Hesperapis regularis* populations declined for any reason, *Clarkia* communities would almost certainly also decline as a result of pollinator limitation to reproduction [29]. In the communities we studied, such declines might occur first in the SX site type, where total *Clarkia* abundance is consistently lower than in the other two site types [23,43].

Finally, our research provides some insight into how different species of bees interact phenologically with their host plants but is only a snapshot from one year and should be expanded. Work in plant-pollinator systems in the future should continue to investigate the species-specific diversity of responses to environmental changes in a variety of plant communities and incorporate information on bee population abundance both over the course of growing seasons and across years.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Author Contributions

ACA wrote the original draft and edited; ARMJ conceptualized the study, performed data analysis, designed the methodology, collected data, made visualizations, wrote the original draft, and reviewed and edited; EM curated the data, wrote the original draft, and reviewed and edited; MAG conceptualized the study, secured funding, supervised, performed project administration, and reviewed.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.ecochg.2021.100031.

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