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ARTICLE

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Phenological mismatch is less important than total nectar availability for checkerspot butterflies

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Abstract

Changes in phenology are a conspicuous fingerprint of climate change, leading to fears that phenological mismatches among interacting species will be a leading cause of population declines and extinction. We used quantile regression to analyze museum collection data and estimate changes in the phenological overlap of Baltimore checkerspot butterflies and 12 common nectar plant species over several decades in two geographic regions. We combined these museum data with field estimates of each species' flower density and nectar sugar production to estimate changes in resource availability caused by shifts in phenological overlap. Phenological overlap (measured as the proportion of plant flowering during the flight period of an average butterfly) decreased through time, primarily because the flowering period of nectar plants was longer, but the flight period of butterflies was shorter in recent years. Our study was also motivated by the hypothesis that phenological mismatches may be more severe in the southern region due to a midsummer dearth in floral resources, but this hypothesis was not supported by our data. Although phenological overlap was somewhat smaller in the southern region, changes in overlap through time were similar in both regions. When phenological overlap was weighted by nectar sugar production of different species, the overlap increased in the southern region but decreased in the northern region (the opposite of our prediction). Overall, nectar resources were much more abundant at study sites in our northern region than in our southern region, possibly due to differences in land management. Our study demonstrates the complexities of phenological mismatch of interacting species and highlights that phenological changes may have small impacts on population viability.

KEYWORDS
climate change, *Euphydryas phaeton*, floral resources, habitat management, herbarium, historical collections, latitudinal gradient, phenological overlap, phenology, pollinator conservation

INTRODUCTION

Changes in phenology—the timing of annual life cycle events such as dormancy and reproduction—are a long-standing and prominent biological fingerprint of climate change (Parmesan & Yohe, 2003; Walther et al., 2002). In and of themselves, phenological changes could be a sign of resilience to climate change, in the sense that organisms are adjusting the timing of life cycle events to new environmental conditions. However, these changes could also lead to mismatches in the timing of activity of interacting species (see, e.g., Kudo & Cooper, 2019; Visser et al., 1998). Such phenological mismatches are of particular concern in trophic interactions because phenological sensitivity tends to decrease with trophic level (Thackeray et al., 2016). As expected with different temperature sensitivities among species, the phenological overlap of consumers and their resources has changed in many pairs of interacting species (Kharouba et al., 2018), leading to concerns that phenological mismatches could exacerbate direct effects of climate change, leading to further species declines or extinctions.

In spite of the potential importance of phenological mismatches, recent studies have also raised several caveats. Most of what we know comes from studies that relate slopes of the timing of peak activity of a consumer to the timing of peak activity of its resource (Kharouba et al., 2018). However, phenology is a distribution of activity, not a point estimate, and overlap could be changing more or less than expected from changes in peak activity dates (Inouye et al., 2019; Ramakers et al., 2020). Furthermore, perfect phenological overlap may not be optimal. In one recent meta-analysis, consumers had higher fitness if they emerged before their resource, possibly because early emergence allowed preemptive consumption (Kharouba & Wolkovich, 2023). Perfect phenological overlap may also not be necessary because there may be times when resource abundance exceeds consumers' needs (Ramakers et al., 2020). Finally, for consumers of many resources, the significance of changes in phenological overlap with different resources depends on the quality and quantity of each different resource (Twining et al., 2022).

In light of these concerns, butterflies and their nectar plants are in many ways an ideal model system for detecting and understanding the consequences of phenological mismatch. Nearly all butterflies consume nectar from plant flowers as adults, as well as consuming plant leaves as larvae. Although larval feeding is typically specialized to some extent in butterflies, most butterfly species are nectar generalists as adults. Butterfly species obtain 35%–70% of the carbon used in reproduction from their adult nectar diet (O'Brien et al., 2004). Furthermore, butterflies and nectar plants are most easily identified during the life stages at which they interact (adult butterflies and plants in flower). Therefore, it is possible to extract their historical timing from scientific collections (Kharouba et al., 2014; Vellend et al., 2013). From historical data, we know that phenological shifts of interacting butterflies and nectar plants are likely; Kharouba and Vellend (2015) used collections to quantify sensitivity to temperature and found that both groups tended to have earlier phenology in warmer years and locations, but that the sensitivity of plants was stronger than that of butterflies. Finally, there is good reason to believe that phenological overlap of butterflies and nectar predicts resource availability to butterflies because plants produce new crops of nectar every day (cf. Kearns & Inouye, 1993; Schultz & Dlugosch, 1999); unlike consumers of a fixed resource pool (e.g., birds eating caterpillars or caterpillars eating leaves), it would not be possible to preemptively consume resources by arriving earlier than the resource emerges.

Here, we evaluate spatial and temporal variation in the phenological overlap of Baltimore checkerspot butterflies (*Euphydryas phaeton*) and 12 commonly used nectar plant species. In this study, we compare historical (1980s) and contemporary (2010s) phenological overlap of Baltimore checkerspots and nectar plants. Inference about change in phenology through space and time is based on historical specimens throughout the Baltimore checkerspot range and is compared to phenology and plant abundance at study sites in eastern Massachusetts and Maryland (approx. 600 km southwest of the Massachusetts sites). Baltimore checkerspots are thought to be declining in Maryland, especially in the eastern half of the state where our study sites were located (Frye et al., 2013), but they are generally stable in abundance in Massachusetts (Breed et al., 2013; Michielini et al., 2021). Geographic variation in population viability has been attributed to climate change (Abarca et al., 2019; Frye et al., 2013) and possibly geographic differences in larval host breadth (specifically, pre-diapause oviposition on a common non-native plant; Michielini et al., 2024). We speculated that phenological overlap with nectar plants could also contribute to differences in population viability because the Baltimore checkerspot flight period is in mid-summer; if early-season plants are advancing in phenology and late-season plants are delaying flowering (Pearson, 2019; Sherry et al., 2007), longer growing seasons in the Maryland sites could lead to fewer flowering plants during the Baltimore checkerspot flight season (cf. Aldridge et al., 2011; Timberlake et al., 2019).

In this study, we use a combination of historical specimens and field data to evaluate the magnitude of phenological shifts between Baltimore checkerspots and their

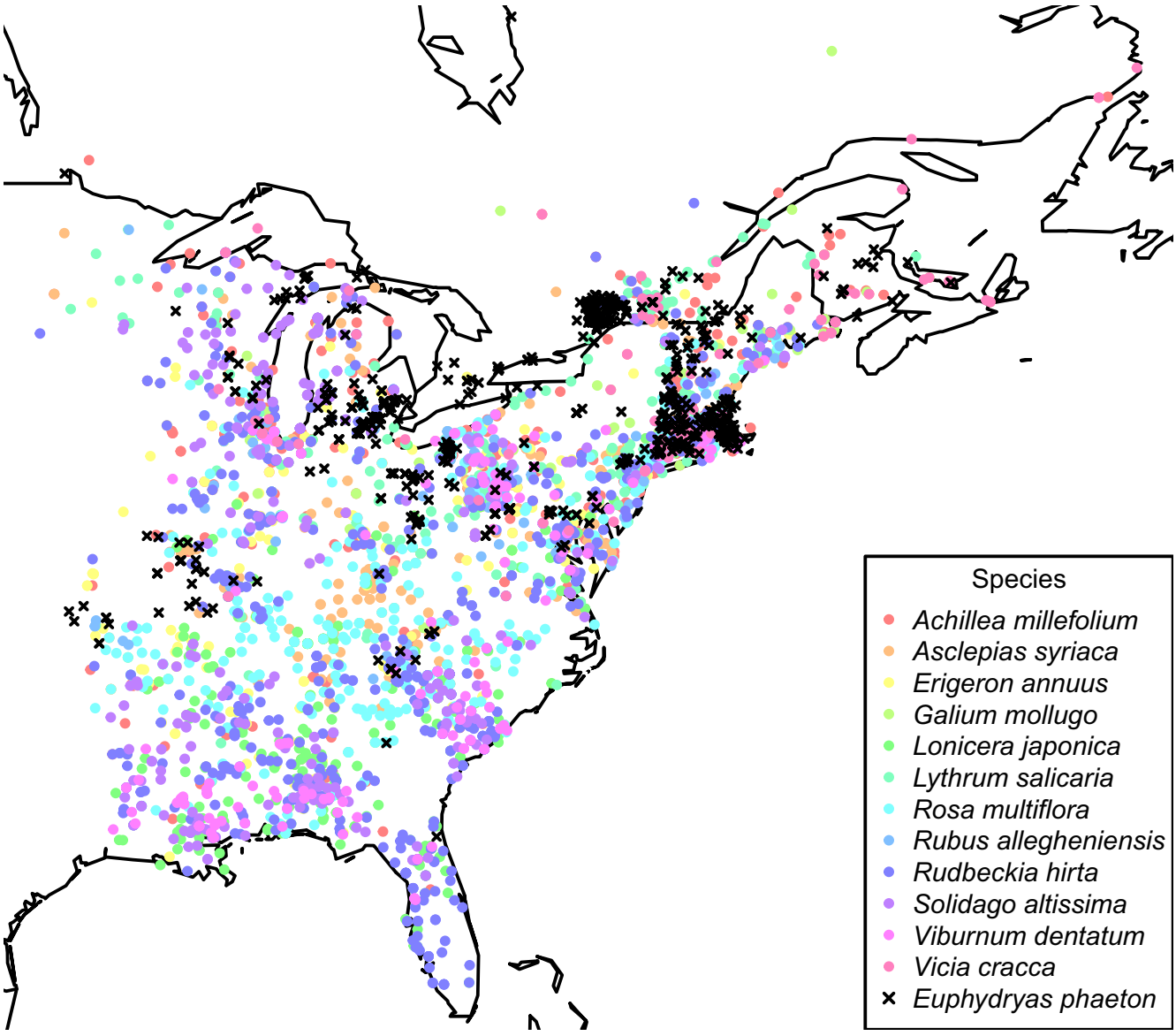

FIGURE 1 Map of herbarium and zoological museum specimens used for quantile regression of collection dates.

nectar plants, and whether these differed between our northern (Massachusetts) and southern (Maryland) study regions. Using historical specimen data from throughout eastern North America (Figure 1), we asked (1) How does the distribution of activity of each species vary as a function of latitude and year? We predicted that phenology would, in general, be earlier in warmer time periods and places, that is, earlier in more recent years and at the Maryland field sites. Following Kharouba and Vellend (2015), we also predicted that plants would show greater phenological sensitivity than butterflies. Following Aldridge et al. (2011) and Sherry et al. (2007), we predicted that early-season plants would flower earlier, and late-season plants would flower later in warmer periods and places, leading to a greater decrease in phenological overlap in Maryland than Massachusetts. Next, we combined historical specimen data with contemporary field data on plant abundances and nectar sugar production to ask (2) How does the overlap of checkerspots and nectar differ among regions, and how has this overlap changed through time? In a simple sense, one would expect changes in nectar availability to mirror changes in relative phenology of butterflies and plants, especially because we considered only phenological change, and used static estimates of plant abundance and nectar production from modern field surveys (in part, this decision was based on data availability; see *Methods* and *Discussion*). However, this might not be the case if, for example, the phenology of abundant plant species was changing differently than rare ones (cf. Inouye et al., 2019). Thus, in a general sense, we expected the same patterns in nectar overlap as in phenological shifts if the flowering times of all nectar

plant species were changing in similar ways, but possibly different patterns if species differed both in their importance as nectar resources and in their phenological responses.

In the process of setting up the fieldwork, it became apparent that nectar plant communities and nectar abundance differed considerably among sites and regions. In other butterfly species, among-site differences in nectar plants can be as important for butterfly abundance as among-site differences in larval host plant densities (Murphy et al., 1984; Schultz & Dlugosch, 1999). Therefore, we also used our field data to ask (3) How does the abundance of flowers and total nectar production differ among sites and regions, especially in relation to the magnitude of changes in phenological overlap? This last question is important for contextualizing the importance of changes in phenology. If effects of phenological change are large relative to other sources of variation, it would broadly support the notion that changes in phenology are a leading driver of population viability. If effects of phenological change are small relative to other sources of variation in nectar sugar, it suggests that they are less important as a driver of population viability, might be overwhelmed by other sources of environmental heterogeneity, and could potentially be mediated by habitat management.

METHODS

Study system

Baltimore checkerspots are a nymphalid butterfly native to wetlands and wet meadows of Eastern North America. The Baltimore checkerspot is univoltine and lays eggs in mid-summer which overwinter as fourth instar caterpillars, emerging in the subsequent spring. Pre-diapause caterpillars feed primarily on a single hostplant, *Chelone glabra*, though in some parts of their range, they also feed on *Plantago lanceolata* (Bowers et al., 1992). Post-diapause caterpillars feed on a wider range of plant species, but still perform best on their pre-diapause host plant species (Arriens et al., 2021; Brown et al., 2017). Adult butterflies nectar on a variety of native and non-native flowers, often in upland meadows adjacent to wetlands with their larval host plants. In a closely related species (*Euphydryas chalcedona*), about one-third of the sugar used for reproduction came from nectar consumed by adult butterflies (O'Brien et al., 2004), indicating the importance of nectar for population viability.

We conducted field research in two geographic regions: eastern Maryland, near the warm thermal limit of the Baltimore checkerspot's geographic distribution; and eastern Massachusetts, near the thermal center of the Baltimore checkerspot's geographic distribution. In Maryland, where the Baltimore checkerspot is relatively rare, we chose three field sites on private land based on where staff from the Maryland Department of Natural Resources were aware of recent checkerspot population sightings: Alesia (lat, lon = 39.7, −76.8), Norrisville (39.7, −76.5), and White Hall (39.7, −76.6). In Massachusetts, where Baltimore checkerspots are relatively common, we chose three field sites based on sightings from the Massachusetts Butterfly Club: Appleton (42.6, −70.9), Harvard (42.5, −71.6), and Upton (42.2, −71.7). For reference, our study regions differ in average annual temperature by ~3°C, and the average temperature change over time during the time period of our historical data was ~1.25°C in both regions (https://www.ncei.noaa.gov/access/monitoring/climate-at-a-glance; accessed January 3, 2024).

Historical specimen data

We used historical museum specimen records to analyze trends in phenology of Baltimore checkerspots and their nectar plants from 1980 through the present. We initially compiled all available records and cleaned them as described in the following paragraphs (see Appendix S1: Table S1). After building the database, we analyzed data from 1980 through 2018 for plants and 2017 for Baltimore checkerspots (the years of data compilation) to evaluate recent trends in phenology through time. We chose 1980 because it was the start of the period of rapid climate warming (Kharouba et al., 2018; Pielke, 1998). We also filtered plant specimens to include observations only from the eastern United States and Canada, specifically, US states east of (and including) the north–south line from Minnesota through Louisiana, and Canadian provinces east of (and including) eastern Manitoba (Figure 1). This region overlaps broadly with the Baltimore checkerspot's geographic range and is a region in which temperature decreases roughly monotonically from south to north (Crozier & Dwyer, 2006; Dorian et al., 2023).

Data for Baltimore checkerspot records were downloaded from the Symbiota Collections of Arthropods Network (https://scan-bugs.org/portal/), the Global Biodiversity Information Facility (https://www.gbif.org), Butterflies and Moths of North America (https://www.butterfliesandmoths.org), and eButterfly (http://www.e-butterfly.org). Specimen data were also recorded in person from the collections at the American Museum of Natural History, the University of Connecticut, the University of Wisconsin-Madison, and the McGuire Center for Lepidoptera and Biodiversity. Data from the collections at the Smithsonian National Museum of Natural History were provided by Jayme Lewthwaite. We

selected a set of nectar plant species for herbarium analysis based on knowledge of common plants that co-occurred with Baltimore checkerspots from observations during past fieldwork (e.g., Arriens et al., 2021; Brown et al., 2017; Brown & Crone, 2016): *Achillea millefolium*, *Asclepias syriaca*, *Galium mollugo*, *Rudbeckia hirta*, *Solidago altissima*, and *Vicia cracca*. Additional species (primarily non-native) were added to have overlap with the most common species at our field sites (see *Methods: Contemporary field data*): *Erigeron annuus*, *Lonicera japonica*, *Lythrum salicaria*, *Rosa multiflora*, *Rubus allegheniensis*, and *Viburnum dentatum*. Data for herbarium records were downloaded from the Consortium of Northeastern Herbaria (http://portal.neherbaria.org/portal/) and the Consortium of Midwest Herbaria (http://midwestherbaria.org/portal/). All analyses were based only on records that were documented by historical specimens in museum or herbarium collections; we excluded non-documented and exclusively photodocumented observations from all data sources.

For both plant and butterfly specimens, only specimens in the appropriate life stage (adult butterflies and plants known to be flowering) and that had a specific day, month, and year of collection were used. If a range of dates was given, the median day was used (i.e., July 12 for July 11–13). We only used specimens that had a county-level or more precise location. For records where coordinates were not provided, we used either GEOLocate (https://www.geo-locate.org/default.html) or Google Maps (https://www.google.com/maps) to find the coordinates. Due to the amount of time required to find precise coordinate locations, many records were georeferenced to the county center. All of the coordinates, both provided and calculated, were checked to make sure that they were in the proper state and county and recalculated if needed. If we were unable to find coordinates for a specimen, it was removed. If there were multiple specimens collected from the same day and place, only one was included in the dataset, to avoid including multiple, nonindependent, observations from single collection events. To remove duplicates, we removed any specimens that were collected on the same day and at the same latitude and longitude (within 0.1°) as another of that species. To remove specimens for which the life stage may have been mis-coded, we removed any records where the plants were listed as flowering (without a picture provided) but were over a week earlier/later than the earliest/latest confirmed flowering specimen of that species.

Contemporary field data

We conducted floral abundance surveys in 2019 at three sites in Maryland and three sites in Massachusetts. Each site included 9–10, 20-m × 1-m belt transects. At sites in Massachusetts, where Baltimore checkerspot sightings were common, transect locations were selected by randomly sampling locations from areas where Baltimore checkerspot butterflies were sighted in the previous year (L. M. Brown et al., unpublished data) and then randomly generating a compass direction for the other end of the transect. At sites in Maryland, where Baltimore checkerspot sightings were relatively rare, transects were established by spacing points evenly throughout the site and then randomly generating a compass direction for the other end of the transect. We surveyed most sites four times during the field season; one site (Appleton in MA) was surveyed five times. For each survey, we counted all open non-graminoid flowering units in each transect. The flowering unit for each species was determined based on what was most intuitive to count for that plant. A unit was one flower for species where flowers grow singly, one inflorescence for species with inflorescences, and one flower head for composite species. Hereafter, we refer to the species included in these counts as "nectar plants" for simplicity, although we only sampled nectar on a subset of species and did not verify that all non-graminoid flowers produced nectar.

We estimated the total number of flowering units and total nectar sugar production for each common species following the general approach used by Schultz and Dlugosch (1999). Their equation for total sugar produced for species j (TS_j) is:

$$TS_j = S_j \times D_j \times F_j \times U_j \quad (1)$$

where S_j is the daily sugar produced in milligrams, D_j is the number of days a flower is open (i.e., producing nectar), F_j is the number of flowers per flowering unit, and U_j is the number of flowering units per square meter at the site. We estimated flowering units per square meter (U_j) for each species from transect data, using the maximum recorded density at each site. For each species, we counted the number of total possible flowers per unit (F_j), including buds and open flowers, for at least 15 units. We determined the number of days that an individual flower stayed open (D_j) by labelling at least 15 buds of each species and then tracking them each day until they were done flowering. Samples were collected opportunistically during other fieldwork, so were irregularly distributed across sites and regions (Appendix S1: Table S2).

To collect nectar samples to calculate daily sugar produced per flower (S_j), we used the "washing" method (Morrant et al., 2009). In brief, after bagging flowers for 24 h, we removed a flower and shook it for 1 min in a vial with 5 mL of distilled water. The flower was then

removed from the vial and the vials were stored for laboratory analysis. Sample vials were stored in a cooler while still in the field and temporarily stored in a standard freezer until transfer to a −80°C freezer. We analyzed the sugar content of nectar samples in the laboratory following the anthrone reagent method used by Schultz and Dlugosch (1999). In cases with composite flowers or very small flowers where several were washed together, the total sugar was divided by the number of open flowers/florets washed. As above, samples were collected opportunistically during fieldwork (Appendix S1: Table S2).

To calculate sugar availability, we multiplied each element of the above equation to get the TS_j for each species. For analyses of focal plant species (our Question 2), we summed U_j and TS_j across the 12 focal plant species. For analyses of overall plant communities (our Question 3), our aim was to include all common plant species (see *Results*).

Data analyses

All analyses were conducted in R version 4.2.2 (R Core Team, 2022). We evaluated each research question as described below.

How does the distribution of activity of each species vary as a function of latitude and year?

We used quantile regression, implemented with the quantreg package in R (Koenker, 2022), to evaluate phenological trends in the historical data. Quantile regression analyzes trends at different points in the distribution of observations through time in a way that is robust to changes in sample size (Michielini et al., 2021). We evaluated average trends through time for the 0.1 quantile of observations (hereafter, the "onset" of the butterfly flight or plant flowering period), the 0.5 quantile (the median of both periods), and the 0.9 quantile (hereafter, the "end" of the butterfly flight or plant flowering period). For this analysis, we fit statistical models with latitude, year, and their interaction as predictor variables. SE and *p*-values were calculated using the SE = "boot" option, with the number of bootstrap replications set to 2000. We analyzed responses across all species and three quantiles (39 *p*-values) for each predictor variable: year, latitude, and the year × latitude interaction. To account for multiple comparisons, we used Fisher's method to test whether the distribution of *p*-values across nectar plant species differed significantly from the null expectation (see Sokal & Rohlf, 1995, their box 18.1). We interpreted patterns for predictors (i.e., year, latitude, or year × latitude interaction) only when Fisher's test indicated significant results across species. Since there was no overall evidence for a significant year × latitude interaction (see *Results*), inferences about trends were made from models with the interaction removed. To calculate average trends in the onset, median, and end of flowering across nectar plant species, we used linear models to estimate mean values of the slopes at each quantile across species. Here, the slope of each species was the response variable and quantile was the predictor variable; slopes were weighted by the inverse of their SE to account for differences in precision of each estimate.

For nectar plants, we compared trends in phenology of early- versus late-flowering species by analyzing the slope of flowering date with respect to year and latitude (estimated from the statistical models) in relation to flowering season (estimated as the median flowering date in 1980 at the mean specimen latitude of 40.3° N, extracted from quantile regression) across the 12 nectar plant species. We implemented these analyses using two separate linear models: slope of phenology versus latitude in relation to median flowering date and slope of phenology versus year in relation to median flowering date. All models included the slopes of the 0.1, 0.5, and 0.9 quantiles as the response and the median flowering date, quantile value, and their interaction as predictors. In plain language, the main effects of quantiles accounted for possible differences in the slopes of onset, median, and end dates of activity, and the interactions tested whether changes in the onset, median, and end of flowering were related to median phenology in different ways. In these statistical models, the slope for each nectar plant species was a single data point, and species were weighted by the inverse of the SE of their slope estimates.

How does the overlap of checkerspots and nectar differ among regions and through time?

We used a second set of quantile regression models as a descriptive technique to estimate activity curves for each species at specific latitudes and in specific years (see Figure 2 for overview). These curves were the basis for estimating phenological overlap of butterfly flight and nectar plant flowering (our Question 2). The analysis consisted of fitting a set of quantiles evenly distributed over a standard normal probability density function: 0.023, 0.067, 0.159, 0.309, 0.500, 0.691, 0.841, 0.933, and 0.977. For each quantile, we fit a quantile regression model with year and latitude as predictors and day of year (DOY) as the response (Figure 2a,b); the interaction was removed from these models because it was not

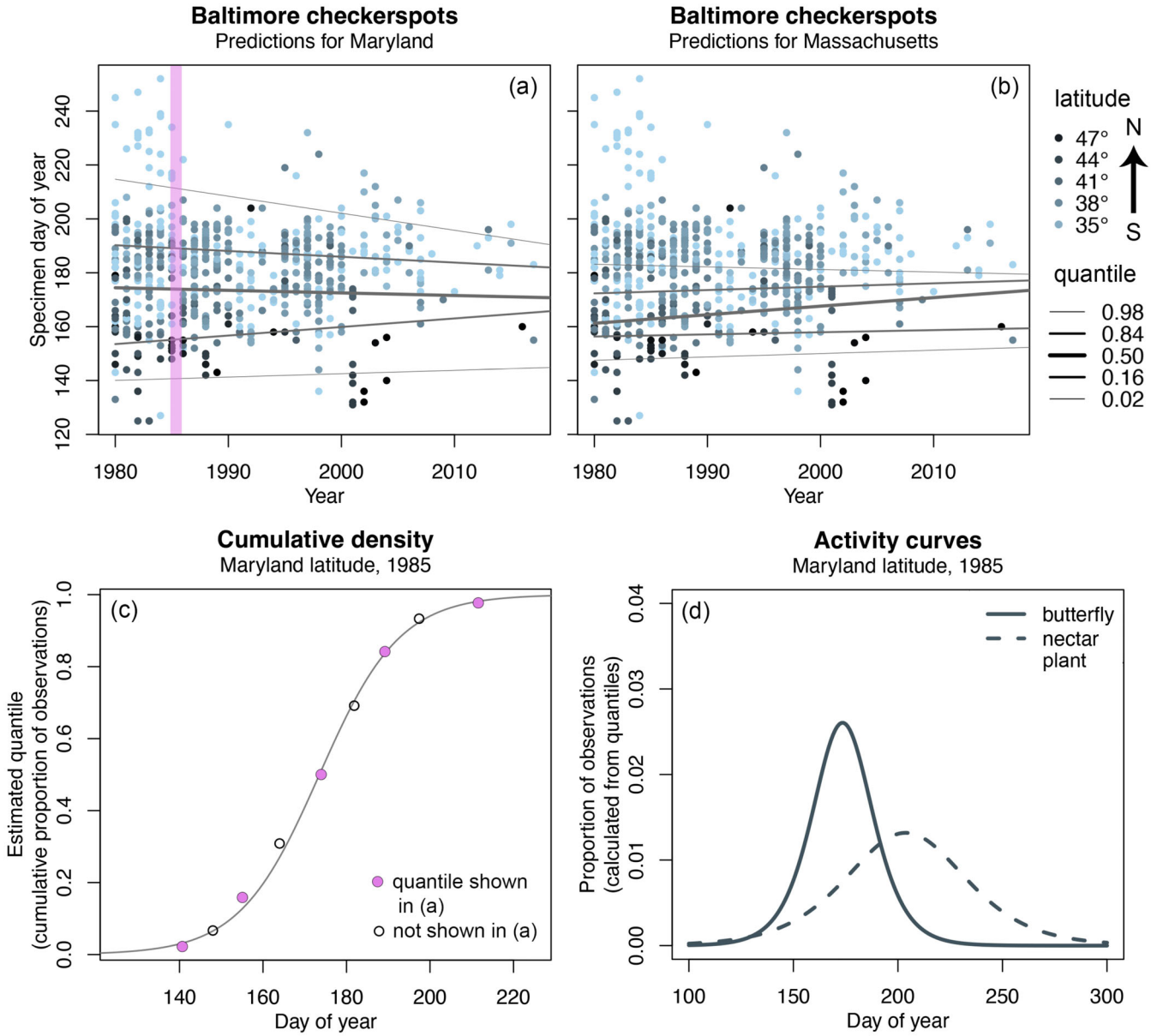

FIGURE 2 Methods for estimating activity curves from historical specimen data. First, we analyzed data with quantile regression models and used them to predict the distribution of specimen dates at a particular place in space or time. Panels (a) and (b) show data for Baltimore checkerspot butterflies through time, with latitudes colored from south (blue) to north (black). The lines are predicted quantiles for activity at the average latitudes of our study sites in (a) Maryland and (b) Massachusetts through time; only five lines are shown here for visual clarity. Next, we used the quantile regression predictions to estimate a cumulative density curve for activity, as shown in (c) for Baltimore checkerspots at the Maryland latitude in 1985. The value of each filled point on the *x*-axis of (c) is the *y*-coordinate of a quantile line at $x = 1985$ in panel (a); other (open) points were from the full set of nine fitted quantiles (see *Methods*). Next, we used Equation (3) to convert the cumulative density to a probability density representing the distribution of activity (flight or flowering) through the year, as shown by the solid line in (d). To calculate the average proportion of plant nectar on a given day of butterfly activity, we used the same procedure to calculate activity curves of plant species, as shown for a representative nectar plant (dashed line). For each nectar plant species, the average proportion of that species' nectar available to a typical butterfly on a day is the product of the values of the two activity curves, for example, the curves in (d), summed over all days (see Equation 4b). For this pair of species, PO ≈ 0.002.

statistically supported in the first set of analyses (see *Results*). To extract an activity curve for a specific latitude and year, we used fitted quantile regression models to predict the day of activity at each of these quantiles for the latitude-year combination of interest. We then fitted the relationship between quantile and DOY using a cumulative logistic model, implemented with the lm() function in R, with DOY as the predictor variable and logit-transformed quantiles as the response variable, that is:

$$\mathrm{E}\left[\ln\left(\frac{\mathrm{CDF_{DOY}}}{1-\mathrm{CDF_{DOY}}}\right)\right]=\beta_0+\beta_1 DOY \quad (2)$$

where $\mathrm{CDF_{DOY}}$ is a fitted quantile associated with each DOY (the day of year for that quantile), β_0 and β_1 are the intercept and slope (respectively) estimated from linear models, and $\ln(x/(1-x))$ is the logistic transformation (Figure 2c). These cumulative logistic models were transformed into a logistic probability density using the standard mathematical relationship (Figure 2d):

$$P[\mathrm{DOY}=x]=\frac{\exp(-\beta_0-\beta_1 x)}{(1+\exp(-\beta_0-\beta_1 x))^2} \quad (3)$$

To quantify phenological overlap, we solved activity curves for the average latitudes of our Massachusetts and Maryland study sites (39.7° N and 42.7° N, respectively) in 1985 and 2015, representing years near the beginning and end of the historical data (see Appendix S1: Table S1). We used these curves to calculate overlap between Baltimore checkerspots and the 12 focal plant species, as measured by the average proportion of flowering by each focal nectar plant species on an average day of butterfly activity (Figure 2d). Recall that the average of a discrete probability distribution is:

$$\sum_i x_i P(x_i) \quad (4a)$$

where x_i is the value being averaged (e.g., the amount of flowering by a nectar plant on day i), and $P(x_i)$ is the proportion of data that have value x_i (e.g., the proportion of butterflies active on day i). If x_i is proportional to the activity density curve for the nectar plant and $P(x_i)$ is the activity density curve for Baltimore checkerspots, then the average availability of that nectar plant to Baltimore checkerspots is the product of the two density curves, summed over all days of the year, that is,

$$PO_j=\sum_{i=1}^{365} x_i P(x_i) \quad (4b)$$

where PO_j indicates phenological overlap of species j with Baltimore checkerspots, x_i is the nectar activity curve evaluated at day i, and $P(x_i)$ is the butterfly activity curve evaluated at day i. This measure of overlap reflects our interest in nectar availability as a food source for butterflies; other measures of overlap are more appropriate for other kinds of interactions (cf. Ramakers et al., 2020; Sevenello et al., 2020). Examples of activity curves and associated values of PO are shown in Appendix S1: Figure S1.

We combined species-specific metrics of phenological overlap in three ways. First, we took the simple average across species:

$$PO=\frac{1}{n}\sum_{j=1}^{n} PO_j \quad (4c)$$

where PO is overall phenological overlap and all parameters are as in Equation (4b).

Second, we calculated the average number of flowering units on a given butterfly activity day by multiplying the average phenological overlap of each species, PO_j, by its density of flowering units (U_j; as described in *Methods: Contemporary field data*, above) averaged over all sites in each region, that is,

$$FO_j=U_j PO_j \quad (5a)$$

and

$$FO=\frac{1}{n}\sum_{j=1}^{n} U_j PO_j \quad (5b)$$

where FO stands for flowering overlap, n is the number of plant species, and all other parameters are as defined above.

Similarly, we estimated the average nectar sugar available from the focal plant species in each region. This calculation is largely similar to FO except that overlap is weighted by sugar production per square meter (TS_j, as estimated above) rather than flowering unit density. In other words

$$SO_j=TS_j PO_j \quad (6a)$$

and

$$SO=\frac{1}{n}\sum_{j=1}^{n} TS_j PO_j \quad (6b)$$

where SO is sugar overlap, and all other parameters are as defined above.

We interpret these metrics of overlap in a descriptive way since there are many unquantifiable sources of variation, such as precision and accuracy of projections from historical data.

How does the abundance of flowers and total nectar production differ among sites and regions?

We compared three metrics of nectar flower abundance: flowering plant species richness, flowering unit density

(U_j in Equation 1), and nectar sugar density (TS_j in Equation 1). For all statistical analyses, we calculated metrics at the transect level so that we could compare them among sites and regions. Therefore, species richness was defined simply as alpha-diversity at the transect × visit level, that is, the average number of species per 20-m × 1-m transect during each visit. Similarly, flowering unit density was summed across each transect during each visit. Nectar sugar was calculated for each transect during each visit by multiplying flowering unit density during that visit by point estimates of S_j, D_j, and F_j (nectar sugar per flower per day, flower longevity, and flowers per flowering unit, respectively), since these were measured from a single pooled sample of observations for each species.

We compared metrics between regions (Maryland vs. Massachusetts) using generalized linear mixed models (GLMMs) with random effects of site and sampling date. Species richness and flowering unit density were analyzed with negative binomial, log-link GLMMs. Nectar sugar density was log-transformed and analyzed with Gaussian (normal) family models. We obtained nectar sugar data for 20 of 68 species observed in our transects (Appendix S1: Table S3). We substituted our estimated nectar sugar from *G. mollugo* for all *Galium* species and *R. allegheniensis* for all *Rubus* species. After this substitution, our nectar data set included 75.4% of all flowering units in Maryland and 92.5% of all flowering units in Massachusetts (see *Results*). Therefore, we conducted two analyses of nectar sugar: a basic analysis using the data for the species we had and a supplemental analysis in which we weighted each observed data point by the proportion of flowering units sampled in that region (e.g., dividing transect totals from Maryland by 0.754 and from Massachusetts by 0.925 to reflect the differences in the proportion of species included).

RESULTS

Question 1: How does the distribution of activity of each species vary as a function of latitude and year?

Fisher's omnibus test of *p*-values across all species (checkerspots and nectar plants) strongly supported trends in phenology in relation to year ($\chi^2 = 139.7$, df = 78, $p < 0.001$; see species specific models in Appendix S1: Table S4) and latitude ($\chi^2 = 533.6$, df = 78, $p < 0.001$; see species specific models in Appendix S1: Table S4). However, the latitude × year interaction did not differ from a null distribution of *p*-values ($\chi^2 = 83.6$, df = 78, $p = 0.312$; see species specific models in Appendix S1: Table S4). Therefore, our inference was based on models with additive effects of year and latitude on phenology of checkerspots and their nectar plants.

Baltimore checkerspot activity occurred earlier at southern latitudes (slopes ± SE of 7.2 ± 0.9, 7.3 ± 1.0,

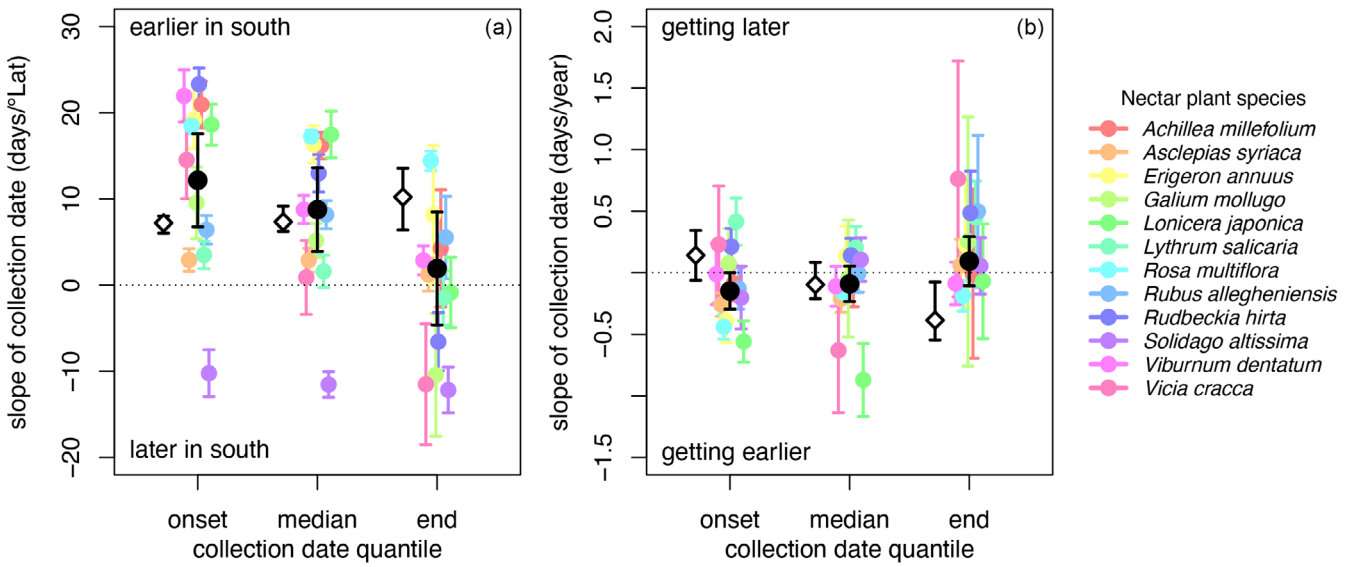

FIGURE 3 Spatial and temporal patterns of collection dates for Baltimore checkerspot butterflies and 12 nectar plant species. (a) Collection date versus latitude. (b) Collection date versus year. In both panels, colored points indicate individual nectar plant species, black circles indicate mean values across all nectar plant species, and open diamonds indicate Baltimore checkerspot butterflies. Error bars indicate 95% CI.

and 10.2 ± 2.7 days per degree latitude for 0.1, 0.5, and 0.9 quantiles, respectively; Figures 2a,b and 3a). Neither the onset nor median of the Baltimore checkerspot flight period were changing through time (slopes ± SE of 0.14 ± 0.14 and −0.10 ± 0.09 days/year for 0.1 and 0.5 quantiles, respectively; Figure 3b). However, the average timing of the end of the Baltimore checkerspot flight period has advanced through time (slope ± SE of −0.38 ± 0.17 days/year for the 0.9 quantile), leading to a shorter activity period.

Across all nectar plant species, the onset and median of flowering tended to be earlier in the south (average slopes ± SE of 12.1 ± 2.6 and 8.8 ± 2.4 days per degree latitude for the 0.1 and 0.5 quantiles, respectively; Figure 3a), although the end of activity did not consistently differ with latitude (2.0 ± 3.2 days per degree latitude for the 0.9 quantile; Figure 3b). In other words, nectar plants at southern latitudes tended to have wider flowering periods due to earlier onset and similar end dates as compared to the same species at northern latitudes. Similarly, the onset of flowering has tended to be earlier (negative slope) in more recent years (slope ± SE of −0.15 ± 0.07 days/year for the 0.1 quantile). The median and end of flowering have not changed consistently across species, though there is a tendency for the median to be getting earlier (negative slope) and the end later (positive slope) through time (slopes ± SE of −0.09 ± 0.07 and 0.09 ± 0.10 days/year for the 0.5 and 0.9 quantiles, respectively).

Trends in phenology differed among nectar plant species (Appendix S1: Table S4), and some of the variation in phenological trends among plant species can be explained by the time of year at which they bloom. Flowering season was associated with both spatial and temporal variation. Latitudinal trends in phenology were significantly associated with flowering season (effect of flowering season on slope of collection day vs. latitude: $F = 47.6$, df = 1, 30, $p < 0.001$, slope coefficient = −0.22). In other words, early-season species flowered earlier in the south, late-season species (e.g., *S. altissima*) flowered later in the south, and mid-season species tended to flower at the same time in both regions. Similarly, in more recent years, early-season species tended to flower earlier, and late-season species flowered later (effect of flowering season on slope of collection day vs. year: $F = 4.5$, df = 1, 30, $p = 0.043$, slope coefficient = 0.0023). Neither effect differed among the slopes for the onset, median, and end of phenology (flowering season × quantile interactions: $F = 0.05$, df = 2, 30, $p = 0.953$ and $F = 0.13$, df = 2, 30, $p = 0.881$ for latitude and year effects, respectively).

Question 2: How does the phenological overlap of checkerspots and nectar differ among regions, and how has overlap changed through time?

Phenological overlap estimated from museum specimens, PO, ranged from 0.0084 at the latitude of our Maryland sites in 2015 to 0.0102 at the latitude of our Massachusetts sites in 1985 (Figure 4a,b; Appendix S1: Figure S2a,b). In both regions, PO was lower in 2015 than in 1985, with a 7.9% decrease at the Maryland latitude and a 7.7% decrease at the Massachusetts latitude. Average PO was also about 12% higher at the Massachusetts latitude than at the Maryland latitude during both time periods. These average changes reflect considerable variation among plant species (Appendix S1: Figure S2a,b). At the Massachusetts latitude, four species (*A. millefolium*, *A. syriaca*, *L. japonica*, and *R. allegheniensis*) were predicted to increase in PO with Baltimore checkerspots; in Maryland, five species (the same four plus *V. dentatum*) were predicted to increase in PO. Of these species, two (*L. japonica* and *R. allegheniensis*) were predicted to increase in PO by more than 10% from 1985 to 2015. Six plant species (*E. annuus*, *G. mollugo*, *L. salicaria*, *R. multiflora*, *R. hirta*, and *V. cracca*) showed >10% lower PO in both regions in 2015.

Weighting phenological overlap by flower densities at our field sites modified, but did not substantially alter, conclusions about changes in phenological overlap through time. Overlap weighted by flower density, FO, ranged from 0.0021 for the Maryland latitude in 2015 to 0.0499 for the Massachusetts latitude in 1985 (Figure 4c,d; Appendix S1: Figure S2c,d). FO declined by 7.3% in at the Maryland latitude and by 11.9% at the Massachusetts latitude. Although trends through time were similar, FO showed much larger geographic variation than PO and was ~20 times higher in Massachusetts than Maryland during both time periods. Because FO is simply PO multiplied by flower densities (U_j in Equation 1), the difference between variation among regions in PO versus FO comes only from differences in nectar plant densities in the field. In particular, *G. mollugo* was very abundant at our Massachusetts sites (Appendix S1: Table S3, Figure S2), which explains most of the difference in average FO between regions. *G. mollugo* is also one of the species with the largest decreases in PO through time, which explains why FO declined more at the Massachusetts latitude than at the Maryland latitude, even though changes in PO were similar.

In contrast, weighting phenological overlap by nectar sugar production substantially altered conclusions

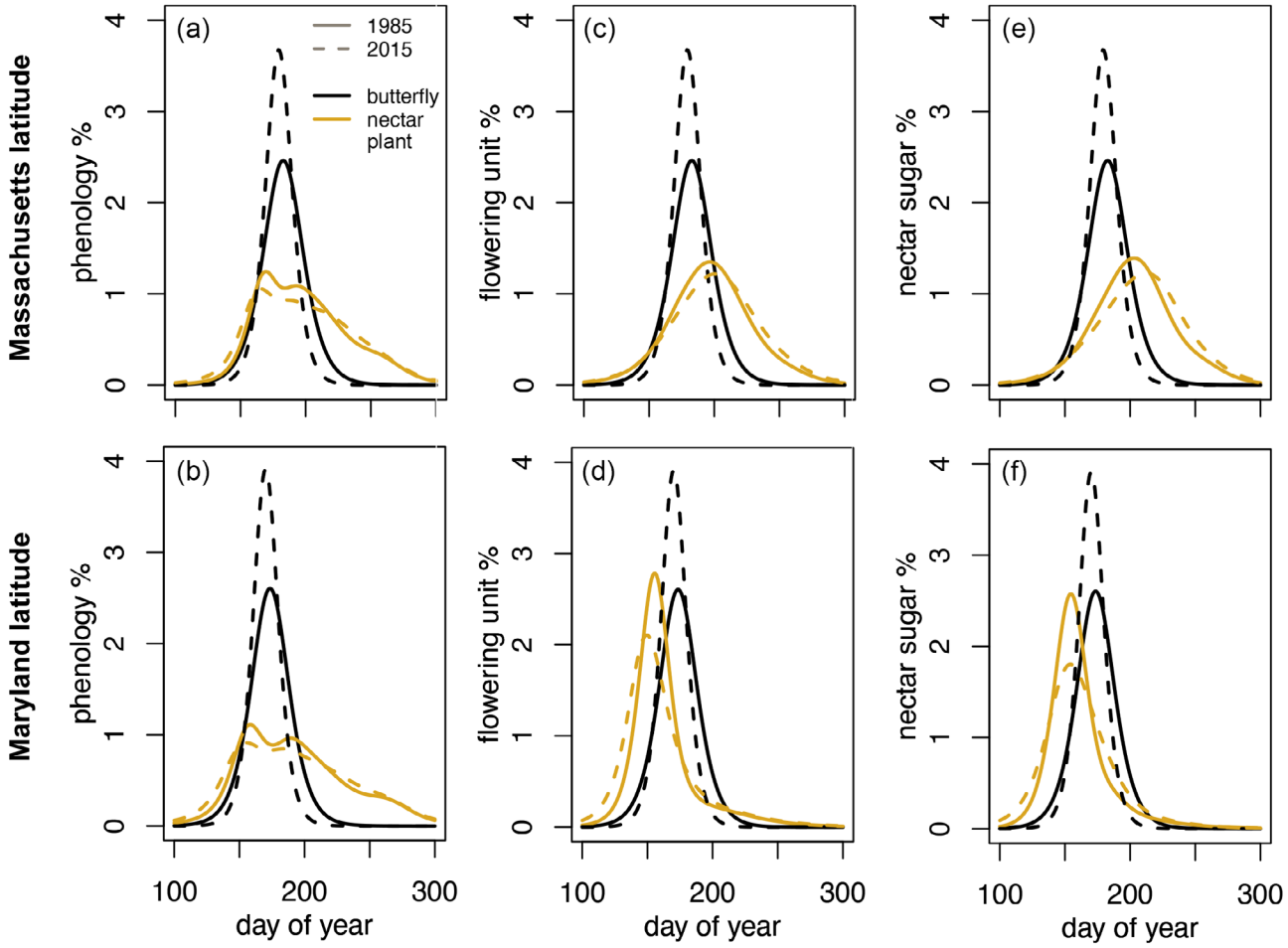

FIGURE 4 Changes in phenological distributions of Baltimore checkerspot butterflies with nectar plant flowering, summarized over all nectar plant species: (a, b) phenology only, with all plant species weighted equally; (c, d) species weighted by abundance; (e, f) species weighted by nectar sugar production. For comparison of butterflies and nectar metrics, curves in this figure were all normalized to have the area sum to 100; therefore, nectar metrics for 2015, in which the flowering period of plants is longer (see *Results*), will tend to have lower peaks than the same metrics in 1985. Average values for each plant species are shown in Appendix S1: Figure S2. The upper row of panels (a, c, e) are calculations for Massachusetts sites, and the lower row of panels (b, d, f) are calculations for Maryland sites. In all panels, the solid lines are calculated for 1985 and the dashed lines for 2015. In all panels, black lines indicate butterflies, and gold lines indicate nectar plants.

about the implications of phenological shifts. Overlap weighted by nectar sugar production, SO, ranged from 0.021 at the Maryland latitude in 1985 to 0.099 at the Massachusetts latitude in 1985 (Figure 4e,f; Appendix S1: Figure S2e,f). SO increased by 9.9% at the Maryland latitude but decreased by 21.0% at the Massachusetts latitude. SO was about four times higher at the Massachusetts latitude than Maryland latitude, though that difference declined through time (4.7× higher in 1985 and 3.4× higher in 2015). The increase in SO at the Maryland latitude is largely due to *R. allegheniensis*, which was abundant at our field sites in Maryland, had one of the larger increases in PO, and produced high nectar sugar per flower (Appendix S1: Table S3, Figure S2).

Question 3: How does the abundance of nectar flowers and total nectar production differ among sites and regions?

By all metrics, nectar was more abundant at our sites in Massachusetts than in Maryland. Species richness per transect survey was more than three times higher in Massachusetts sites than in Maryland sites ($\chi^2 = 17.07$, df = 1, $p < 0.001$; Figure 5a). Species richness varied substantially among sites within regions (log-scale random effect SD = 0.42) and among dates (log-scale random effect SD = 0.28). Across the Baltimore checkerspot flight season, we observed 6, 13, and 27 species at each of the three Maryland sites and 22, 25, and 27 species at each of the three Massachusetts sites. In total, we observed 37 nectar

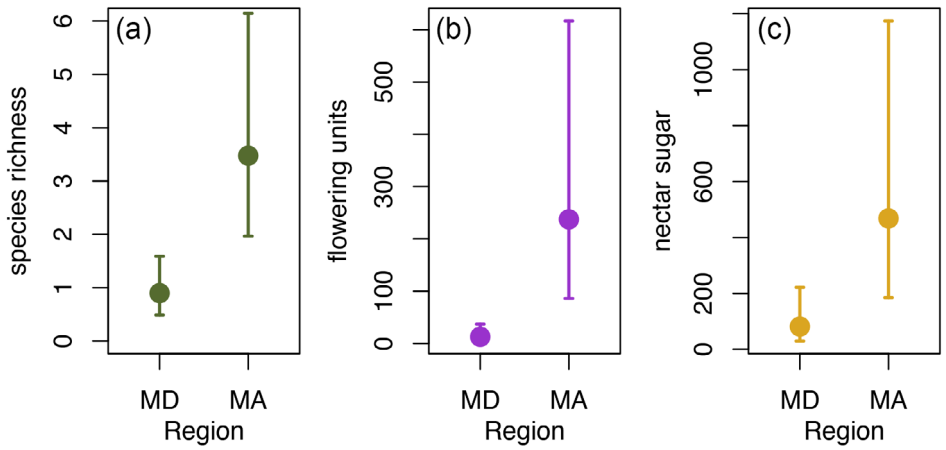

FIGURE 5 Among-region variation in nectar availability, measured as (a) species richness per transect survey, (b) flowering units per square meter per survey or (c) nectar sugar density per square meter. Error bars indicate 95% CIs. MA, Massachusetts; MD, Maryland.

plant species in Maryland, 44 in Massachusetts, and 68 species across the two regions.

The number of flowering units per transect survey was nearly 20 times higher in Massachusetts sites than in Maryland sites ($\chi^2 = 22.96$, df = 1, $p < 0.001$; Figure 5b). Flower unit density also differed substantially among sites within regions and survey dates (log-scale random effect SD's of 0.55 and 1.01, respectively). Similar to species richness, flowering unit density was lower at two of three Maryland sites (site means of 3.1, 6.4, and 105.6 flowering units/survey), compared to the Massachusetts sites (site means of 19.4, 184.5, and 3753.6 flowering units/survey). Regional differences were due in part to extremely high flower densities of one species, *G. mollugo*, at some sites (see Appendix S1: Figure S2). We re-ran analyses with this species removed and still observed significantly higher flowering unit densities in Massachusetts sites than in Maryland sites ($\chi^2 = 33.7$, df = 1, $p < 0.001$; back-transformed means and 95% CIs: 16.6 [10.2, 26.6] and 90.0 [57.1, 140.7] flowering units/m^2/survey in Maryland and Massachusetts, respectively).

Estimated nectar sugar density was about five times higher in Massachusetts sites than in Maryland sites ($\chi^2 = 6.44$, df = 1, $p = 0.011$; Figure 5c). Similar to species richness and flowering unit density, nectar sugar density varied among sites and dates within regions (log-scale random effect SD's of 0.70 and 0.82, respectively). However, unlike species richness and flowering unit density, there was no overlap between site means for nectar sugar density in Maryland (site means of 48.4, 83.2, and 135.4 μg/m^2/survey) compared to Massachusetts (site means of 303.2, 349.4, and 968.9 μg/m^2/survey). Because we did not have nectar sugar estimates for all plant species, these calculations include 91.6% of all flowering units across all sites, 75.4% of flowering units in Maryland, and 92.5% of flowering units in Massachusetts. Re-running the analysis with nectar sugar estimates weighted by regional totals (i.e., divided by the proportion of flowering units sampled in each region; see *Methods*) still suggested significantly higher nectar sugar density in Massachusetts than in Maryland ($\chi^2 = 5.02$, df = 1, $p = 0.025$; back-transformed means and 95% CIs: 106.9 [39.3, 292.3] and 504.6 [198.3, 1272.4] μg/m^2/survey in Maryland and Massachusetts, respectively).

To contextualize our analyses of phenological overlap with 12 focal plant species, we calculated the proportion of the total flowering units and nectar sugar in each region that was produced by these 12 species. Our focal species accounted for 59% of the flowering units in our Maryland transects and 85% of the flowering units in our Massachusetts transects. Our focal species accounted for 94% of the nectar sugar in our Maryland transects and 98% of the nectar sugar in our Massachusetts transects.

DISCUSSION

For Baltimore checkerspot butterflies and their nectar plants, phenological overlap has decreased through time. Although this result was largely expected from past studies (e.g., Kharouba & Vellend, 2015), the mechanisms and ecological significance of phenological changes in this system contrast broadly with general expectations and change interpretation of some past studies. On the one hand, phenological mismatch was due to contrasting changes in activity period of checkerspots versus nectar plants and occurred in spite of similar changes in median activity dates. This result implies that phenological mismatch might be more common than would be inferred from past reviews based only on relative rates of

changes in average or peak activity dates (Kharouba et al., 2018; Kharouba & Vellend, 2015; Thackeray et al., 2016). On the other hand, three aspects of our results suggest that phenological mismatches are not important drivers of population viability in our system. First, in one of our study regions (Maryland), the overall decrease in phenological overlap was completely counteracted by increasing phenological overlap with one common nectar plant species, leading to an estimated increase in available sugar. Second, the change in phenological overlap was much smaller than representative "cartoon" figures designed to illustrate the potential for mismatch (compare, e.g., the changes we see in fig. 4 to fig. 1 in Kharouba & Wolkovich, 2023 or to representative differences in Appendix S1: Figure S1 of this paper). Third, the proportional change in phenological overlap was noticeably smaller than variation among sites within regions and an order of magnitude smaller than the difference in nectar availability between regions. The comparison of phenology effects to between-region variation echoes observations that spatial heterogeneity can offset the impact of phenological mismatches (Hindle et al., 2015) and that differences in phenological overlap among interacting species are much larger than phenological differences within species (Toftegaard et al., 2019). It also points to the importance of interpreting large-scale changes in the phenology of potentially interacting species in the context of how species interact in the field.

For nectar plants, the range of flowering dates is expanding. This result was partly expected, in that we predicted early-season species to flower earlier in the south and earlier in more recent years and late-season species to flower later in the south and later in more recent years. This result echoes past work with plants (Sherry et al., 2007), and this pattern has also been seen in some univoltine insects (e.g., solitary bees; Dorian et al., 2023). A more surprising result is that we observed the same pattern within species. On average, a typical nectar plant species had an earlier onset and similar end of flowering period in the south, compared to the north. Through time, nectar plant species are tending to have an earlier onset and later end to their flowering period in both regions. In a sense, this pattern is intuitive, since longer growing seasons also tend to increase the period of leaf activity in plants (earlier leaf out in spring and later leaf senescence in fall; Gallinat et al., 2015; Jeong et al., 2011). However, individual flowers tend to be shorter-lived in warmer environments, both among (Song et al., 2022) and within (Arroyo et al., 2013; Pacheco et al., 2016) species. At the whole-plant level, flowering duration has been studied less than the onset of flowering or floral longevity, but past studies have also suggested that flowering duration tends to be shorter under warmer climatic conditions (Bock et al., 2014; Črepinšek et al., 2012; Nagahama et al., 2018). One possible explanation for the increases in flowering period that we observed in this study is that early-flowering individuals might be more responsive to temperature than late-flowering individuals, leading to an overall longer flowering duration at the population level (Miller-Rushing et al., 2007).

In contrast to its nectar plants, the Baltimore checkerspot flight period has become shorter through time. In this species, the spatial pattern did not mirror the temporal trend; at southern latitudes, the Baltimore checkerspot flight period was uniformly earlier, but not shorter in duration. One possible explanation for the difference between temporal and latitudinal patterns in our study system is that the magnitude of temperature difference in space (~3°C) was larger than the magnitude of change through time (~1.25°C) (see *Methods*: *Study system*). More generally, it is not unusual for species to respond differently to spatial and temporal variation in temperature (Hodgson et al., 2011; Kharouba & Vellend 2015). A trend toward shorter activity periods could reflect an increase in the number of days that have appropriate weather conditions for activity. In many butterfly species, daily activity and lifetime fitness are limited by the number of days with suitable weather (Dempster, 1983; Doak et al., 2006) and mid-season butterflies like *E. phaeton* are more likely to be active on warmer days (Franzén et al., 2022). It could be that warmer conditions enable Baltimore checkerspots to complete their lifespans more quickly with no fitness costs. However, an alternative explanation for a shorter activity period is higher mortality due to other environmental changes. For example, greater nectar availability increases butterfly lifespans in general (Lebeau et al., 2016), and Baltimore checkerspots without access to nectar have 20% shorter adult lifespans than those with unlimited nectar access (L. M. Brown, unpublished data). A third possibility is that the narrower flight period at the population level reflects more synchronized emergence times of individuals; butterfly development times show notable plasticity in relation to temperature (e.g., Dell et al., 2005; Stålhandske et al., 2015; Van Nouhuys & Lei, 2004), though it is not clear whether this plasticity would lead to higher synchrony within populations through time. These disparate possibilities highlight the importance of understanding the mechanisms of changes in phenology to understand their consequences. In the context of phenological changes, this could be a valuable direction for future research in this system.

Our study also highlights some of the strengths and limitations of historical collections data. One of the most challenging problems in assessing impacts of

environmental change is the need to know the state of the system before these changes began. The spatial and temporal extent of scientific collections provides an important window into this baseline. In combination with the statistical power of quantile regression (Dorian et al., 2023; Michielini et al., 2021), we were able to use historical specimens to quantify how the distributions of butterfly flight and plant flowering have changed in space and time. Indeed, predictions from our statistical models based on collections data aligned well with the dates in which we observed Baltimore checkerspot butterflies and their nectar plants in the field (Appendix S2). However, we were only able to estimate changes in phenology from collections data; all of our abundance data came from contemporary field sampling. The numbers of species records in biological collections can discriminate rare from common species (Gotelli et al., 2023) and inform changes in species geographic distributions (Colla et al., 2012; Duchenne et al., 2020). However, it seems unlikely that collections will be able to inform fine-scale changes in species' abundance through time at local sites (cf. Shirey et al., 2023; Wepprich, 2019). In other words, using historical specimens, we were only able to evaluate how changes in phenology would affect the availability of nectar to checkerspot butterflies under the assumption that the relative abundances of nectar plant species were similar in 1985 to what they were in 2019.

Similarly, another limitation of collections data is they are strongly biased toward certain life stages. Butterfly–nectar plant interactions are an ideal model system for studying long-term phenological change because they are typically collected at the stages during which they interact (flowering plants and adult butterflies). However, in contrast to their generalist adult diets, butterflies are often highly specialized on particular host plant taxa as larvae, with differing implications for phenological mismatch. Past studies have shown conflicting results about whether dietary specialists show larger or smaller levels of phenological change than generalists (Altermatt, 2010; Brooks et al., 2017; Diamond et al., 2011; Dorian et al., 2023; Zografou et al., 2021). It is not clear whether more specialized life stages within a species would be more or less subject to phenological mismatch. In the process of setting up this study, we also compiled historical observation dates for Baltimore checkerspot larvae and their primary host plant, white turtlehead (Appendix S3). Data were much sparser for these rarely collected life stages, for example, 28 vegetative versus 828 flowering turtlehead specimens (Appendix S3: Figure S1). Nonetheless, for this species, phenological mismatch inferred from these specimens was modest at the larval stage, similar to the adult stage (Appendix S3: Figure S2). In general, collections data are unlikely to be highly informative about phenology of immature insect life stages, and finding additional sources of information about their phenology (e.g., digitizing historical naturalist observations) could be an interesting avenue for future research.

Our research was motivated in part by the hypothesis that differences in phenological mismatch with nectar plants could contribute to regional differences in the population viability of Baltimore checkerspot butterflies. In contrast with this prediction, the magnitude of change in resource availability due to changes in any metric of phenological overlap (5%–20%) was much smaller than among site variation in nectar sugar within regions (50%–65%) or differences among regions (~500%). In setting up our study, we were able to locate many Baltimore checkerspot populations in natural areas managed for conservation in Massachusetts. However, all of our study populations in Maryland were located on the edges of private farm fields with few nectar plants, in spite of the fact that they were chosen to represent the best remnant populations in Maryland (Maryland Department of Natural Resources, personal communication). Declines in butterfly populations in agricultural landscapes have been attributed to loss of wildflower diversity and abundance (Lebeau et al., 2016; Wallisdevries et al., 2012). For butterfly populations in general, nectar resources can limit abundance as much as larval food plants (Boggs & Inouye, 2012; Schultz & Dlugosch, 1999). It seems likely that nectar availability does indeed contribute to regional differences in population viability, but that the cause is regional differences in overall nectar plant abundance, not differences in nectar plant phenology. Evaluating the importance of nectar resources for Baltimore checkerspot habitat restoration would be an important direction for future research.

In closing, concerns over phenological mismatch have been motivated primarily by the hypothesis that interacting species at different trophic levels have different phenological cues or responses to those cues (Thackeray et al., 2016). Our results broadly support this hypothesis; they point to the diversity of ways in which phenology can vary in space and time and to the importance of understanding the mechanisms that underpin phenological patterns if we want to predict future changes and their consequences. At the same time, our study suggests that phenological mismatch is not a primary driver of changes in nectar availability for the Baltimore checkerspot butterfly. Although phenological changes are among the most conspicuous signals of environmental change in general, this case study highlights that phenological shifts may not be the most important impacts of those changes for species persistence in changing environments.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data (Crone et al., 2024a) are available in Dryad at https://doi.org/10.5061/dryad.rr4xgxdhk. Code (Crone et al., 2024b) is available in Zenodo at https://doi.org/10.5281/zenodo.13760920.

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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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