Received: 7 March 2025 | Revised: 6 September 2025 | Accepted: 14 October 2025

DOI: 10.1002/ecy.70297

ARTICLE

ECOLOGY
ECOLOGICAL SOCIETY OF AMERICA

Climate and species traits give rise to complex phenological dynamics

Gbolahan A. Reis[1] | **Matthew L. Forister**[2] | **Christopher A. Halsch**[3] | **Clare M. Dittemore**[2] | **Arthur M. Shapiro**[4] | **Zachariah Gompert**[1]

[1]Department of Biology and Ecology Center, Utah State University, Logan, Utah, USA

[2]Program in Ecology, Evolution and Conservation Biology, Department of Biology, University of Nevada, Reno, Nevada, USA

[3]Department of Biological Sciences, Binghamton University, Binghamton, New York, USA

[4]Center for Population Biology, University of California, Davis, California, USA

Correspondence
Gbolahan A. Reis
Email: anthony.reis@usu.edu

Funding information
Utah State University Ecology Center Research Award, Grant/Award Number: A07339-1092; National Science Foundation, Grant/Award Numbers: DEB-2114794, DEB-2114973

Handling Editor: Derek M. Johnson

Abstract

Climate change has substantially shifted the phenology of many organisms. These shifts vary across species and habitats and are shaped by species' natural history traits and local environmental conditions, yet the relative importance of these drivers remains unclear. Moreover, climate can have diverse effects on different aspects of phenology, such as the timing and duration of activity, but this complexity is rarely captured by commonly used phenological metrics. We used multidecadal butterfly surveys and climate data from five montane sites spanning an elevational gradient to investigate how climate affects different aspects of the annual flight period of 135 butterfly species. Using a hierarchical Bayesian framework, we modeled annual probability of occurrence distributions for species using polynomial models that capture changes in abundance, timing, and length of flight. Spring maximum and minimum temperatures and winter precipitation were the best predictors of interannual variation in phenology. High winter precipitation, which usually comes in the form of snow, delayed phenology, while warmer spring maximum temperatures advanced phenology across elevations. Even modest increases in spring minimum (nighttime) temperatures caused strong phenological shifts. Climate effects varied among sites, among species within sites, and even among populations of the same species across sites, with particularly pronounced variation among species at a single location. Variation in climate effects was slightly better explained by local climate than by natural history traits. Among natural history traits, voltinism and overwintering stage were particularly influential. Importantly, climate influenced different aspects of the flight period (e.g., timing versus duration) in distinct ways, with both natural history traits and local climate modulating these responses. Our findings highlight the often-overlooked importance of winter precipitation and nighttime temperatures in shaping phenology and demonstrate the value of considering the entire flight period, rather than distinct aspects alone, to improve our understanding and predictions of species response to climate change.

KEYWORDS

climate change, hierarchical Bayesian modeling, Lepidoptera, long-term monitoring, phenology

https://doi.org/10.1002/ecy.70297

INTRODUCTION

Climate change is rapidly transforming ecosystems worldwide, with numerous studies documenting substantial impacts on the ecology of organisms (Halsch et al., 2021; Inouye, 2022; Parmesan, 2006). Among the most evident biological responses to climate change are phenological shifts, with species experiencing changes in the timing of critical life history events such as migration, flowering, and flight periods (Cleland et al., 2007; Forister et al., 2018; Newson et al., 2016; Parmesan, 2006, 2007). These changes in phenology can disrupt species interactions, alter ecosystem function, and reshape community dynamics (Kharouba et al., 2018; Miller-Rushing et al., 2010; Renner & Zohner, 2018; Thackeray et al., 2010). This has led to growing interest in identifying the ecological and climatic drivers of phenological change across taxa and environments.

In ectothermic organisms, including insects, phenological responses are particularly pronounced because metabolic, and developmental rates are directly influenced by external temperature, photoperiod, and precipitation patterns (Cohen et al., 2018; Deutsch et al., 2008; Parmesan, 2006). In Lepidoptera, earlier flight periods, increased voltinism, and extended flight periods have been widely documented in response to climate change (Colom et al., 2021; Forrest, 2016; Gutiérrez & Wilson, 2021; Habel et al., 2024). However, the magnitude and direction of these shifts vary considerably across species and habitats and appear to be shaped by both natural history traits (e.g., voltinism, overwintering stage) and environmental factors (e.g., elevation, local climate) (Colom et al., 2021; Diamond et al., 2011; Forrest, 2016; Gutiérrez & Wilson, 2021; Habel et al., 2024; Rödder et al., 2021; Zografou et al., 2021), although the relative importance of these factors is not well understood.

Shifts in flight periods are commonly quantified using simple metrics such as the first, mean, or last day of flight (Faltýnek Fric et al., 2020; Parmesan, 2007; Roy & Sparks, 2000; Thackeray et al., 2016). While useful, these metrics are sensitive to factors like species abundance, observation period, detection, and sampling effort. Some are more robust than others; for example, mean flight dates could be less sensitive to species abundance. Nevertheless, these metrics may inaccurately capture changes in the shape, symmetry, or duration of the flight period, leading to poor estimates of the magnitude and direction of phenological shifts (Inouye et al., 2019; Miller-Rushing et al., 2008; Pearse et al., 2017; Van Strien et al., 2008). Furthermore, focusing on a single date collapses the complexity of phenological responses, such as whether climate affects only the start of the flight period, its overall duration, or both, and whether it does so in a consistent direction and magnitude. We risk overlooking how climate affects other important portions of the flight period that could substantially impact species interactions and broader ecological dynamics (Forrest & Miller-Rushing, 2010; Macphie et al., 2023). Recent work on Lepidoptera suggests that different aspects of the flight period can change independently and may be differentially affected by climate depending on natural history traits, such as voltinism, and environmental factors, such as elevation (Habel et al., 2024). For example, we can expect that some species will advance their emergence date without changing flight length, while others will exhibit both earlier emergence and longer durations. These discrepancies could introduce barriers to our understanding of changes in phenology and phenological mismatches and obscure broader patterns, particularly as meta-analyses and cross-study comparisons often synthesize studies that quantify different components of the flight period (Cohen et al., 2018). Modeling the full phenological curve, which is the approach we take here, offers a more robust and comprehensive framework for quantifying changes in flight periods (Dennis et al., 2016; Macphie et al., 2023).

In this study, we use a long-term butterfly monitoring dataset, encompassing over 150 species across various elevations and habitat types in the Sierra Nevada of western North America, to understand changes in flight periods by modeling annual occurrence distributions, that is, the probability of occurrence or detection each day across the flight period for each species at each site in each year (Figure 1). Montane habitats are particularly vulnerable to climate change, with temperatures rising more rapidly at higher elevations (Ohmura, 2012; Rödder et al., 2021). Previous studies at these sites have focused on the effect of climate on abundance (as captured by the average probability of occurrence for a butterfly species in a year) rather than phenology. These studies showed that the effects of climate on butterfly abundance vary substantially among different sites, highlighting the heterogeneous nature of climate responses (Nice et al., 2019). Some work has been done with these data on phenology but only in a limited and focused way. For example, drought events were shown to compress flight windows in univoltine species and reduce species richness, indicating the potential for climate extremes to alter flight periods (Forister et al., 2018).

We combine this butterfly dataset (repeated presence/absence observations and natural history trait data) with climate data and use hierarchical Bayesian generalized linear models to assess the effects of climate on interannual variation in butterfly occurrence distributions. Our analysis allows us to model the effects of climate on the probability of occurrence of butterflies across the season (i.e., the occurrence distribution) in three

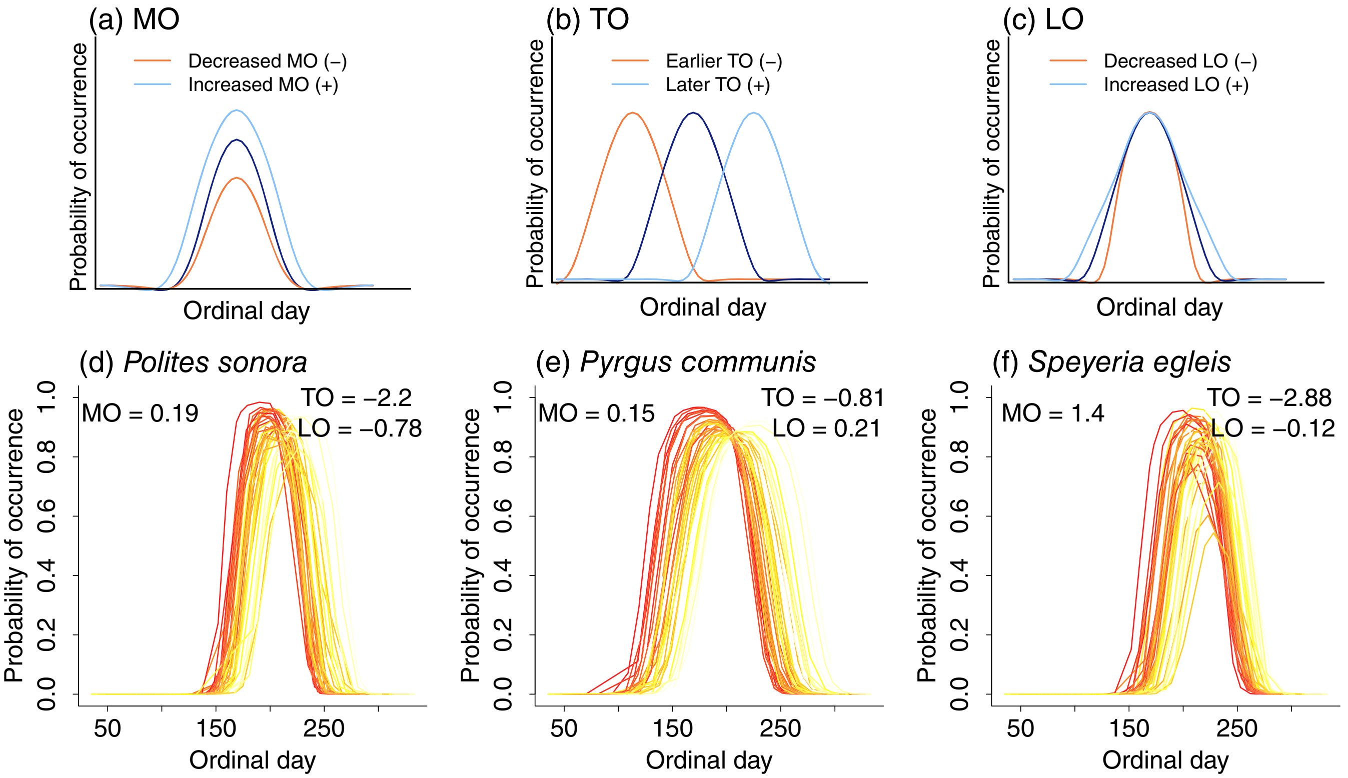

FIGURE 1 Effects of each predictor variable (climate variables or year) on the annual occurrence distribution of butterfly species. Panel (a) indicates the effect of the predictor variable on mid-season occurrence (MO), with negative effects denoting a decreased probability of occurrence and positive effects indicating an increased probability of occurrence across the flight period. Panel (b) shows the impact of the predictor variable on the timing of occurrence (TO) (interaction between predictor variables and ordinal day), with negative effects indicating a shift to an earlier flight period and positive effects suggesting a shift to a later flight period. Panel (c) presents the effect of the predictor variable on the length of occurrence (LO) (interaction between predictor variables and ordinal day^2), with negative values indicating a shorter flight period and positive values indicating a longer flight period. Panels (d), (e), and (f) show estimates of interannual variation in flight periods for three representative species, *Polites sonora*, *Pyrgus communis*, and *Speyeria egleis*, at Donner Pass from our climate model. Each line represents the probability of occurrence on each day across a year, with colors indicating average spring maximum temperatures for that year (darker colors indicate higher spring maximum temperatures). Thus, the effects of spring maximum temperature on MO, TO, and LO for each species are shown in each plot.

distinct ways. Specifically, our models include climatic effects on: (i) the mid-season probability of occurrence (MO), which is an intercept term that parameterizes the probability of occurrence on ordinal Day 0 (after centering, hence the term mid-season) but is related to the probability of occurrence throughout the entire flight season; past work has shown that the probability of occurrence across the flight period is a useful metric of abundance and thus the effect of climate on MO captures the effect of climate on population density (Casner et al., 2014; Halsch et al., 2024); (ii) the timing of the flight period (i.e., the timing of occurrence or TO); and (iii) the duration of the flight season, which we refer to as the length of occurrence (LO) (Figure 1). This approach accounts for species- and site-specific responses, providing a nuanced understanding of how climatic effects could differ by species and sites.

We address four main questions: (i) How does interannual variation in climate affect MO, TO, and LO across species? (ii) Do the effects of climate vary more strongly across sites, among species within sites, or among populations of the same species across sites? (iii) Are these differences in the climate effects best explained by natural history traits or by local environmental factors? (iv) Is there a consistent and generalizable relationship among the effect of climate on aspects of the flight period (MO, TO, LO) across species? Specifically, we sought to determine whether knowing the effect of climate on one component (e.g., timing of flight period) allows us to reliably predict its effect on others (e.g., length of flight period), or whether each aspect of the flight period shifts independently, with species exhibiting a range of response patterns. We hypothesize that annual weather will impact the flight period of species and that variation among species within sites will be most pronounced, reflecting the diversity of life history strategies. We further expect that the relationship between the effect of climate on each aspect of the flight period would differ by species and that this is shaped by both local environmental factors and species' natural history traits. For instance, multivoltine species may have greater capacity to adjust their phenology in response to warming than univoltine species, whose life cycles are more constrained. Similarly, we expect other natural history traits to be important, such as overwintering stage, diet breadth, residency (local breeding at a site), and ruderal status (association with disturbed habitats and exotic hosts). Furthermore, we expect extension of the flight period at high-elevation sites to be constrained by earlier winter onset despite warming.

MATERIALS AND METHODS

Butterfly dataset

The butterfly dataset used in this study derives from a long-term monitoring program that was begun in the early 1970s by one of us (AMS), encompassing 10 sites across Northern California. Since 2018, monitoring at the highest elevation sites has been conducted by three of us (MLF, CAH, CMD) using the same methodology. We found no evidence that changes in observers impacted detection of temporal trends (Appendix S1: Figure S1). Here, we focused on observations from five sites in the Sierra Nevada–Castle Peak (CP), Donner Pass (DP), Lang Crossing (LC), Sierra Valley (SV), and Washington (WA)–spanning an elevational gradient from 800 to 2800 m (Figure 2a,b). These sites exhibit diverse climatic conditions (Figure 2c–e) and habitat types. Surveys at these sites are conducted every other week during the butterfly flight season on days conducive to butterfly activity, typically beginning shortly after snowmelt in the spring and ending in the fall, before snowfall or when temperatures become too cold to support butterfly activity. Surveys were conducted without missing any scheduled visits. During each survey visit, observers follow a fixed, permanent route and record the presence or absence of all butterfly species. The number of years that each site has been monitored varies, some starting as early as 1973 (DP), while others began later (SV in 1982, WA in 1988). For the present analyses, data for sites that

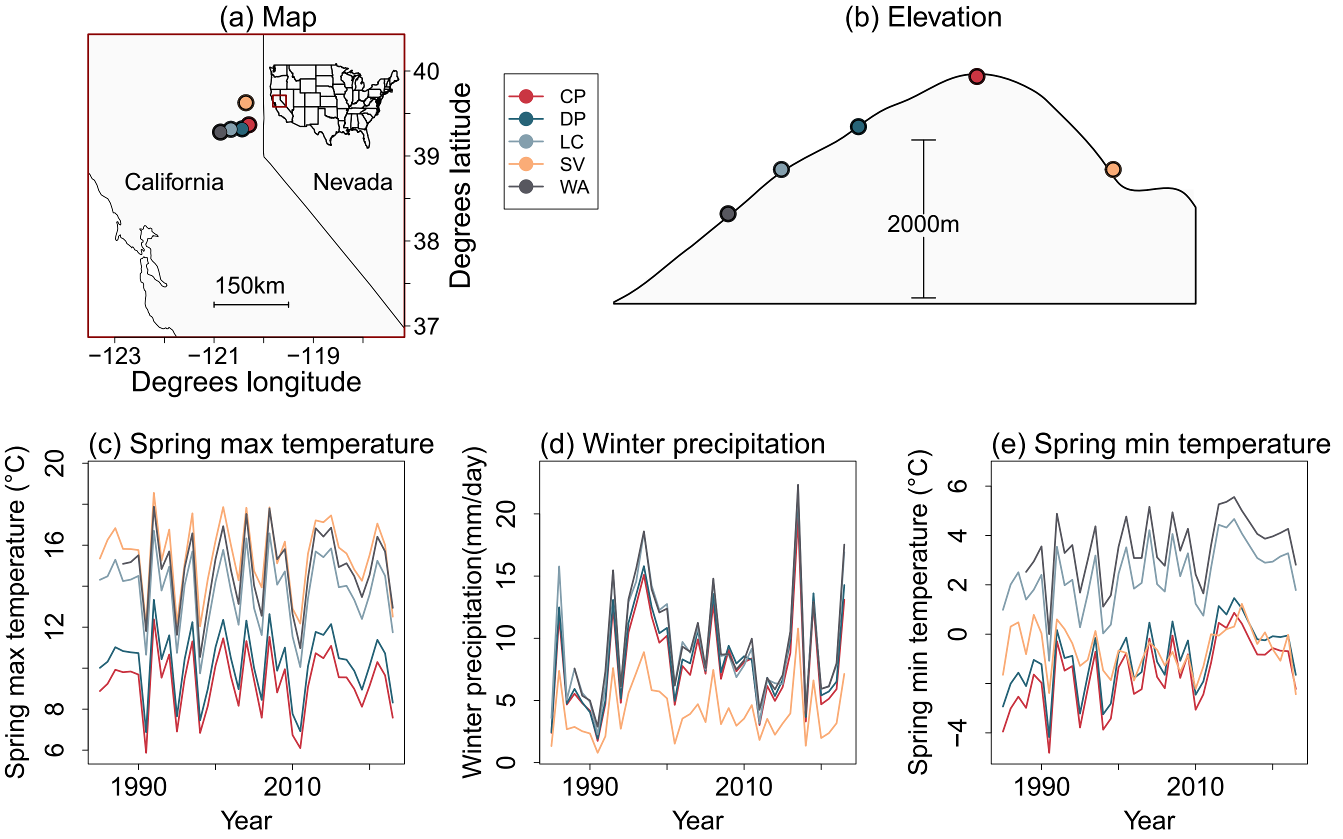

FIGURE 2 Site locations and annual climatic variation. Panel (a) is a map showing the five study sites in the Sierra Nevada with an inset of a USA map with the focal area enclosed in a box. Panel (b) shows the elevation at each site. Washington (WA): 850–1200 m, Lang Crossing (LC): 1500–1700 m, Donner Pass (DP): 2000–2200 m, Castle Peak (CP): 2400–2775 m, and Sierra Valley (SV): 1500 m. Panels (c), (d), and (e) display interannual variation in average spring maximum temperature (c), average winter precipitation (d), and average spring minimum temperature (e) across sites from 1985 to 2023.

were monitored before 1985 were truncated so that the earliest observations begin in 1985, providing consistency in time series length. Detailed information on each site and the corresponding survey routes can be found in Shapiro (2024). For this study, at each site, we focused on butterfly species observed on at least 10 visits throughout the study years, excluding strays and infrequent species. This selection resulted in a total of 135 unique species observed across all study sites: 64 at CP, 88 at DP, 83 at LC, 70 at SV, and 80 at WA. Of these, 104 species were found at two or more sites, and 26 were found at all five sites (Appendix S1: Figure S2).

Temporal occupancy modeling

To quantify shifts in butterfly flight periods, we modeled their annual occurrence distributions using a hierarchical Bayesian framework. Butterfly occurrence on a given day was modeled as a Bernoulli random variable, where the presence of a butterfly on a specific ordinal day was classified as a success. We modeled the probability of occurrence for species *i* on ordinal day *j* in year *k* (denoted as $P_{i,j,k}$) using a generalized linear model (Equations 1 and 2). Since the probability of occurrence of butterflies typically follows a parabolic pattern within a year–first increasing and then decreasing–we included a quadratic polynomial for ordinal day (i.e., including both ordinal day and ordinal day^2 terms) to capture these dynamics. Multivoltine species at these sites typically show a distinct occurrence peak within a year rather than multiple distinct peaks (Appendix S1: Figures S3–S15) likely due to the short flight season at these elevations. First, we fit a baseline time model and then considered various suites of climatic variables. For the time model, the design matrix ($\mathbf{X}$) included ordinal day, ordinal day^2, year, and the interactions between year and both ordinal day and ordinal day^2. For the climate models, the design matrix ($\mathbf{X}$) included climate variables, ordinal day, ordinal day^2, year, and the interactions between each climatic variable and both ordinal day and ordinal day^2.

We estimated species-specific intercepts (α_i) and effects for explanatory variables ($\boldsymbol{\beta}_\mathbf{i}$)–all of which were Z-standardized–within the matrix ($\mathbf{X}$) (Equation 2). Here, $\boldsymbol{\beta}_\mathbf{i}$ is a vector of effects for species *i*, with one coefficient per explanatory variable. The hierarchical means ($\boldsymbol{\mu}$) and hierarchical standard deviations ($\boldsymbol{\sigma}$) describe the mean and variability of the species-specific effects of each explanatory variable at each site (these are vectors with lengths equal to the number of explanatory variables) (Equation 3).

The model specification was as follows:

$$Y_{i,j,k} \sim \mathrm{bernoulli}\left(P_{i,j,k}\right), \tag{1}$$

$$\mathrm{logit}\left(P_{i,j,k}\right) = \alpha_i + \boldsymbol{\beta}_\mathbf{i}^\top \mathbf{X}_{i,j,k}, \tag{2}$$

$$\boldsymbol{\beta}_\mathbf{i} \sim \mathrm{normal}(\boldsymbol{\mu}, \boldsymbol{\sigma}), \tag{3}$$

$$\boldsymbol{\mu} \sim \mathrm{normal}(0, 20), \tag{4}$$

$$\boldsymbol{\sigma} \sim \mathrm{gamma}(2, 0.1), \tag{5}$$

$$\alpha_i \sim \mathrm{normal}(0, 1.5). \tag{6}$$

The main effect for each explanatory variable (climate variable or year) represents the direct effect of that variable on MO, where negative and positive effects indicate decreased and increased overall probabilities of occurrence (and thus abundance), respectively. The interaction effect between each explanatory variable and ordinal day represents the effect of that variable on TO, with negative effects indicating a shift to an earlier flight season and positive effects indicating a shift to a later season. These shifts apply to the entire probability of occurrence distribution. The interaction effect between each explanatory variable and ordinal day^2 represents the effect of that variable on LO, where negative values indicate a shorter flight season, and positive values indicate a longer season (this assumes a concave function for the probability of occurrence across the season) (Figure 1a–c).

These curves that were modeled using the biweekly presence and absence observations effectively describe the timing, length, and mid-season occurrence of butterfly species, capturing changes in the probability of occurrence across the flight period (Figure 1).

Separate models were fitted for each site. Our hierarchical approach enabled us to estimate the effects of each explanatory variable at two levels: for individual species within a site (captured by the β coefficients estimated for each explanatory variable at that site, this was estimated for each species) and across all species at a site (captured by the parameter μ estimated for each explanatory variable at that site), thus capturing both species-specific and site-level effects and variability (with the latter captured by the parameter σ estimated for each explanatory variable at that site). To maintain consistent interpretation of the regression coefficients, we excluded species whose peak probability of occurrence was at the beginning and end of the flight season, that is where the probability of occurrence distribution was convex rather than concave (this is expected, e.g., for some species that are most abundant very early in the season including species that overwinter as adults). This included five species at CP, one species at LC, and two species at SV.

All analyses were conducted in R (Version 4.2.2). We used relatively vague priors for all parameters estimated in our analysis (Equations 3–6). Posteriors were sampled using Hamiltonian Monte Carlo in Stan via the RStan package (Version 2.21.8). Four chains were run, each with 4000 iterations, and the first 2000 iterations were considered as the burn-in period. Model convergence was assessed through Gelman–Rubin diagnostics and trace plots (Gelman & Rubin, 1992; Vats & Knudson, 2021). Models were compared using Pareto-smoothed importance sampling and posterior predictive checks using the loo package (Version 2.5.1). The posterior distribution of each estimated parameter was summarized by calculating its median and 95% credible interval (CrI).

Temporal trends in flight period

To examine overall temporal trends in butterfly abundance and phenology, we fitted a baseline time model using the year (effect of year on MO), ordinal day of occurrence within that year, ordinal day^2, interaction between year and ordinal day (effect of year on TO), and interaction between year and ordinal day^2 (effect of year on LO) as explanatory variables. This initial model provided a framework to capture time-related changes in the period of flight, serving as a baseline to assess temporal trends. However, while time reflects overall patterns, it is not a causal factor. Thus, we further examined specific climatic factors that may underlie these trends and also explain the interannual variation in flight period.

Effect of climate on the annual flight period

To investigate the effects of climate on annual flight periods, we obtained daily climate data for each site, including minimum temperature, maximum temperature, precipitation, and snow water equivalent (SWE), from Daymet daily surface weather and climatological summaries, corresponding to the Daymet grid pixel (1 × 1 km spatial resolution) (Thornton et al., 2022). Minimum temperature, maximum temperature, and precipitation were averaged at both annual and seasonal levels, with seasons defined as follows: fall summaries represented the average daily climate data from September to November of the previous year, winter summaries covered December of the previous year through February of the current year, and spring summaries included March to May of the current year. We also calculated the mean daily SWE from September 1 of the previous year to May 31 of the current year. Using daily minimum and maximum temperature, we estimated growing degree days (GDD) accumulated from January 1 to May 31 of the current year using methods described in Cayton et al. (2015) with a minimum and maximum threshold of 10 and 30°C respectively. We considered 11 climatic variables, including the mean daily precipitation, daily minimum temperature, and daily maximum temperature for fall, winter, and spring, as well as GDD and SWE. We specifically focused on climate summaries from the previous fall, winter, and spring to understand how climate influences phenology as mediated through overwintering and early season developmental stages.

We employed a forward model selection approach to identify the combination of climatic variables that best predicts annual flight period across sites and among populations of species (Appendix S1: Table S1). This approach allowed us to compare the effects of climatic variables across sites. For each site, we first fit 11 single-climate variable models for each site, each incorporating a climatic variable as an additional variable beyond the baseline time model (this included effects of the variable on MO, TO, and LO). For every fitted model, we estimated the expected log pointwise predictive density (ELPD) via approximate leave-one-out cross-validation using the loo package (v2.5.1) in R. We then averaged ELPD values across sites to identify the single-climate variable model with the best predictive performance. The model with the highest average ELPD was selected as the best model (Vehtari et al., 2017). Building from this best-performing single-variable model, we added a second climatic variable to create ten two-climate variable models for each site and evaluated whether the additional variable improved model predictive performance. If performance improved, we retained the best two-climate variable model and repeated this process iteratively to test models with three climatic variables. Model building stopped once adding another climatic variable no longer improved predictive performance (Appendix S1: Table S1). All models incorporating climatic variables outperformed the baseline time model, suggesting that climate could account for additional variation in flight period. The model that included spring maximum temperature, spring minimum temperature, and winter precipitation (primarily snow at these montane sites) as climatic variables best predicts flight period of butterflies on average across sites (Appendix S1: Table S1). Model comparisons further showed that including year improved predictive accuracy relative to models without year (Appendix S1: Table S2). Correlations between year and these three climate variables were low (Appendix S1:

Figure S16), suggesting minimal confounding. Therefore, we used the model with year and these climate variables to investigate the effects of climate on the annual MO, TO, and LO of butterfly species.

Quantifying variation in climate responses across sites and species

To identify the scale at which variation in the effect of climate on flight periods is most pronounced, we quantified and compared variation in effects at three distinct levels. First, we assessed how the average effects of each climatic variable on MO, TO, and LO varied across sites by calculating the standard deviation of the estimated mean effects (the μs) across the five sites. Second, we evaluated the level of variation among species within sites by estimating the mean of all hierarchical standard deviations among species within each site (i.e., the mean of the estimated σ parameter for each climate variable averaged across sites). Lastly, we quantified variation among populations of species found in multiple (two or more) sites. This was accomplished by estimating the standard deviation in species-specific effects of climate on populations of each of the 104 species inhabiting two or more sites (out of 135 species total) and averaging these estimates across species.

To determine whether differences in the average effects of climatic factors at each site were caused by differences in species compositions versus differences in how the same species were affected by climate, we calculated correlations in climate effects among species shared between pairs of sites. High correlations between sites would suggest that differences in species composition drive differences in average effects among sites, whereas low correlations would suggest different effects of climate on the same species at different sites.

Disentangling the drivers of variation in climate effects on MO, TO, and LO

To evaluate the relative importance of the natural history traits of species and local climate conditions in driving variation in the effects of climate on different aspects of the flight period (MO, TO, and LO), we conducted redundancy analysis (RDA) and partial redundancy analysis (pRDA) using the vegan package (version 2.6-8) in R. First, we conducted an RDA using both species-level natural history traits and site-level climate variables as predictors, with the estimated effects of each climate variable on MO, TO, and LO as the response variables. To partition the independent contributions of each set of predictors, while accounting for potential collinearity, we then performed two pRDAs. In the first, we included only climate variables as predictors and conditioned on natural history traits. In the second, we included only natural history traits as predictors and conditioned on climate variables. The climate variables included site-level means and standard deviations of spring maximum temperature, spring minimum temperature, and winter precipitation calculated across all years at each site. The natural history traits considered were voltinism (univoltine or multivoltine), overwintering stage (egg, larva, pupa, or adult), diet breadth (monophagous or polyphagous, based on host plant genera), residency status (whether species breed and overwinter at the site), and ruderal status (whether species are typically associated with disturbed environments and exotic hosts).

To further assess the contribution of each natural history trait individually, we conducted an RDA using all five traits as predictor variables and the estimated climate effects on MO, TO, and LO as response variables. We then performed five separate pRDAs, each using one focal trait as the predictor while conditioning on the other four. Species without complete data on the five natural history traits were excluded from these analyses.

Trait and spatial variation in the relationships among the effect of climate on MO, TO, and LO

To investigate the possibility of consistent and generalizable relationships among the effects of climate on aspects of the flight period across species, we estimated the correlation between the species-specific effect of each climatic variable on TO versus LO, TO versus MO, and MO versus LO at each site. Because climate variables are multifaceted, often correlated, and could interact with each other, we also employed a multivariate approach using principal components analysis (PCA). This approach allowed us to simultaneously consider all climate variables and examine how their effects on different facets of the occurrence distribution were correlated. For each site, a PCA was performed using the species-specific effects of each climatic variable on each aspect of the flight period for species observed at that site. To examine whether species' natural history traits could influence how the effects of climate on different facets of the occurrence distribution are correlated, we quantified differences between groups under each trait (e.g., univoltine and multivoltine). We calculated Euclidean distances in multivariate space based on the first two PCA axes from the previous analysis (using the species-specific effects of each climatic variable on each aspect of the flight period for species observed at that site) and conducted a permutation test to assess whether the observed differences were greater than expected by chance. Finally, to determine whether relationships between the effects of climate on different aspects of the flight period are influenced by local climate at each site, we conducted an additional PCA that focused only on species found at all sites, ensuring that differences in species composition do not influence the results. For this, PCA was performed using species-specific effects of each climatic variable on each aspect of the flight period across all five sites.

RESULTS

Temporal trends in the occurrence distributions

We examined temporal changes in flight period as captured by the effect of year on MO, TO, and LO parameters describing the probability of occurrence across the flight period. Despite species-specific variability, we observed a consistent decline in MO across all sites, indicating a general decline in the average probability of occurrence for butterflies over time (Figure 3a). Additionally, species-level variation was evident in TO, with some species shifting toward earlier emergence, while others had a delayed flight season (Figure 3b). Similar species-specific patterns were observed for LO, with varying trends in the length of the flight period across species (Figure 3c).

Effects of climate on the occurrence distributions

Models incorporating climatic variables outperformed the time model, suggesting that climate explains additional variation in annual occurrence distributions and thus in phenology. The model with the highest predictive power across sites included spring maximum temperature, spring minimum temperature, and winter precipitation as predictors, suggesting these climatic factors explain interannual variation in butterfly abundance and phenology (Appendix S1: Figures S17–S61).

Overall, we did not detect credible site-level effects or consistent species-specific effects at each site for most climatic variables on MO, and thus on the overall probability of occurrence across the year, which is related to abundance (Figure 4a–c). However, a subset of species exhibited credible effects of each climatic variable on MO at each of the five sites. Moreover, at CP, we found a credible negative site-level effect of spring maximum temperature (−0.47, 95% CrI: −0.72 to −0.23) that was consistent across species with credible species-specific effects, suggesting that higher spring maximum temperatures reduced MO (Figure 4a). Similarly, at DP, we found a credible negative site-level effect of spring minimum temperature (−0.38, 95% CrI: −0.58 to −0.18), and this was consistent across species with credible species-specific effects, suggesting that higher spring minimum temperatures reduced MO (Figure 4c).

We found a consistent credible negative site-level effect of spring maximum temperature on TO at all sites: CP (−1.26, 95% CrI: −1.52 to −1.01), DP (−1.73, 95% CrI: −1.99 to −1.49), LC (−1.23, 95% CrI: −1.48 to −1), SV (−0.66, 95% CrI: −0.9 to −0.43), and WA (−1.2, 95% CrI: −1.48 to −0.94). Negative effects were also observed for all species with credible species-specific effects within each site. This suggests that higher spring maximum temperatures are associated with earlier flight seasons across all sites and for many species (Figure 4d). Winter precipitation had a credible positive site-level effect on TO at higher elevation sites, CP (0.71, 95% CrI: 0.48–0.94) and DP (0.85, 95% CrI: 0.64–1.06). This positive effect was also consistent across all species with credible species-specific

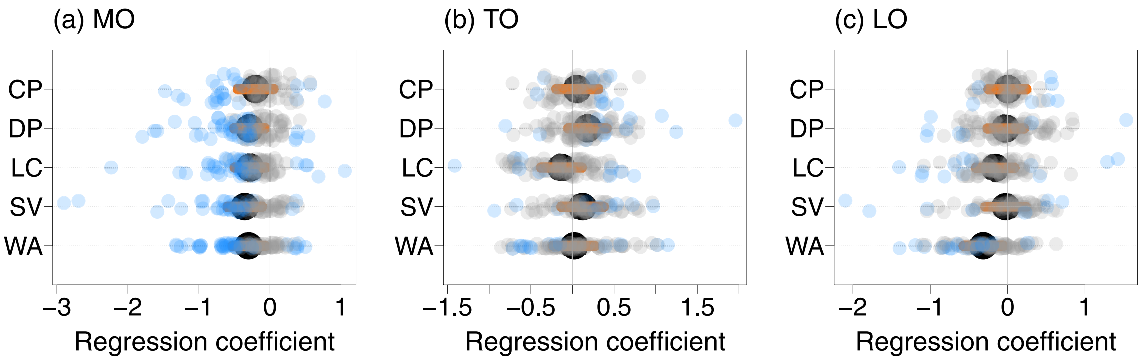

FIGURE 3 Temporal trends in butterfly flight period at each site. Each panel shows the effect of year on the (a) mid-season occurrence (MO), (b) timing of occurrence (TO), and (c) length of occurrence (LO) for each butterfly species at each site. In each panel, large black points with orange bars show the site-level response and 95% credible intervals (CrIs). The small points show population-specific responses; blue colored points denote credible population-level effects, whereas gray colored points indicate cases where 95% CrIs for population effects include 0.

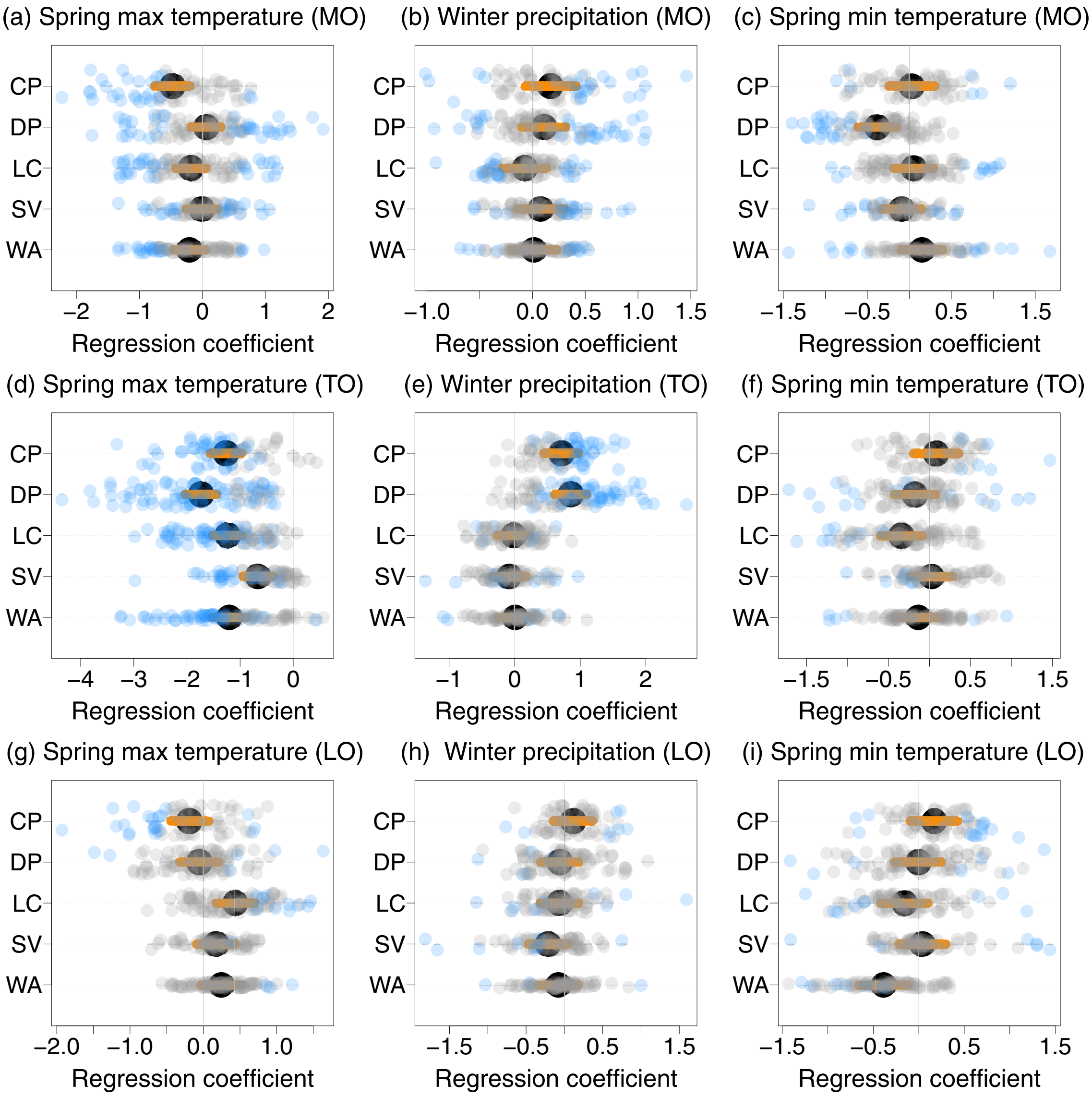

FIGURE 4 Effect of climate on butterfly flight period at each site. Results are shown for the effect of (a) spring maximum temperature on the mid-season occurrence (MO), (b) winter precipitation on the mid-season occurrence (MO), (c) spring minimum temperature on the mid-season occurrence (MO), (d) spring maximum temperature on the timing of occurrence (TO), (e) winter precipitation on the timing of occurrence (TO), (f) spring minimum temperature on the timing of occurrence (TO), (g) spring maximum temperature on length of occurrence (LO), (h) winter precipitation on length of occurrence (LO), (i) spring minimum temperature on length of occurrence (LO). In each panel, large black points with orange bars show the site-level response and 95% credible intervals (CrIs). The small points show species-specific responses; blue colored points denote credible population-level effects, whereas gray colored points indicate cases where 95% CrIs for population effects include 0.

effects at both sites suggesting that increased winter precipitation is associated with later flight periods at these two high-elevation sites. We found heterogeneity in the effect of winter precipitation among species at other sites (Figure 4e). The effect of spring minimum temperature on timing was also heterogeneous within sites, except at LC, where we found a credible negative site-level effect, indicating that higher spring minimum temperatures are associated with earlier flight periods (Figure 4f).

In general, we did not find credible site-level or consistent species-specific effects of climatic variables on LO (Figure 4g–i). Nonetheless, a modest subset of species exhibited credible effects of each climate variable on LO at each of the five sites. In addition, at LC we found a credible positive site-level effect of spring maximum temperature (0.43, 95% CrI: 0.20–0.67), suggesting that higher spring maximum temperatures were associated with a longer season for most species (Figure 4g). Conversely, at WA, we found a credible negative site-level effect of spring minimum temperature (−0.39, 95% CrI: −0.63 to −0.14), indicating that higher spring minimum temperatures were associated with shorter seasons (Figure 4i).

Quantifying variation in climate responses across sites, within sites, and among populations

We analyzed variation in the effect of climate on different aspects of the occurrence distribution (MO, TO, and LO) at three levels: variation in the average effect of a climatic variable across sites, variation in species-specific effects among species within a site averaged across sites, and variation in species-specific effects for each species among sites (populations) averaged across species. The results revealed substantial heterogeneity in the effects of all climatic variables (spring maximum temperature, winter precipitation, and spring minimum temperature) on each facet of the probability of occurrence distribution (Figure 5). The greatest heterogeneity was found among

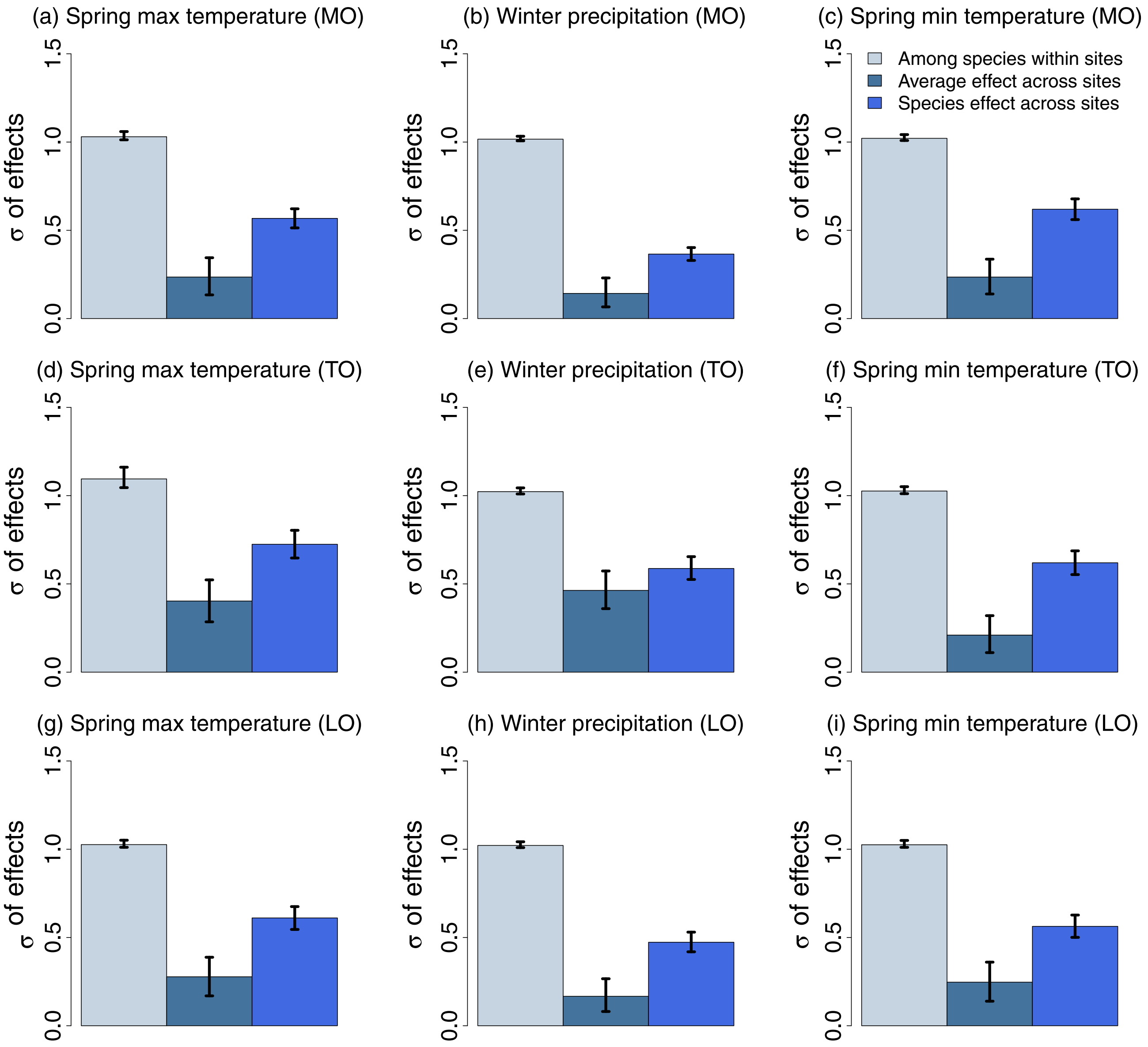

FIGURE 5 Variability in the effect of each climatic variable on butterfly flight period among species within a site (among species within sites), across all sites (average effect across sites), and among populations of a species across sites (species effect across sites). Results are shown for the effect of (a) spring maximum temperature on the mid-season occurrence (MO), (b) winter precipitation on the mid-season occurrence (MO), (c) spring minimum temperature on the mid-season occurrence (MO), (d) spring maximum temperature on the timing of occurrence (TO), (e) winter precipitation on the timing of occurrence (TO), (f) spring minimum temperature on the timing of occurrence (TO), (g) spring maximum temperature on length of occurrence (LO), (h) winter precipitation on length of occurrence (LO), (i) spring minimum temperature on length of occurrence (LO). Colored bars denote the estimated standard deviations (**σ** of effects) and error bars denote 95% credible intervals on these estimates. Higher standard deviation indicates higher variability. The greatest heterogeneity was found among species within sites, followed by populations of the same species across different sites, with the least heterogeneity observed for mean effects across sites.

species within sites, followed by populations of the same species across different sites, with the least heterogeneity observed for mean effects across sites (Figure 5).

The heterogeneity we detected in the effects of climate across sites was not solely due to differences in species composition across sites (Appendix S1: Figure S62). Specifically, with the exception of CP versus DP, which responded similarly to climate overall (Figure 4), species-level effects of climate on flight period were only weakly correlated for pairs of sites (Appendix S1: Figure S62a–e). In other words, the same climatic factor often had distinct effects on a given species at different sites.

Disentangling the drivers of variation in climate effects on MO, TO, and LO

When examining the relative importance of natural history traits of species and local climate conditions in driving variation in the effects of climate on MO, TO, and LO, we found that both sets of predictors together significantly explained 32.8% of the total variation. Local climatic conditions alone explained 16.2% of this variation (49.5% of the variation explained by the full model), even after controlling for natural history traits. This indicates a strong association between local climate and the effects of climate on different aspects of the flight period. Natural history traits, when controlling for local climate, accounted for 15.4% of the variation (47.0% of the explained variation) (Table 1).

When examining the contribution of each natural history trait individually, we found that the five traits collectively explained 16.6% of the variation in the effects of climate on MO, TO, and LO. Overwintering stage and voltinism explained the most variation in climatic effects on phenology, 5.3% and 2.8% of the variation after accounting for the effects of other traits (32.1% and 17.0% of the explained variation), respectively. Diet breadth accounted for an additional 1.1% of the variation (6.6% of the explained variation). In contrast, residency status explained none of the variation, and ruderal status had no significant effect. Notably, the largest percentage of the variation explained by the full model (43.1%) could not be uniquely attributed to any of the five traits. This suggests that multiple traits covary in ways that make it impossible to attribute effects to any one trait individually (Appendix S1: Table S3). Overall, these results indicate that variation in how climate affects MO, TO, and LO is jointly driven by local environmental conditions and natural history traits. Local conditions appear to be slightly more influential. Among traits, voltinism and overwintering stage are particularly important.

Trait and spatial variation in the relationships among the effect of climate on MO, TO, and LO

To determine the extent to which the species-specific effect of each climatic variable on one facet of the occurrence distribution was associated with its effect on others, we estimated correlations between the species-specific effects of each climatic variable on MO and TO, MO and LO, and TO and LO at each site. Overall, we found that these correlations were weak such that climatic factors have largely independent effects on different aspects of the flight period (Figure 6). There were some notable exceptions to this general pattern, which suggest a stronger coupling of phenological properties at the highest elevation sites. For example, we found moderate positive correlations between the effect of spring maximum

TABLE 1 Results of partial redundancy analysis (pRDA) decomposing the influence of local climate and species natural history traits on the effects of climate variables (spring maximum temperature, spring minimum temperature, and winter precipitation) on each aspect of the flight period (mid-season occurrence, timing of occurrence, and length of occurrence).

RDA/partial RDA models	Variance	R^2	$p(>F)$	Proportion of explainable variance	Proportion of total variance
Full model: $F =$ natural history + local climate	0.914	0.328	0.001	1	0.328
Pure Climate: $F =$ local climate | (natural history)	0.452	0.162	0.001	0.495	0.162
Pure Natural history trait: $F =$ natural history | (local climate)	0.430	0.154	0.001	0.470	0.154
Confounded effects of climate and natural history traits	0.032			0.035	0.012
Total unexplained	1.875				0.672
Total variance	2.789				1

Note: The proportion of explainable variance refers to the fraction of total constrained variation explained by the full model. | indicates that the effect of the variable on the left is assessed while controlling for the variables in parentheses.

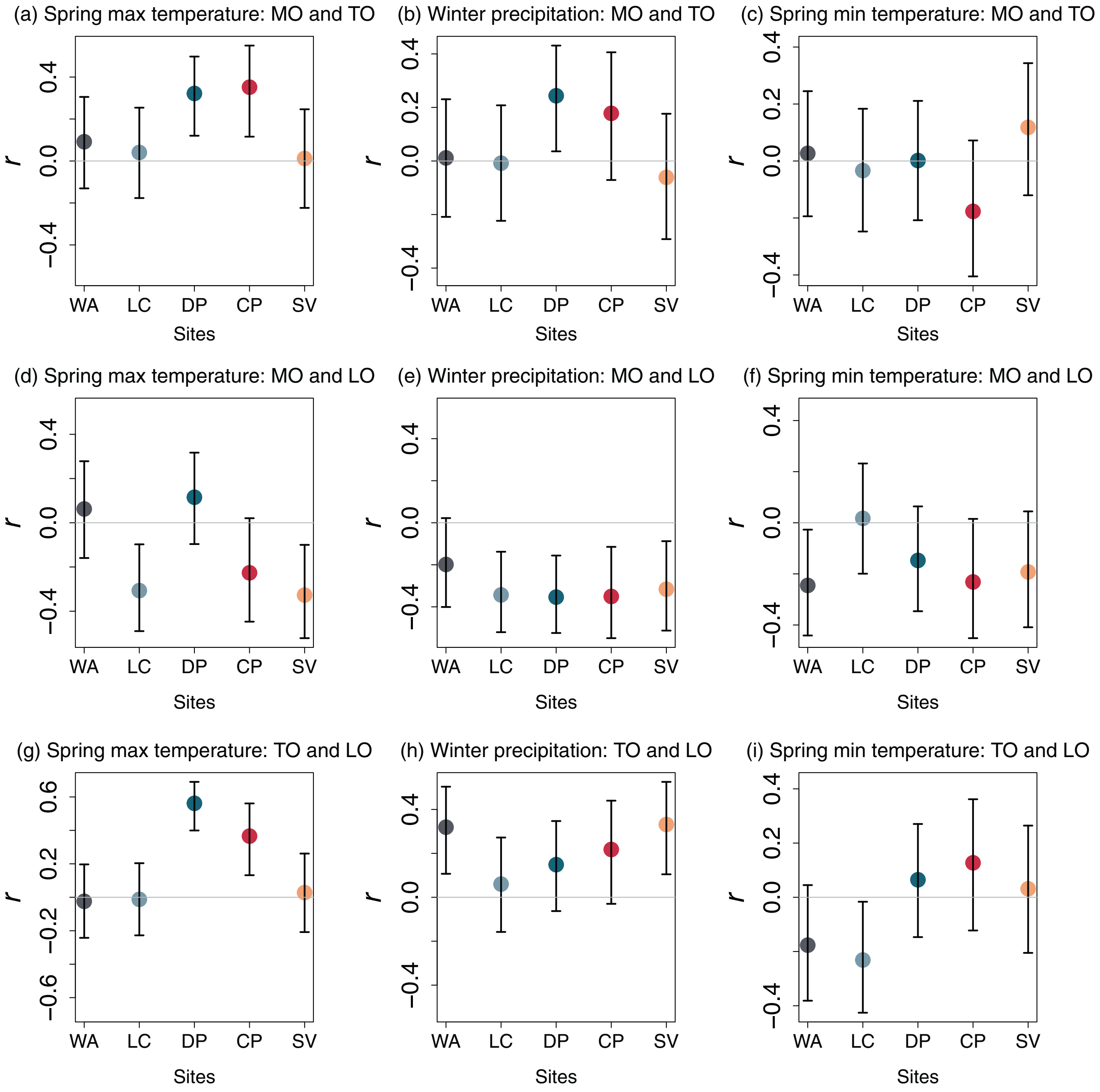

FIGURE 6 Relationship between the effect of each climatic variable on different aspects of the occurrence distribution of species at each site as captured by the Pearson correlation coefficient (*r*). The panels show (a) the correlation between the effects of spring maximum temperature on the mid-season occurrence and timing of occurrence (MO and TO), (b) the correlation between the effects of winter precipitation on the mid-season occurrence and timing of occurrence (MO and TO), (c) the correlation between the effects of spring minimum temperature on the mid-season occurrence and timing of occurrence (MO and TO), (d) the correlation between the effects of spring maximum temperature on the mid-season occurrence and length of occurrence (MO and LO), (e) the correlation between the effects of winter precipitation on the mid-season occurrence and length of occurrence (MO and LO), (f) the correlation between the effects of spring minimum temperature on the mid-season occurrence and length of occurrence (MO and LO), (g) the correlation between the effects of spring maximum temperature on the timing and length of occurrence (TO and LO), (h) the correlation between the effects of winter precipitation on the timing and length of occurrence (TO and LO), and (i) the correlation between the effects of spring minimum temperature on the timing and length of occurrence (TO and LO). The correlation coefficient indicates the similarity in the effect of each climatic variable on two compared aspects of the occurrence distribution of species at each site. The error bars denote 95% CIs.

temperature on MO and TO at CP (0.35, 95% CI: 0.12–0.55) and DP (0.32, 95% CI: 0.12–0.50), suggesting that the effects of spring maximum temperature on MO and TO covary more strongly at high elevations. Similarly, we detected moderate correlations in the effect of spring maximum temperature on TO and LO at CP

(0.37, 95% CI: 0.13–0.56) and DP (0.56, 95% CI: 0.40–0.69), again indicating higher covariance at higher elevations. Lastly, there were moderate negative correlations in the effect of winter precipitation on MO and LO at CP, DP, LC, and SV (CP: −0.35, 95% CI: −0.55 to −0.11, DP: −0.35, 95% CI: −0.52 to −0.16, LC: −0.34, 95% CI: −0.52 to −0.14, and SV: −0.32, 95% CI: −0.51 to −0.09) (Figure 6).

To simultaneously assess the influence of multiple climatic variables and examine how their species-specific effects on different facets of the occurrence distribution are correlated, we used a PCA. This approach enabled us to move beyond pairwise correlations and detect broader patterns of how each climate variable impacts various aspects of the occurrence distribution simultaneously. The first two principal components explained 48.6%, 51.4%, 39.8%, 39.9%, and 41.7% of the variance at CP, DP, LC, SV, and WA, respectively. At CP and DP (the highest elevation sites), the first principal component explained variation in the effect of climate on TO and MO, while the second principal component (PCA 2) captured variation in climatic effects on LO (Figure 7a,b). This indicates that the effects of climate on flight season length diverge from its effects on the timing and abundance of butterflies at these sites. Interestingly, this pattern was not detected at the lower elevation sites–LC, SV, and WA (Figure 7c–e), suggesting site-specific associations.

We found that at CP, DP, SV, and WA, the relationship between the effects of climate on different aspects of the flight period differed significantly between multivoltine and univoltine species, with Euclidean distances of 1.64, 1.85, 1.03, and 1.24, respectively. Permutation tests confirmed that these differences were statistically significant ($p < 0.05$), suggesting that voltinism may influence, or be associated with, how climate effects on different facets of the occurrence distribution are correlated. No significant difference was observed at LC (Appendix S1: Figure S63). Similarly, the relationship between climate effects on MO, TO, and LO differed significantly between resident and nonresident species at CP, DP, and LC (Euclidean distances: 1.65, 1.69, and 1.72; $p < 0.05$), but not at SV or WA (Appendix S1: Figure S64). These results indicate that residency status may shape how species experience climatic influences on different aspects of their flight periods. We also found significant differences between ruderal and nonruderal species at CP, DP, and WA (Euclidean distances: 1.71, 1.49, and 1.24; $p < 0.05$), suggesting that ruderal status may play a role in modulating the effect of climate on flight periods. No significant differences were observed at LC or SV (Appendix S1: Figure S65). In contrast, we did not detect differences between monophagous and polyphagous species in the relationship between climate effects on MO, TO, and LO at any site (Appendix S1: Figure S66). For overwintering stage, significant differences in the relationship between the effect of climate on different aspects of the flight period were observed only between specific groups at CP and SV: species overwintering as eggs or pupae differed significantly from those overwintering as larvae and pupae ($p < 0.05$). At DP, we found significant differences between all compared overwintering stages. However, no significant differences were found at LC or WA (Appendix S1: Figure S67). Finally, we examined whether the associations between the effects of climate on different aspects of the flight period show similar patterns across sites. Our analysis showed that patterns of association were often site-specific. However, these patterns were more similar between geographically proximate sites, such as CP and DP, and LC and WA (Figure 7f).

DISCUSSION

Climate change is having widespread consequences for the phenology of wild plants and animals (Cohen et al., 2018; Forister et al., 2018; Newson et al., 2016; Parmesan, 2006, 2007). Long-term datasets that span diverse habitats and elevational gradients, such as the dataset analyzed in this study, provide critical insights into the effects of climate on the timing of life history events, like the flight of adult insects. By examining both site- and species-level responses, we quantified the distinct effects of climate at both the species and community levels. Consistent with prior studies, we found that the flight periods of butterfly species are changing over time (Colom et al., 2021; Habel et al., 2024). Furthermore, our results indicate declines in MO over time across all sites, suggesting that butterfly populations are becoming increasingly scarce and less abundant. Similar recent declines in abundance have been documented across the United States and in previous studies of data from our focal sites that modeled abundance without considering phenology (that is, studies that did not allow the probability of occurrence to vary across the season within years) (Edwards et al., 2025; Forister et al., 2021; Halsch et al., 2024; Wepprich et al., 2019).

Our findings complement and extend earlier research reinforcing the idea that climate is a major driver of phenological shifts in butterfly populations. Specifically, our models identified spring maximum temperature, winter precipitation, and spring minimum temperature as the most influential climatic predictors (among those considered) of butterfly flight period across all sites. TO was particularly sensitive to spring maximum temperatures, with warmer temperatures resulting in earlier emergence

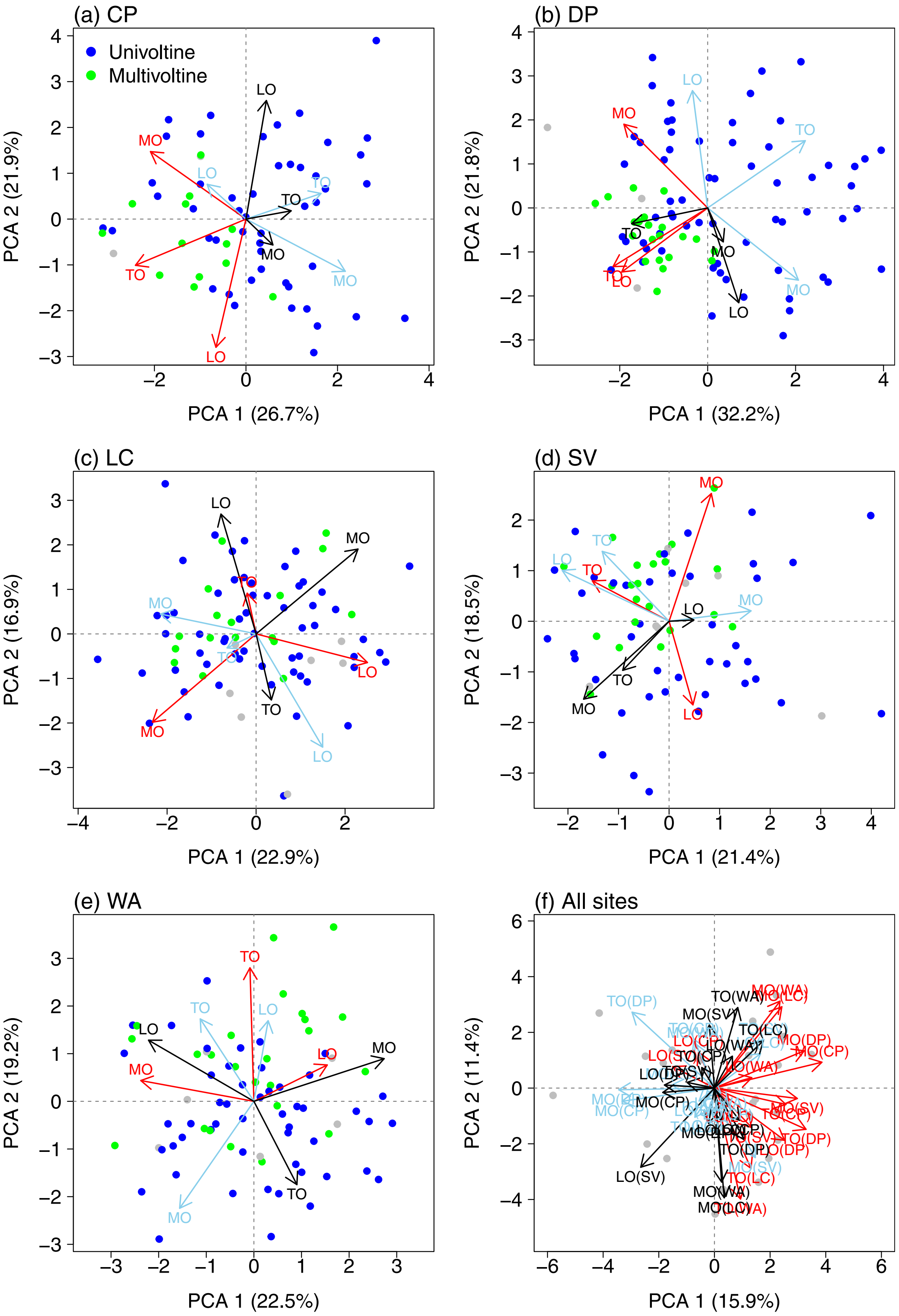

FIGURE 7 Legend on next page.

at all sites. This finding is consistent with previous studies that report earlier emergence of butterfly species under warming conditions (Colom et al., 2021; Forister & Shapiro, 2003; Gutiérrez & Wilson, 2021; Habel et al., 2024; Parmesan, 2007), likely due to increased developmental rates of larva and pupa at higher temperatures. At higher elevation sites–CP and DP–we observed a pronounced effect of winter precipitation on TO, with increased precipitation leading to delayed TO. Higher winter precipitation, which usually comes in the form of snow at these elevations, could act as a thermal buffer, insulating the ground and maintaining cooler temperatures that slow the development of overwintering stages of butterflies as well as their host plants and nectar sources (Inouye, 2008; Konvicka et al., 2021). This finding further highlights the critical role of winter precipitation, particularly in montane habitats, emphasizing the idea that changes in winter precipitation are as crucial as temperature changes in shaping the phenology of insects and other ecological processes.

In addition, our results underscore the substantial influence of even modest increases in spring minimum (nighttime) temperatures on the flight period. Nighttime temperatures can impact caterpillar growth, survival, and behavior (Yang et al., 2025). However, studies on insect phenology or abundance have often focused on daily maximum temperature or average daily temperatures, overlooking the impact of nighttime temperatures, which are increasing more rapidly due to climate change at these sites and in many other regions (Speights et al., 2017; Vasseur et al., 2014). Our findings suggest that nighttime warming may elicit different physiological and phenological responses compared to daytime warming. These varying responses to extreme daily (minimum nighttime and maximum daytime temperatures) conditions can be obscured when using average daily temperatures as a metric (Ma et al., 2015). By considering both minimum and maximum daily temperatures, rather than relying solely on averages, we can obtain a more nuanced understanding of ecological responses to unusual weather events, daily fluctuations, or specific temperature thresholds, which are often critical but underappreciated in phenology studies.

We observed the highest heterogeneity in the effect of climate among species within sites, followed by populations of the same species across different sites, with the least heterogeneity observed for the average effect of climate across sites. Local climate appears to be slightly more influential than species natural history traits in driving variation in how climate affects MO, TO, and LO. Among traits, voltinism and overwintering stage are particularly important.

Our analysis further reveals that climate affects different facets of the occurrence distribution in distinct ways. MO, TO, and LO did not respond uniformly to climate variables across species, reinforcing the limitations of focusing exclusively on metrics such as the day of first flight. Knowing how climate affects one aspect of the flight period (e.g., timing) does not reliably predict its effect on others (e.g., duration), as these components often shift independently, with species exhibiting a variety of response patterns. Importantly, we observed site-specific patterns that were not solely attributable to differences in species composition, suggesting that local environmental conditions such as slope, exposure, geology, and microclimatic variation likely play a critical role in shaping how climate drives changes in each aspect of the butterfly occurrence distributions at different locations. This complicates predictions of phenology and population dynamics across unmonitored parts of the flight period. Such complexities can confound meta-analyses that synthesize studies that quantify different components of the flight period, potentially leading to overgeneralization or obscuring the true extent of phenological change. Such misinterpretations may ultimately hinder our understanding of climate-driven phenological mismatches and their ecological consequences. However, we find that species' natural history traits including voltinism, residency status, ruderal status, and overwintering stage are associated with how climate effects on different facets of the flight period are related. This suggests some consistency and the possibility for generalizable relationships among the effects of climate on aspects of the flight period (MO, TO, LO) among groups of species that share similar traits. Our findings complement and extend earlier research suggesting that the natural history traits of species play a significant role in determining their phenological responses to climate (Diamond et al., 2011; Zografou et al., 2021).

FIGURE 7 Principal component analysis (PCA) of the effects of all climate variables on different aspects of the flight period (mid-season occurrence [MO], timing of occurrence [TO], length of occurrence [LO]) across species observed at (a) Castle Peak, (b) Donner Pass, (c) Lang Crossing, (d) Sierra Valley, (e) Washington, and (f) all sites. Red arrows represent the effect of spring maximum temperature, blue arrows represent the effect of winter precipitation, and black arrows represent the effect of spring minimum temperature. Blue points represent univoltine species while green points represent multivoltine species. The first two principal components explained 48.6%, 51.4%, 39.8%, 39.9%, and 41.7% of the variance at CP, DP, LC, SV, and WA, respectively.

Our findings emphasize the importance of winter precipitation and night temperature on phenology, especially flight periods of ectotherms in montane environments, and reveal that climate impacts on different aspects of the flight period vary among species and populations of the same species across sites. This variation is modulated by both species' natural history traits and local climatic conditions, with local climate appearing slightly more influential overall. Among traits, voltinism and overwintering stage emerge as particularly important. We also highlight the value of considering the entire flight period to better improve our understanding and predictions of how species will respond to climate change. Conservation strategies must recognize that populations of the same species may respond differently to climate change depending on their traits, location, and ecological context. We acknowledge that some species observed at these sites (albeit a minority) are migratory and do not directly experience winter or spring weather conditions at these sites, as they overwinter in different areas. However, climate patterns are increasingly becoming more spatially and temporally auto-correlated in the face of climate change, making it plausible for climate conditions in the study area to have indirect associations with offsite climate effects (Di Cecco & Gouhier, 2018; Liebhold et al., 2004) (also see Figure 2c–e). Finally, this study highlights the complexity of predicting climate-driven changes in phenology and stresses the need for species- and site-specific approaches, as local adaptation could buffer or exacerbate the effects of global climate trends on a regional scale. By adopting a more holistic view of phenological responses, we can gain deeper insights into how species respond to changing climatic conditions, better inform conservation strategies, and improve our ability to predict future phenological patterns in a warming world.

AUTHOR CONTRIBUTIONS

Gbolahan A. Reis: Conceptualization (equal); data curation (equal); formal analysis (lead); funding acquisition (equal); methodology (equal); visualization (lead); writing—original draft preparation (lead); writing—review and editing (equal). **Matthew L. Forister:** Conceptualization (equal); data curation (equal); investigation (equal); funding acquisition (equal); writing—review and editing (equal). **Christopher A. Halsch:** Data curation (equal); investigation (equal); writing—review and editing (equal). **Clare M. Dittemore:** Data curation (equal); investigation (equal); writing—review and editing (equal). **Arthur M. Shapiro:** Data curation (equal); investigation (equal); writing—review and editing (equal). **Zachariah Gompert:** Conceptualization (equal); data curation (equal); funding acquisition (equal); methodology (equal); supervision (lead); and writing—review and editing (equal).

ACKNOWLEDGMENTS

We gratefully acknowledge the support and resources provided by the Center for High Performance Computing at the University of Utah. This work was also supported by the National Science Foundation (DEB-2114974 to Zachariah Gompert, DEB-2114973 to Matthew L. Forister), the Utah State University Ecology Center Research Award (A07339-1092), and the American Philosophical Society grant to Gbolahan A. Reis.

FUNDING INFORMATION

National Science Foundation, Grant/Award Numbers: DEB-2114794 and DEB-2114973, and Utah State University Ecology Center Research Award A07339-1092.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Reis et al., 2025) are available in Dryad at https://doi.org/10.5061/dryad.sxksn03h0.

ORCID

Gbolahan A. Reis https://orcid.org/0000-0002-3967-6118

Matthew L. Forister https://orcid.org/0000-0003-2765-4779

Christopher A. Halsch https://orcid.org/0000-0003-1381-1905

Clare M. Dittemore https://orcid.org/0000-0003-2182-9320

Zachariah Gompert https://orcid.org/0000-0003-2248-2488

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SUPPORTING INFORMATION

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

How to cite this article: Reis, Gbolahan A., Matthew L. Forister, Christopher A. Halsch, Clare M. Dittemore, Arthur M. Shapiro, and Zachariah Gompert. 2026. "Climate and Species Traits Give Rise to Complex Phenological Dynamics." *Ecology* 107(1): e70297. https://doi.org/10.1002/ecy.70297