

# Evolved Phenological Cueing Strategies Show Variable Responses to Climate Change

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**ABSTRACT:** Several studies have documented a global pattern of phenological advancement that is consistent with ongoing climate change. However, the magnitude of these phenological shifts is highly variable across taxa and locations. This variability of phenological responses has been difficult to explain mechanistically. To examine how the evolution of multitrait cueing strategies could produce variable responses to climate change, we constructed a model in which organisms evolve strategies that integrate multiple environmental cues to inform anticipatory phenological decisions. We simulated the evolution of phenological cueing strategies in multiple environments, using historic climate data from 78 locations in North America and Hawaii to capture features of climatic correlation structures in the real world. Organisms in our model evolved diverse strategies that were spatially autocorrelated across locations on a continental scale, showing that similar strategies tend to evolve in similar climates. Within locations, organisms often evolved a wide range of strategies that showed similar response phenotypes and fitness outcomes under historical conditions. However, these strategies responded differently to novel climatic conditions, with variable fitness consequences. Our model shows how the evolution of phenological cueing strategies can explain observed variation in phenological shifts and unexpected responses to climate change.

**Keywords:** phenological shifts, climate change, evolved cueing strategies, cryptic genetic variation, novel climates, cue integration.

## Introduction

Recent years have seen increasing interest in the study of phenological shifts. While organisms around the world have generally shown a “globally coherent fingerprint” of advancing phenology with climate change (Parmesan and Yohe 2003; Parmesan 2007; Thackeray et al. 2010), several studies also point to substantial unexplained variation in phenolog-

ical shifts (Parmesan 2007; Thackeray et al. 2010; Pearse et al. 2017). This variation in the responses to climate change is an important factor driving phenological mismatch and the disruption of species interactions (Parmesan 2006; Khrouba et al. 2018). It has become increasingly clear that understanding how organisms integrate multiple environmental cues will be necessary to anticipate phenological shifts (Forrest and Miller-Rushing 2010; Visser et al. 2010; Pau et al. 2011; Chmura et al. 2019).

Although several studies have suggested factors that correlate with variation in phenological shifts (e.g., Parmesan 2007; Thackeray et al. 2010), relatively few studies have examined mechanistic explanations for this variation (Chmura et al. 2019). For example, while taxonomic groupings are often strong predictors of phenological shifts (Parmesan 2007; Davis et al. 2010; Thackeray et al. 2010, 2016; Davies et al. 2013), the mechanisms behind these groupings remain idiosyncratic or unclear (e.g., Parmesan 2007; Thackeray et al. 2010). The mechanisms for other proposed explanatory factors are similarly unresolved. Chmura et al. (2019) reviewed nine factors that have been suggested to structure variation in phenological shifts (including latitude, elevation, habitat, trophic level, life history, specialization, seasonal timing, thermoregulation, and generation time) and concluded that most studies either do not suggest specific underlying mechanisms or do not evaluate alternative mechanistic hypotheses.

Our current study builds on previous modeling studies that explored phenological cueing strategies in a general context. These studies represent a progression from single-cue to multicue models and toward more realistic environmental conditions. For example, Reed et al. (2010) used an individual-based model to examine plastic responses to simulated variation in a single cue and found that plasticity buffered fitness from environmental variation if the cue provided reliable information about environmental conditions but had the opposite effect when the correlations between cues and conditions were weakened or when environmental

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variability was high. McNamara et al. (2011) developed a general analytical model based on a regression and correlation framework to explore the relationship between cues and optimal phenological timing under changing environments and showed that environmental changes can affect the information value of cues in complex ways; as a result, they suggest that multiple cues could provide more robust predictive power than single cues (see also Tauber and Tauber 1976; Danks 2007; Marchin et al. 2015). Chevin and Lande (2015) developed a multicue model to evaluate the evolution of multiple reaction norms in response to simulated environmental variation that included multiple correlated but fluctuating cues. This work showed that singular reaction norms can evolve to show plasticity that appears maladaptive when evaluated outside the multicue context, as a result of the correlated nature of environmental cues.

Here we present a generalized model that demonstrates how the evolution of integrated multitrait cueing strategies can yield variable phenological responses to climate change. This model advances key themes established in previous studies by allowing cue integration strategies to evolve in the context of more complex real-world environmental conditions. While previous modeling studies show that optimal multicue integration strategies depend on correlations among environmental cues (e.g., Chevin and Lande 2015), those results were based on simulated environments with known correlations. Our model aims to examine general mechanisms that emerge when organisms evolve to use the predictive information within real-world climatic data from different locations. Real-world climatic data are characterized by complex correlations among variables, and we assume that this correlation structure varies across locations, with relatively similar properties in nearby locations and increasingly different properties in distant locations. Specifically, we examine how phenological cueing strategies could evolve to use correlations among climate variables to anticipate future events and how these evolved strategies could contribute to observed phenological variation when historical correlations among climatic variables are disrupted.

We hypothesized that variation in cueing strategies could arise if organisms experiencing different environmental histories evolve different phenological strategies, caused by consistent differences in the reliability of predictive information provided by different kinds of environmental cues (Reed et al. 2010; McNamara et al. 2011; Chevin and Lande 2015). If the evolution of phenological cueing strategies was shaped by past environmental conditions in predictable ways, we expected that similar phenological strategies would evolve when organisms experienced similar historical climates. Conversely, variation among evolved strategies could persist under the same historical climate if different strategies were able to yield similar fitness outcomes. We further

hypothesized that variation among evolved cueing strategies in their reliance on climatic and nonclimatic cues could contribute to observed variation in phenological responses to climate change (Bonamour et al. 2019; Chmura et al. 2019).

### Model and Methods

Our model simulates the evolution of a generalized, annual, asexually reproducing organism in a simplified environment defined by daily maximum temperature, total daily precipitation, and day of the year (hereafter, temperature, precipitation, and day, respectively). These conditions provide cues to anticipate future environmental conditions and determine the fitness of individuals in the population (fig. 1).

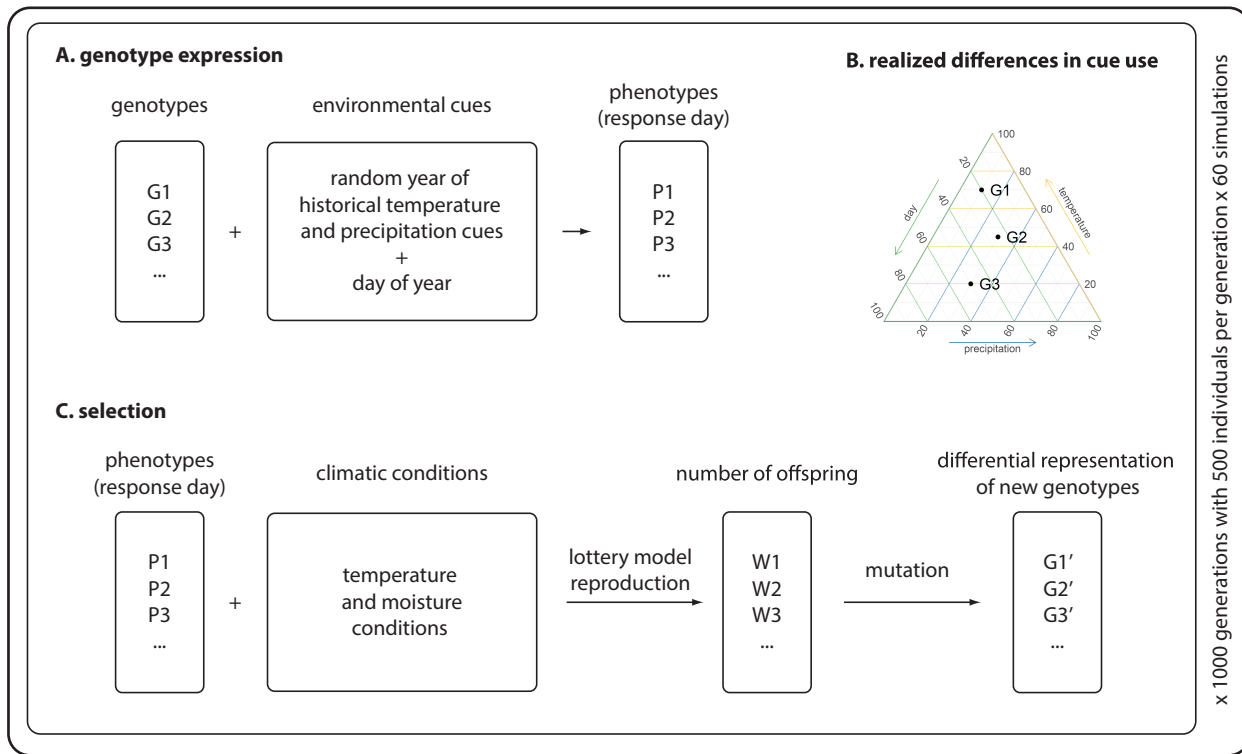
Our model combines the following three key features: (1) organisms combine multiple environmental cues using a weighted sum, (2) organisms make a phenological decision in response to a threshold of this weighted sum, and (3) organismal sensitivity to each environmental cue is an evolved trait. Each of these features has been described across a wide range of organisms in nature (Gu et al. 2008; Wilczek et al. 2010; Burghardt et al. 2014; Seeholzer et al. 2018). We implemented the simulation model and all analyses in R (R Core Team 2019).

#### *Cue Integration*

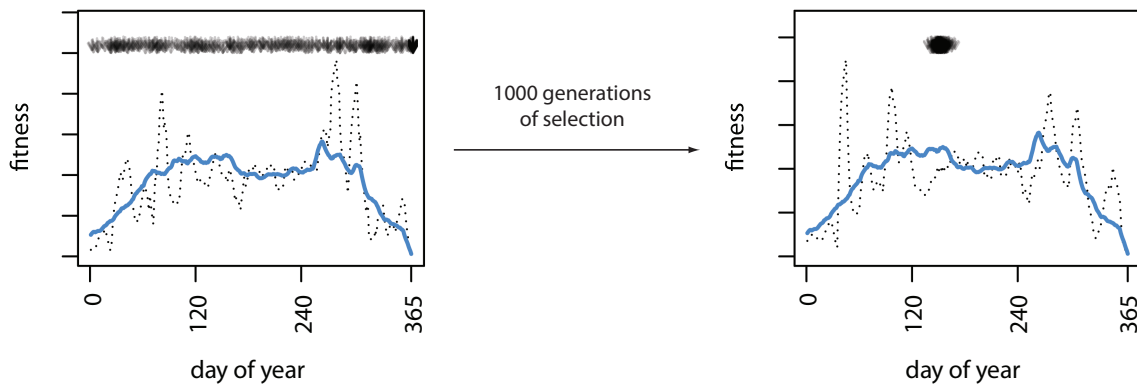
In our model, the set of environmental cues  $E$  is composed of cumulative annual daily maximum temperature ( $\gamma_{\text{temp}}$ ), cumulative annual daily precipitation ( $\gamma_{\text{precip}}$ ), and day of the year ( $\gamma_{\text{day}}$ ):

$$E = [\gamma_{\text{temp}}, \gamma_{\text{precip}}, \gamma_{\text{day}}]. \quad (1)$$

The set of environmental cues begins to accumulate on the first day of each year, and the cues change each day in each year of each location based on historical climatic data (we omit daily, yearly, and location subscripts for simplicity in this notation; see “Environmental Data” below). The use of cumulative annual temperature and precipitation assumes that organisms are aware of and can be influenced by past environmental conditions, consistent with degree-day models of development and phenology. Day of the year provides a proxy for a consistent and nonclimatic environmental cue, assuming that organisms are able to infer the day of the year (e.g., from photoperiod) with equal accuracy across all locations. Although the amplitude of seasonal photoperiodic changes is larger at higher latitudes, this assumption is supported by studies showing that tropical species are able to detect extremely small changes in photoperiod near the equator (Hau et al. 1998; Dawson 2007). More fundamentally, this assumption allows us to conservatively infer



**D. evolution of phenological cueing strategies**



**Figure 1:** Schematic diagram of the model. *A*, Genotypes combined with environmental cues (including cumulative annual daily temperature maximums, cumulative annual daily precipitation totals, and day of year) result in expressed phenotypes (day of response). *B*, Trait effect ( $T$ ), the proportional contribution of each trait to the response decision (a representation of the interaction between genotype and environment), can be expressed as a composition and presented on a ternary plot. *C*, Fitness of different phenotypes is determined by climatic (temperature and moisture) conditions during a 10-day window after the response threshold is crossed. A lottery model of reproduction determines the number of offspring produced by each individual, and mutation results in new genotypes for the next generation. *D*, Selection results in evolved phenological cueing strategies that anticipate favorable conditions and avoid unfavorable conditions. The solid blue line represents the long-term expected fitness outcome for each day under historical conditions, while the dotted black lines represent the fitness outcomes for the first and last year of the simulation for the left and right panels, respectively. The black arrows at the top of each panel represent the response day of each individual of the population. Initially, the timing of phenological response is spread across the year, but after 1,000 generations of selection, most of the population shows similar phenological timing. This example shows the results of one simulation using climatic data from Davis, California.

the relative information content of a climatically invariant cue across multiple locations, separate from the effect of increasing photoperiodic amplitude at higher latitudes. Using actual cumulative photoperiod produced qualitatively similar results (e.g., fig. S1; figs. S1–S17 are available online).

Each individual in our model has a genotype ( $G$ ) defined by three traits ( $\tau$ ), which reflect its phenological sensitivity (sensu Chmura et al. 2019) to the three environmental cues:

$$G = [\tau_{\text{temp}}, \tau_{\text{precip}}, \tau_{\text{day}}]. \quad (2)$$

Each day of the simulation, each individual combines its cues and genotype into a weighted sum, which represents the response sum ( $S$ ):

$$S = \frac{\gamma_{\text{temp}}}{\tau_{\text{temp}}} + \frac{\gamma_{\text{precip}}}{\tau_{\text{precip}}} + \frac{\gamma_{\text{day}}}{\tau_{\text{day}}}. \quad (3)$$

On the first day of the year when this sum exceeds the response threshold  $S \geq 1$ , the organism makes an irreversible phenological decision in anticipation of future fitness conditions. The genotype  $G$  thus represents the inverse weights of our weighted sum. We use  $1/\tau$  as the weight for the response sum for interpretability and consistency; genotypic traits are represented in the same units as the cue itself, and trait values indicate the critical cue value that would trigger a phenological response in the hypothetical absence of other cues. This also means that fixed increases or decreases to traits have the same effect regardless of trait value (e.g., increasing  $\tau_{\text{day}}$  by 1 means that in the absence of other cues, the organism would respond 1 day later, regardless of whether  $\tau_{\text{day}}$  was previously 1 or 100). As a consequence, large trait values correspond to low sensitivity, and low trait values correspond to high sensitivity. Additive models of cue integration like this have been described in many organisms (Ernst and Banks 2002; Gu et al. 2008; Seeholzer et al. 2018), and similar assumptions have been applied in previous models (e.g., Jong 1990; Scheiner 1993; Lande 2009; Chevin and Lande 2015). While many organisms are likely to use more complex phenological cueing strategies across their life history (i.e., using multiple cues sequentially, as with chilling requirements for germination), additive models of cue integration provide a simple, commonly used, and plausible representation of how multiple cues are combined to form complex phenological cueing strategies.

### *Fitness*

Individuals reproduce at a rate proportional to the sum of the daily fitness they accrue over a fixed window starting 1 day after exceeding their response threshold. The fitness gained on any given day is the product of two skew-normal function outputs: one based on temperature, the other on moisture (see eq. [4]). These two fitness functions are com-

bined to yield a two-dimensional fitness surface akin to a quantitative version of a two-dimensional Hutchinsonian niche (e.g., fig. S2; Hutchinson 1957). Our model assumes that these two fitness factors interact multiplicatively rather than additively, so that favorable conditions in both dimensions are nonsubstitutable requirements for fitness, consistent with the Hutchinsonian niche concept. We used a skew-normal distribution because the thermal performance curves of ectotherms are generally asymmetrical, where fitness increases gradually as temperature increases toward the optimum and then declines sharply above the optimum (Huey and Stevenson 1979; Sinclair et al. 2016). For simplicity, we used the same skew-normal functional form (with a skew parameter of  $-10$ ) for both temperature and moisture, though this model showed qualitatively similar results with alternative fitness functions (see the appendix, “Sensitivity Analyses”). Environmental moisture ( $m$ ) was calculated based on daily precipitation totals ( $p$ ) using a formula that includes a proportional retention constant ( $\alpha$ ) to represent the partial retention of moisture in the surrounding environment over time, as well as the input of new precipitation each day (eq. [4]):

$$m_t = m_{t-1}\alpha + p_t. \quad (4)$$

We set the retention constant to 0.8 in our simulations (see the appendix, “Sensitivity Analyses”). At its limits,  $\alpha = 0$  represents daily precipitation, and  $\alpha = 1$  represents cumulative annual precipitation. We use  $\alpha = 0.8$  to reflect the assumption that organismal activity typically depends on moisture retained in the environment rather than daily precipitation. In contrast, cumulative annual precipitation was used in the cue integration model to reflect the assumption that organisms are aware of accumulated environmental information throughout the year. Changing the retention constant for environmental moisture produced qualitatively similar results, even when  $\alpha = 0$ .

Temperature and moisture performance functions were parameterized separately for each location, such that the peak for each occurred at the 90th percentile of all daily observations for a given location and each function had a value that was 10% of the peak when the cue was at the 10th percentile of all daily observations. This parameterization assumes that potential fitness values are maximized under relatively warm and moist conditions at each location. However, this approach applies equally well to locations that are not characterized by these combined conditions because we simulate reproduction using a lottery model based on relative, realized fitness. Parameterizing by location without assuming performance constraints across sites (e.g., a universal minimum or maximum temperature across all locations) allows the interpretation of spatial patterns in evolved cue use without confounding differences in performance curves. This approach assumes that organisms are

locally adapted to climatic conditions in a comparable way, so that evolved differences between locations are likely to be conservative, compared with a model in which universal constraints affect locations differently. To evaluate the robustness of observed results, we tested this model at a range of alternative fitness parameterizations, including different optimal quantiles, and observed qualitatively similar results (see the appendix, “Sensitivity Analyses”).

The raw fitness of each individual ( $W_i$ ) was calculated as the sum of these daily fitness payoffs over a 10-day window beginning 1 day after the response sum exceeded the response threshold (e.g., fig. S3). These raw fitness values combine the products of two probability densities and provide a relative measure of fitness; they have inherently small values and are not scaled to reflect expected numbers of offspring. Our model assumes a relatively short fitness accumulation window each year, where this window could represent any period when environmental conditions have a strong effect on fitness in the life history of our model organism. For example, it could represent the entire active, nondiapause phase of an organism’s life history or a short period of establishment in a longer life history (i.e., a seasonal window of opportunity *sensu* Yang and Censer 2020); for simplicity, we assume that environmental conditions do not have fitness effects outside of this window. Varying the duration of this window produced qualitatively similar results (see the appendix, “Sensitivity Analyses”). We use the sum of daily fitness payoffs to represent systems where the fitness benefits of favorable conditions accumulate over a window of time; while this is likely to represent some systems well, it would not adequately represent systems where daily fitness effects are multiplicative (e.g., a system in which a single extreme frost event has the potential to persistently damage flowers). We set this fitness window to begin 1 day after the response threshold is exceeded in order to simulate a delayed developmental process that required minimal anticipatory forecasting. Functionally, this 1-day lag reduced the overall correlation between observed cues and experienced conditions. Increasing this lag further makes it more difficult for strategies to anticipate future conditions but does not qualitatively change the behavior of this model (see the appendix, “Sensitivity Analyses”). All organisms in this model were constrained to have annual life histories with one generation per year; organisms that did not respond by the end of the year received zero fitness. This constraint prevented the evolution of multiple generations per year or multiannual life histories, allowing us to focus on the seasonal phenology of relatively short-lived annual organisms.

Individuals reproduced asexually with mutation (see “Heritability and Mutation”), with population size held constant and expected realized fitness of each individual proportional to its calculated relative fitness. Reproduction was

implemented as a lottery model to incorporate competition and allow for demographic stochasticity. With a constant population size each generation, individuals compete for representation in the next generation, with their probability of representation proportional to their raw fitness value ( $W_i$ ). For each evolved strategy (genotype) in the final generation, we calculated the geometric mean of its raw fitness across all years of environmental conditions. This fitness was proportional to its expected long-term relative fitness in that environment.

#### *Heritability and Mutation*

Offspring were given the same genotypes as their parent, modified by mutation. We modeled mutation by adding small random numbers (drawn from a normal distribution with a mean of zero and a small standard deviation) to the parental traits. We set the standard deviation of mutation for each trait to be 0.5% of the overall cue range in order to produce mutation distributions with the same expected effect size in each location. In the case of the day cue, we used 360 as the maximum, leading to a standard deviation of 1.8 for mutation rate of the day trait in all locations. We assumed that each trait mutated for each individual in order to increase the overall rate of simulated evolution and improve computational efficiency.

#### *Environmental Data*

All available years of daily maximum temperature (°C) and daily precipitation (mm rainfall equivalent) data were obtained from the NOAA Climate Data Online portal (NCEI 2018) for 82 locations in North America and Hawaii. Locations were chosen to ensure spatial representation across the range of available data. After filtering for data quality and imputing missing daily values (see the appendix, “Environmental Data”; the appendix is available online), we arrived at a climatic data set of daily maximum temperatures and daily precipitation for 78 locations, with an average duration of 98 years (SD = 18.9 years, interquartile range = 114–84 years; see supplemental table 1, available online).

To ensure that cue values were always nonnegative, the temperatures for each location were shifted so that the minimum transformed temperature for that location was zero. Day of the year was represented as an integer value reflecting the number of days since January 1 of each year inclusive. The 366th day was truncated from leap years in the data set.

#### *Initialization and Execution*

For each location, we ran 60 simulations with the same parameter set (see data deposited in the Dryad Digital Repository, <https://doi.org/10.25338/B8TG95>; Edwards and Yang

2020). Each simulation included 1,000 years (i.e., 1,000 generations) of climatic data independently resampled from the historic data set with replacement; as a result, the climatic history for each simulation was different but drawn from the same historical climate distribution for that location (fig. 1; supplemental table 1). Each simulation maintained a population of 500 individual organisms with individual genotypes. In the initial generation of each simulation, each individual was assigned uniform random trait values between 0 and 4 times the maximum cue value in that location (or 360 in the case of the day cue). This resulted in an initial population of individuals with a broad range of trait values (e.g., figs. 1D, S4). Each simulation proceeded with the expression of a phenotype, accumulation of resulting fitness payoffs, differential reproduction in a lottery model, and mutation in each generation. Thus, each simulation reflects a unique realization of the climatic history from a given location, with a randomly generated initial population. These simulations could be interpreted as replicates in an evolutionary experiment with systematic differences in the climatic means of locations and stochastic variation in the specific sequence of climatic years and the specific genotypes of the initial population. Alternatively, each simulation could be interpreted as separate species that experience the same climate regime and have the same temperature and moisture requirements.

#### *Assessing Realized Relative Cue Use*

Trait values represent cue sensitivity; in our model, these can be interpreted as threshold values that would trigger a phenological response in the absence of other cues. Thus, the same trait values produce different behavior in different locations, depending on the environment. In order to compare strategies across locations, we define the trait effect ( $T$ ) as a metric of proportional cue use. Each trait effect is a value from 0 to 1 that quantifies a strategy's realized reliance on a given cue in a way that is comparable across locations. Specifically, this metric represents the proportion of the response sum  $S$  that is contributed by each  $\gamma/\tau$  term of equation (3) on the day the response threshold is exceeded. Together, the trait effects of all three cues form a mathematical composition (here, a vector that sums to 1) that represents a realized cueing strategy. Thus, we calculate mean strategies within simulations and locations, using Aitchison compositional means (van den Boogaart and Tolosana-Delgado 2013), and plot these compositional means on ternary plots to show the three components of each strategy.

#### *Climate Change Scenarios*

We examined how the individuals from the final generation of each simulation performed in novel climate regimes

using two simple climate change scenarios. In the shift scenario, we advanced the historic temperature and precipitation regime in each year by 5 days. In the warming scenario, we increased all daily temperatures by 3°C and left the precipitation regime unchanged. These two scenarios are not intended to represent detailed or realistic climate change scenarios; instead, they reflect exposure to novel climates using a simple and systematic erosion of the key correlations in historical climatic data. In the shift scenario, the historical correlations between climatic conditions (temperature and moisture regime) and day of the year are weakened, but the key correlation between the temperature and moisture regimes is maintained. Because of this, the seasonal fitness landscape (the time series of potential daily fitness payoffs) in any given year remains unchanged, except that it is advanced by 5 days. In contrast, the warming scenario weakens historical correlations with temperature relative to the other two environmental cues and also fundamentally changes the seasonal fitness landscape in any given year. Thus, while these two novel climate scenarios both represent important departures from the historical climate regime, the warming scenario presents a more profound departure from historical seasonal fitness landscapes. In both scenarios, we calculated the response day and fitness that would have been realized for each individual of our final populations in each unique year of the modified climate regime for each of 30 simulations. This allowed us to assess how climate change affected the phenotype and fitness consequences of each genotype that evolved under historical conditions.

For both climate change scenarios, we assessed correlations between each historic trait effect ( $T$ ) and the change in response day and between each trait effect and the change in geometric mean fitness for each evolved genotype. We used linear mixed models with location as a random factor, allowing intercepts and slopes to vary. For these analyses, we report effect sizes ( $\beta$ ) as the slope coefficient of each fixed explanatory factor; in these analyses, the effect size represents the expected change in response day or geometric mean fitness with a one-unit change in the trait effect.

#### *Sensitivity Analyses*

We tested several model structures, cues, and parameter values to assess the robustness of our results (see the appendix, "Sensitivity Analyses").

### **Results**

In many simulations, populations evolved to a region of successful trait combinations relatively quickly, with selection, mutation, and drift leading to gradual shifts in the average

population genotype, as well as the branching and pruning of lineages over time (e.g., fig. S4). Some simulations experienced large shifts in trait use over time, often with concurrent changes ramifying across multiple traits. The individuals in the final generation of any single simulation typically emerged from the dominant evolved lineage and showed similar combinations of traits. Thus, individual variation within each simulation was well represented by the mean strategy for that simulation.

#### *Variation within Locations*

Mean evolved strategies often showed considerable variation between simulations, within locations. This variation in strategies can be observed in ternary plots of trait effects (figs. 2A–2D, S5) and mapped to locations (fig. S6). While some locations evolved tight clusters of similar strategies, most locations show a broad range of strategies using different sets of cues. These diverse strategies often showed geometric mean fitnesses that were similar to the fittest mean genotype across all simulations (figs. 2A–2D, S5, S7). This occurred because most locations were characterized by high-performance fitness volumes that spanned a wide range of trait values, rather than a single clear optimal strategy. In three-dimensional trait space, these high-performance fitness volumes resembled the hull of a boat or layers in a quartered onion (figs. 2E–2H, S8E–S8H), reflecting a wide range of evolved cueing strategies with similarly high geometric mean fitnesses (figs. S7, S9). These broad regions of trait space yielded similar fitness outcomes because they produced similar phenological behavior under historical conditions (figs. 2I–2L, S8I–S8L).

#### *Variation between Locations*

We found considerable spatial variation in the mean evolved strategies across locations. Spatial patterns in mean cue use are visible when mapped (fig. 3A) and showed strong positive autocorrelation on a continental scale (fig. 3B–3D). This result indicates that similar mean strategies evolved under similar climates, suggesting a degree of underlying predictability in the evolution of phenological cueing strategies, despite the variability of evolved strategies among simulations within each location.

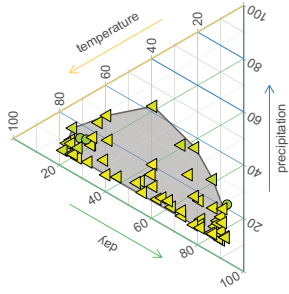
We analyzed several climatic and location variables as potential correlates of evolved mean cue use at each location (appendix, “Analysis of Explanatory Factors”; figs. S10, S11). While several factors emerged as potentially meaningful predictors of phenological cue use in this analysis, most of the variation in cue use was unexplained even in models that combined all 17 factors ( $T_{\text{day}}$ , marginal  $R^2 = 0.102$ ;  $T_{\text{temp}}$ , marginal  $R^2 = 0.110$ ;  $T_{\text{precip}}$ , marginal  $R^2 = 0.308$ ).

#### *Responses to Climate Change Scenarios*

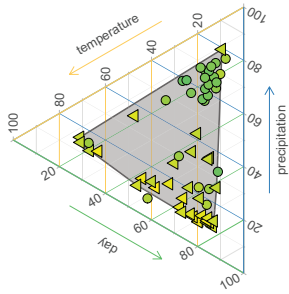
In the shift climate change scenario, populations generally advanced their mean phenology but showed highly variable changes in their realized fitness when comparing between (fig. 4A) and within (fig. 5A, 5C, 5E, 5G) locations. These effects were nonrandom; as expected, organisms that relied more on day cues were less likely to advance their phenology on pace with the changed climate ( $\beta = 4.6$  days per unit  $T$ , SE = 0.02,  $P < .0001$ ), while organisms that relied more on temperature or precipitation cues were more likely to advance their phenology (temperature,  $\beta = -2.5$  days per unit  $T$ , SE = 0.19,  $P < .0001$ ; precipitation,  $\beta = -2.2$  days per unit  $T$ , SE = 0.1,  $P < .0001$ ). Because the seasonal fitness landscape retained the same shape but advanced by 5 days in this scenario, organisms that relied more on day cues generally showed a weak pattern of more negative fitness consequences ( $\beta = -0.00023$  units  $W_i$  per unit  $T$ , SE = 0.00007,  $P = .0009$ ; fig. 4A), while those that relied more heavily on temperature or precipitation cues showed weakly positive fitness consequences (temperature,  $\beta = 0.00017$  units  $W_i$  per unit  $T$ , SE = 0.00005,  $P = .002$ ; precipitation,  $\beta = 0.00009$  units  $W_i$  per unit  $T$ , SE = 0.00005,  $P = .04$ ). While most locations experienced a reduced mean fitness under the changed climate, some locations showed higher overall fitness (fig. 4A). Simulations within locations showed similarly variable responses in both advancement and fitness (fig. 5A, 5C, 5E, 5G). The behavior of individual genotypes within each location (fig. S12A) shows how small changes in phenological response phenotype can drive large changes in mean fitness outcomes under the shift scenario.

Under the warming scenario, populations also advanced their mean phenology, both between (fig. 4B) and within (fig. 5B, 5D, 5F, 5H) locations. Mean strategies with greater reliance on day or precipitation cues showed reduced phenological advancement (day,  $\beta = 8.1$  days per unit  $T$ , SE = 1.2,  $P < .0001$ ; precipitation,  $\beta = 7.7$  days per unit  $T$ , SE = 1.0,  $P < .00001$ ), while those that relied more on temperature showed greater phenological advancement (temperature,  $\beta = -15.4$  days per unit  $T$ , SE = 1.5,  $P < .00001$ ). This effect of day was more apparent in the shift scenario than the warming scenario when comparing across locations (fig. 4A vs. fig. 4B) but is apparent in both scenarios when comparing within locations (fig. 5). Organisms with greater reliance on day and precipitation showed higher fitness in the warming scenario (day,  $\beta = 0.0006$  units  $W_i$  per unit  $T$ , SE = 0.0002,  $P = .0026$ ; precipitation,  $\beta = 0.0007$  units  $W_i$  per unit  $T$ , SE = 0.0003,  $P = .01$ ), while those that relied more on temperature showed reduced fitness ( $\beta = -0.001$  units  $W_i$  per unit  $T$ , SE = 0.0002,  $P < .00001$ ). Many locations showed larger and less predictable changes in mean fitness outcomes under the

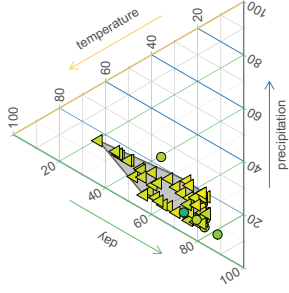
A. Davis, CA, USA



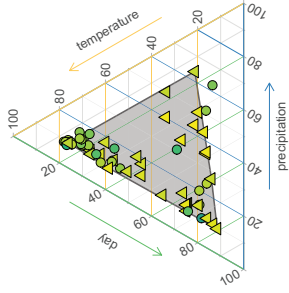
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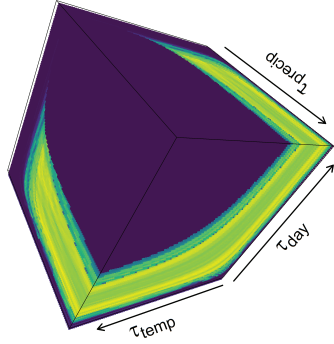
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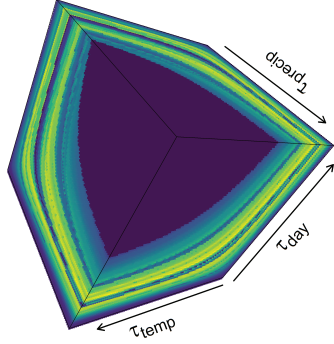
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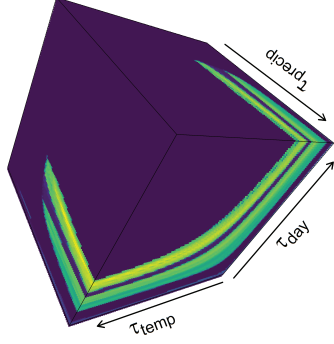
E. Davis, CA, USA



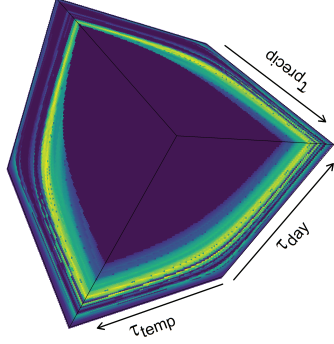
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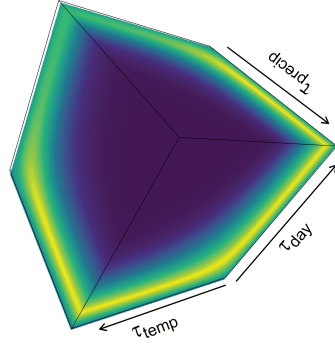
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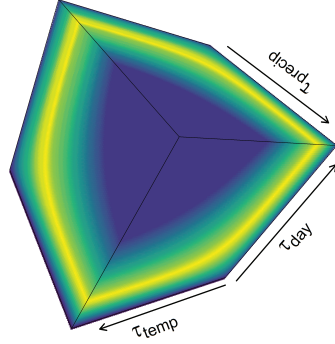
H. Rapid City, SD, USA



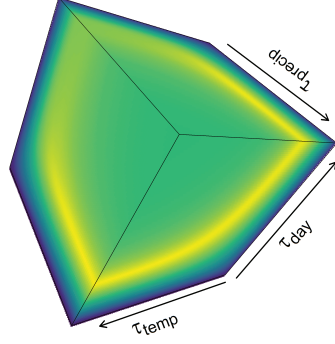
I. Davis, CA, USA



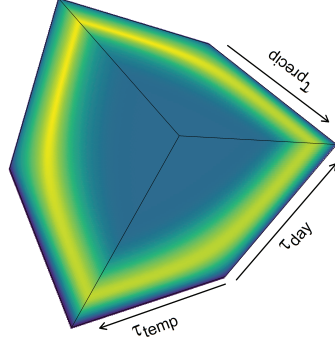
J. Ithaca, NY, USA



K. Honolulu, HI, USA



L. Rapid City, SD, USA





warming scenario than in the shift scenario (e.g., figs. 4, 5, S12).

### Sensitivity Analyses

Our findings were qualitatively robust across a wide range of model variants using different cues (daily precipitation, daily temperature, photoperiod, quadratic measures of cues), fitness functions, and fitness window durations (see the appendix, “Sensitivity Analyses”). Differences in historic data set length did not explain a meaningful proportion of the climatic variation across locations (see the appendix, “Sensitivity to Data Set Length”).

### Discussion

This model suggests two key findings. First, we see that the evolution of phenological cueing strategies was shaped by environmental history in broadly predictable ways across locations (fig. 3), despite substantial variation in cueing strategies within locations (figs. 2A–2H, S5). Second, evolved cueing strategies showed highly variable responses to simulated climate change (figs. 4, 5).

#### *Predictability and Variation in the Evolution of Phenological Cueing Strategies*

The observation that similar mean strategies evolved in locations with similar climates likely reflects continental-scale spatial patterns in the relative reliability of temperature, precipitation, and day cues (fig. 3). The spatial autocorrelation of evolved strategies indicates that evolution tended to produce similar phenological cueing strategies under similar environmental histories. Our model assumes that selection will favor cues based on their ability to pre-

dict future environmental conditions that are relevant to fitness—both the ability to consistently trigger a phenological response ahead of favorable conditions and the ability to avoid triggering a phenological response ahead of unfavorable conditions. Thus, this result suggests that broad patterns in phenological cue use may be predictable based on the relative information content of different cues.

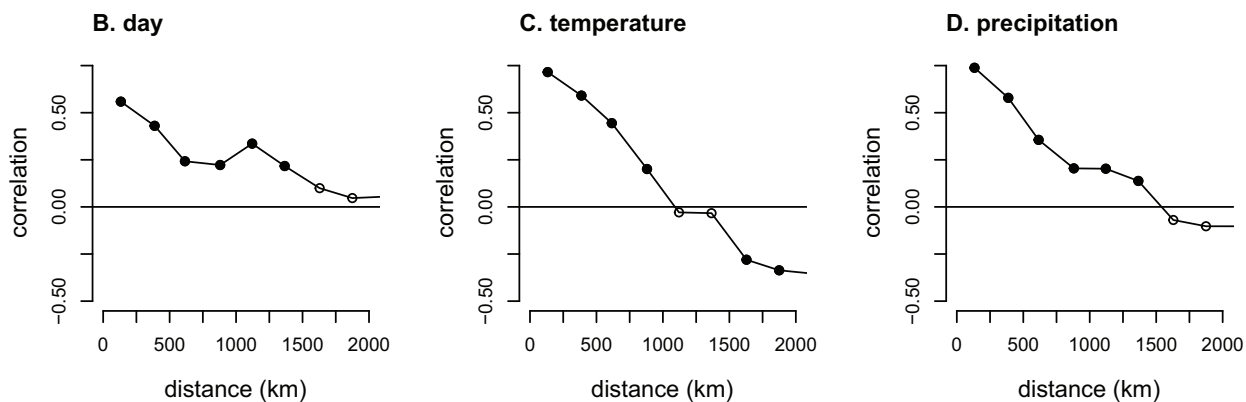
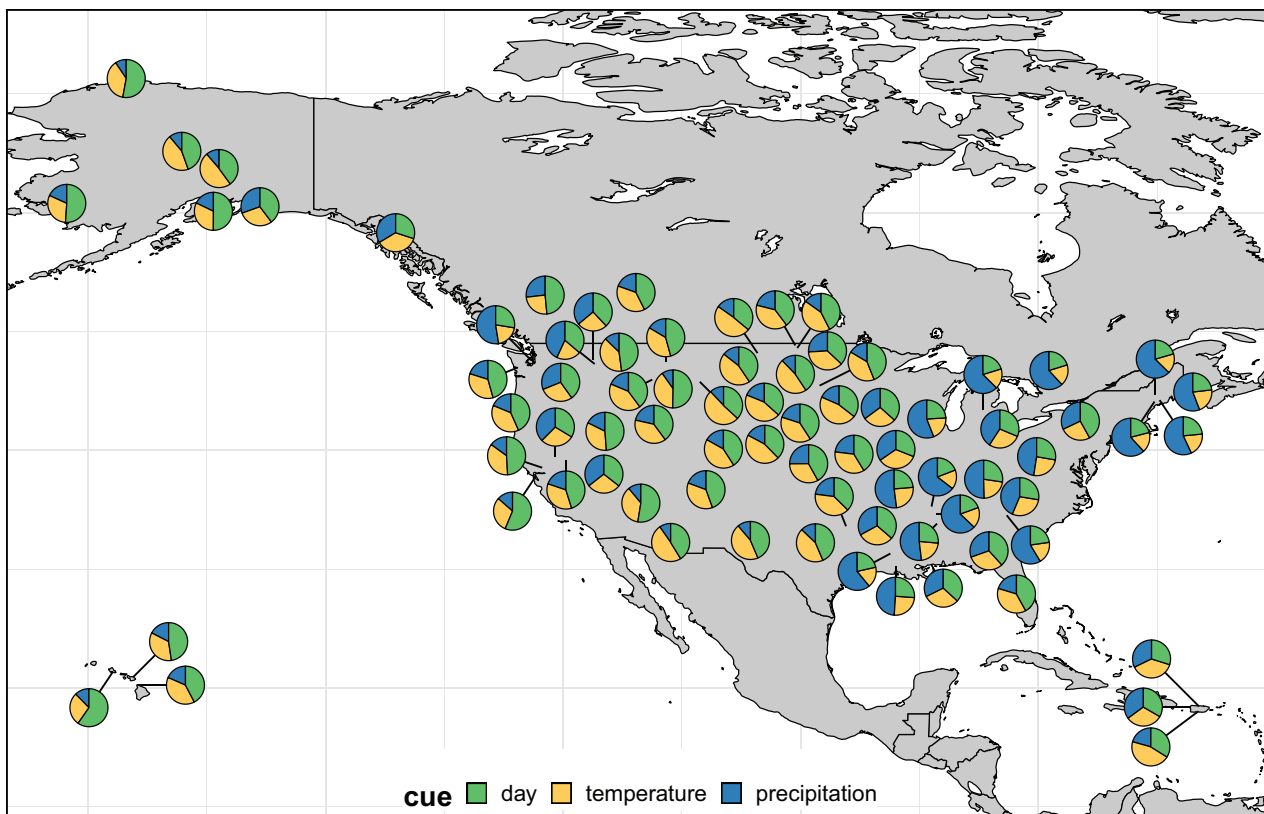
Across locations, we observed a broad and complex range of strategies evolving in response to real-world climatic data. In some locations, this resulted in strategies that relied heavily on climatic cues to track factorable climatic cues across year-to-year variation (e.g., figs. 2, S5). In other locations, this resulted in the evolution of bet-hedging strategies with a greater reliance on climatically invariant day-of-year cues (e.g., figs. 2, S5). While broad patterns of phenological cue use may be predictable based on the relative reliability of environmental cues in an organism’s evolutionary history, simple climatic or location variables were only marginally successful at characterizing the relevant differences between locations in our model, and the majority of observed variation in evolved cue use could not be explained by a model including all evaluated climatic and location variables (appendix, “Analysis of Explanatory Factors”; figs. S10, S11). This likely reflects the fact that most of the a priori descriptive variables we used were too coarse, static, or general to capture the aspects of climatic predictability that are most relevant to our model organisms. For example, many of these descriptive variables were metrics of annual climatic variability averaged across years, and such general descriptors likely failed to capture the specific predictability of cues in most relevant part of the season for our model organisms.

In addition to the variation we observed in mean cueing strategies between locations, we also observed substantial variation in evolved cueing strategies across simulations

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**Figure 2:** A–D, Ternary plots illustrate proportional cue use at the time of response for four selected locations. Each point represents the mean strategy at the end of one simulation; each strategy is represented as a composition of the trait effects ( $T$ ) in percentages, representing relative cue use. Point color reflects geometric mean fitness of genotypes across all years of the climate as a percent of the maximum observed geometric mean fitness ( $\bar{W}$ ) for each location. Simulations within 10% of the maximum observed geometric mean fitness in each location are shown as triangles and included in a gray convex hull. All other points are shown as circles. Ternary plots for all 78 locations are presented in figure S5, and locations are described in supplemental table 1 (both are available online). E–H, Geometric fitness in the three-dimensional trait space of our organisms, with each dimension representing phenological sensitivity to a different cue (where low trait values mean high sensitivity). For each location, the yellow region represents strategies that were at or near the highest observed fitness. This region generally spans a wide range of trait values, reflecting the breadth of potentially successful trait combinations. These plots show that diverse genotypes can produce similarly high fitness phenotypes. To generate these plots, we evaluated a  $100 \times 100 \times 100$  grid spanning trait values ranging from the 10th to the 90th percentiles of observed cues in each location for fitness and response day in each recorded year of climate. I–L, Response similarity is plotted for the same trait ranges in each location. Response similarity is a metric that quantifies the proportional similarity of phenological responses for each trait combination (genotype) compared with the phenological responses of the trait combination with the maximum geometric mean fitness across all available years. We calculate the response similarity as one minus the proportional response dissimilarity, which was defined as the mean distance (in days) between the response day of each genotype compared with that of the fittest genotype, divided by the greatest distance in each year. Bands of high similarity span most of the trait space, demonstrating that many different combinations of traits can lead to similar response phenologies. Comparisons with E–H show that regions of high response similarity generally overlap with regions of high fitness, illustrating that the observed similarity in fitness between diverse strategies is generally due to the expression of similar phenological phenotypes rather than alternative phenotypes with equivalent fitness.

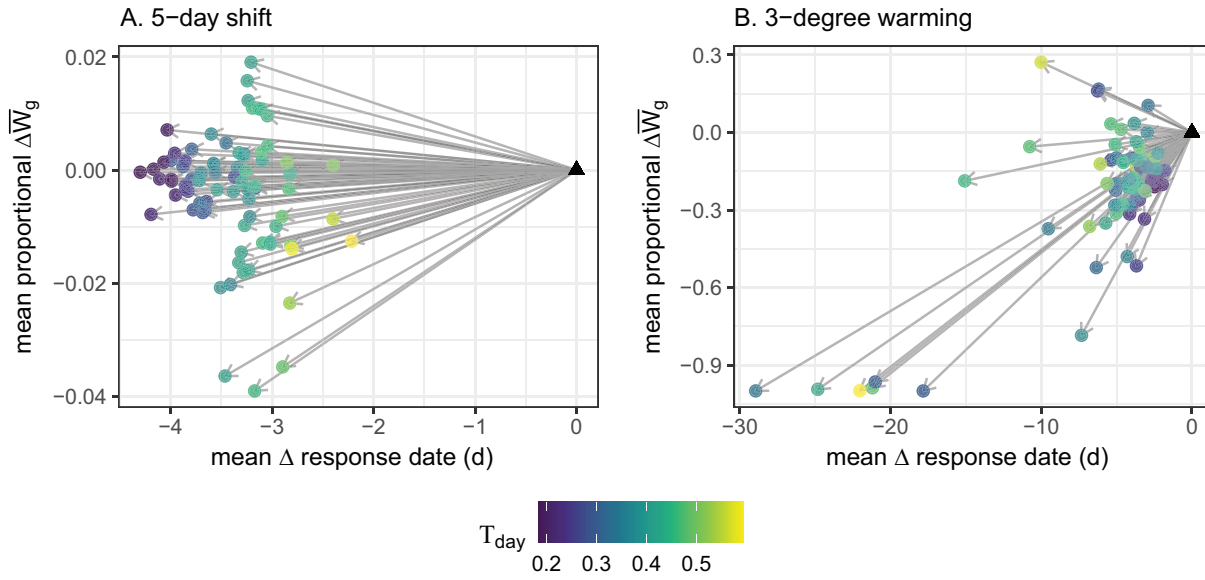
## A. map of mean evolved strategies in each location



**Figure 3:** Evolved strategies show spatial autocorrelation in relative cue use (trait effect,  $T$ ); similar strategies evolve in nearby locations with similar climates, and different strategies evolve in distant locations with different climates. A, Map representing the mean evolved strategy for each of 78 locations across all years. Evolved strategies show significant positive spatial autocorrelation (Moran's  $I$ ) in reliance on day (B), temperature (C), and precipitation (D) cues up to at least 1,000 km. Filled circles are significantly correlated; open circles are not.

within locations (figs. 2A–2D, S5). This variation emerges because a wide range of trait value combinations (i.e., cueing strategies or genotypes; fig. 2A–2D) yield similar response phenotypes (e.g., fig. 2I–2J) with similar fitness outcomes (e.g., fig. 2E–2H). This is a fundamental consequence of

multicue integration when there are correlations among climatic cues; when these conditions are met, changes in one component of a cueing strategy can often be compensated for through changes in another. This feature of cue integration can lead to a broad range of multicue strategies



**Figure 4:** Variability of mean phenological responses to climate change scenarios and their fitness consequences across locations (see also fig. 5 for variation across simulations within locations). Changes in phenology and mean fitness under a shift scenario (A), where both temperature and precipitation regimes advance by 5 days, and under a warming scenario (B), where temperatures are warmed by 3° across the year. Under these two scenarios, organisms with different environmental histories generally respond earlier but show variable degrees of advancement and highly variable fitness consequences. Note differences in the scales of the vertical axes between the shift scenario and the warming scenario. The position of each circle represents the mean change in the response date and the proportional change in geometric mean fitness (averaged across all evolved genotypes of 30 simulations for each of 78 locations) relative to the historical climate in that location, represented by a black triangle. Thus, this figure shows the variability of phenological responses and fitness consequences to climate change across locations (see fig. S12 [available online] for plots of phenological responses and fitness changes across all locations). The color of each circle represents the historical trait effect of day ( $T_{\text{day}}$ ), indicating the relative use of a climatically invariant cue.

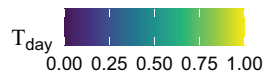
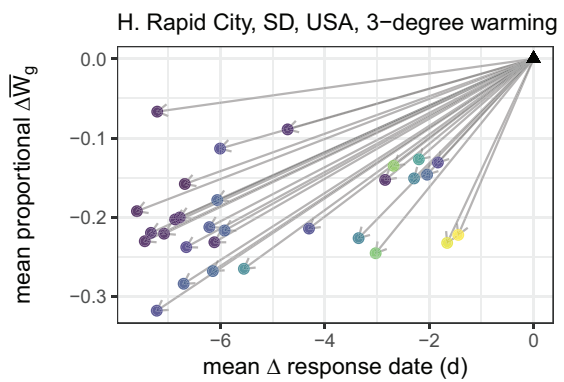
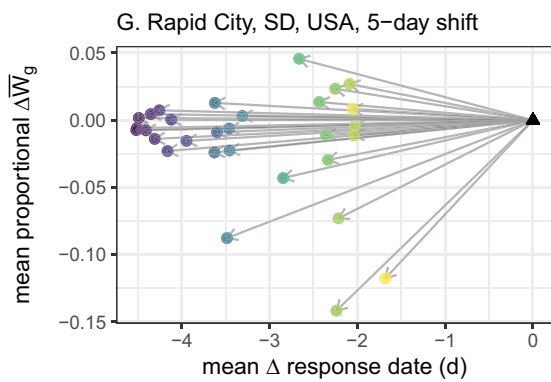
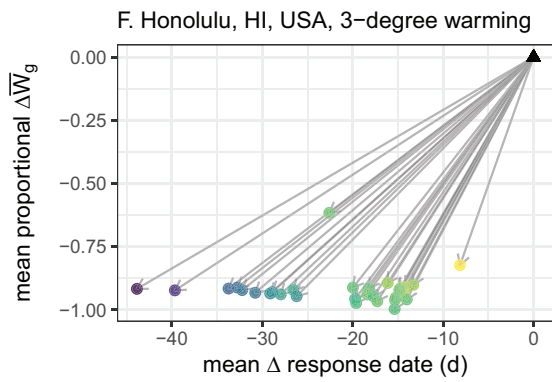
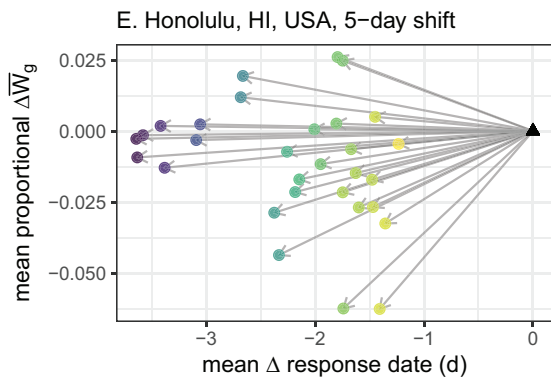
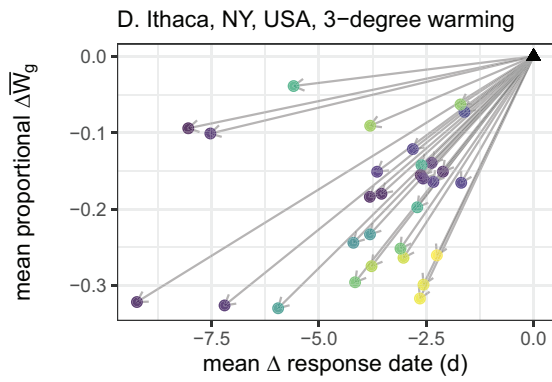
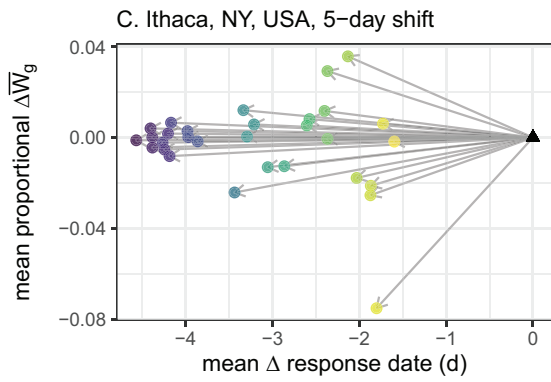
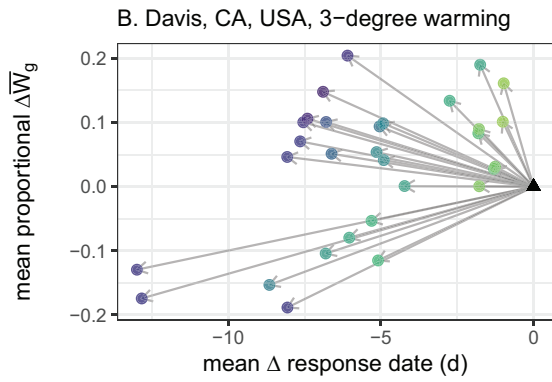
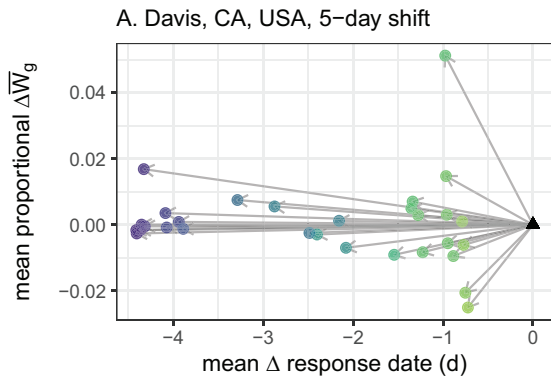
that can appear counterintuitive when singular cue responses are examined in isolation (cf. Chevin and Lande 2015). This fundamental property of multicue integration predicts that organisms showing similar phenologies under historical climates could have widely divergent underlying phenological strategies that use different cues to different degrees. This prediction is consistent with the findings of empirical studies demonstrating differences in cue use between interacting species that generally show phenological synchrony (e.g., Iler et al. 2013).

This fundamental consequence of cue integration is further complicated by nonadditive interactions among traits in our model. This is partly due to our response threshold model, which creates inherent nonlinearities in the relationships between traits and the phenotype. It also reflects the variable nature of real-world climatic dynamics across each year, which cause the effects of one trait to depend on the effects of the other traits in an individual's genotypic background in complex and nonadditive ways. As an extreme example, a trait that confers a very high sensitivity to one cue can nullify the effects of other cues, because even a small value of one cue will cause the organism to exceed its response threshold. More generally, the effects of any

trait on both phenotype and fitness depend on the other traits in the organism's strategy and the seasonal dynamics of its environment. These nonadditive interactions between traits are akin to epistasis (Phillips 2008) and create the potential for a more diverse and complex range of cueing strategies with similar fitness outcomes in any given location (Fenster et al. 1997).

#### *Novel Climates Result in Ecological Surprises*

Our second key finding is that phenological strategies that produced similar phenotypes under historical conditions showed strong phenotypic and fitness differences under simulated climate change (figs. 4, 5, S11). These effects depended on the degree to which our climate scenarios broke key correlations in the historic climate. In the shift scenario, temperature and precipitation regimes were advanced in unison, and so the correlations between temperature and precipitation were unchanged. Thus, organisms that were more sensitive to climatic cues showed greater phenological advancement and more positive fitness consequences, while those that relied more heavily on climatically invariant day-of-year cues showed reduced advancement and



more negative fitness consequences (figs. 4, 5, S11). This result is consistent with expectations about the costs of using invariant day-of-year (e.g., photoperiodic) cues under climate change (Coppack and Pulido 2004; Way and Montgomery 2015). However, in the warming scenario, greater reliance on the invariant day-of-year cue was generally favorable, while organisms that relied more on temperature unexpectedly showed reduced fitness (figs. 4, 5, S11). This result occurs because the warming scenario increased temperatures independently of precipitation, thus breaking historic correlations between temperature- and precipitation-based factors. Because fitness is a function of both temperature and precipitation in our model (fig. S2), the warming scenario changed the seasonal fitness landscape in complex and novel ways. These changes to the seasonal fitness landscape made the fitness consequences of phenological advancement less predictable. As a result, many locations showed large and counterintuitive changes in mean fitness outcomes under the warming scenario (figs. 4, 5, S11).

A comparison of the shift and warming scenarios suggests some general insights. The specific ways in which these two scenarios differed had important consequences. The increased unpredictability of fitness responses under the warming scenario suggests that even a relatively small decoupling of the historical temperature and precipitation regimes could increase the likelihood and costs of maladaptive plasticity. These results are consistent with the hypothesis that organisms are more likely to show maladaptive and counterintuitive plasticity in environments that differ most from those in their evolutionary history (Ghalambor et al. 2007; Chevin et al. 2010; Reed et al. 2010; McNamara et al. 2011; Chevin and Lande 2015; Duputié et al. 2015). Thus, while intuition suggests that a greater reliance on climatic cues (as opposed to climatically invariant cues) would allow for more adaptively plastic responses to a changing climate, our findings suggest that this may not always be the case.

At the intersection of our two key findings, a wide range of strategies that show predictable and consistent behavior under historical conditions can show unpredictable and counterintuitive behavior in a novel environment. This is consistent with the idea that multicue phenological strategies create the potential for cryptic genetic variation to be expressed under climate change. Cryptic genetic variation is genetic variation that is not normally expressed but that can yield phenotypic variation under changed conditions (Rutherford 2000; Gibson and Dworkin 2004; Gibson and

Reed 2008; McGuigan and Sgrò 2009; Paaby and Rockman 2014). Cryptic genetic variation appears to be widespread in eukaryotes and may be particularly characteristic of systems where response thresholds provide a mechanism of “genetic buffering” (Rutherford 2000). In the context of our model, the mechanisms that maintain genotypic variation while minimizing fitness differences under historic climate conditions could contribute to the maintenance of cryptic genetic variation, increasing the potential for ecological surprises under novel climates.

### Context and Broader Implications

Our model examines the evolution of multicue strategies and its implications for variation in phenological responses to climate change. Previous studies have identified important patterns of phenological shift in nature (e.g., Parmesan 2007; Thackeray et al. 2010) and examined the behavior of increasingly complex phenological cueing models under increasingly realistic simulated environments (e.g., Reed et al. 2010; McNamara et al. 2011; Chevin and Lande 2015). Our current study provides a complementary approach to examine how evolution and cue integration could affect patterns of variation in phenological shifts. We find that phenological cueing strategies that evolve in the context of real-world climatic data show patterns of cue use that can be broadly understood in the context of cue reliability, consistent with previous modeling studies (Reed et al. 2010; McNamara et al. 2011). However, these evolved patterns of cue use can also show a great deal of complex and sometimes cryptic variability, consistent with our understanding of multicue integration from previous models (e.g., Chevin and Lande 2015). This variability in evolved cue use can lead to high variability in phenological responses to climate change, with phenotypic and fitness consequences that are increasingly difficult to predict under increasingly novel climate regimes. This result is consistent with expectations about the limits of adaptive plasticity in novel environments (e.g., Ghalambor et al. 2007; Chevin et al. 2010; Duputié et al. 2015) and suggests that many organisms may show increasingly counterintuitive responses to climate change.

Our model results suggest that we should expect to see substantial variation in phenological shifts, even if organisms experience similar environmental changes. Chmura et al. (2019) proposed a key distinction between organismal and environmental mechanisms of variation in phenological

**Figure 5:** Variability of mean phenological responses to climate change scenarios and their fitness consequences across simulations within locations (see also fig. 4 for variation across locations). This figure is constructed like figure 4 but shows changes in phenology and mean fitness for each of 30 simulations from four example locations (rows) under both the shift scenario (*left*; A, C, D, G) and the warming scenario (*right*; B, D, F, H). Each colored circle represents the mean response of a single simulation relative to the historical condition, represented by a black triangle. The color of each circle represents the historical trait effect of day ( $T_{\text{day}}$ ), indicating the relative use of a climatically invariant cue. Note differences in the scales of the vertical axes between the shift scenario and the warming scenario.

shift, with the former driven by differences among organisms in their sensitivity to cues and the latter driven by differences in the environmental change that different organisms experience. In this context, our model is focused on the evolutionary origins of variation in organismal mechanisms. In our climate change scenarios, we control and hold constant the environmental change that each population experiences. As a result, the substantial variation in phenological responses to climate change observed in our simulations is driven by differences in cueing strategy. The results of our model suggest that even when we limit the potential mechanisms of variation in phenological shifts, evolved differences in cueing strategies would contribute to a great deal of observed variation in phenological responses to climate change.

#### *Scope, Aims, and Limitations*

Our model was developed to explore general mechanisms for the variability of phenological shifts and does not attempt to make quantitative predictions about the evolution of cueing strategies at specific locations for any specific organism. For example, the patterns of cue use shown on the map in figure 3A represent only one possible model outcome, generated under one set of model parameters and assumptions. In the absence of a specifically parameterized model, these results should not be interpreted as meaningful predictions for any given system. We present this figure as an example to illustrate a more general finding—that similar mean strategies tend to evolve in locations with similar climates, while different strategies tend to evolve under different environmental histories. Unlike specific patterns of cue use in specific locations, this is a robust result that we see across a wide range of model parameters. More specific questions will require more detailed models, and we hope that this general theoretical framework will encourage more specific studies in the future.

#### *Future Directions*

Future studies could extend this model by increasing model complexity or evaluating our general findings in specific systems. Potential extensions of this model include modeling organisms with alternative life histories, using a broader range of environmental cues, considering more complex cue integration mechanisms, allowing sexual recombination of traits to increase standing genetic variation, or allowing gene flow between locations. It would be particularly useful to study whether more complex cueing strategies could allow greater resilience or robustness in the face of climate change. However, our ability to apply models to make predictions relevant to specific systems is likely to be more limited by our current knowledge of key parameters in specific systems rather than our ability to develop more com-

plex models. Future empirical and observational studies could build a groundwork for these studies by identifying key cues and cue integration mechanisms and by documenting variation in phenological cueing strategies within and across populations.

While we used different locations to represent different environmental conditions in this model, the general findings of this model could also potentially be extended to consider other factors that structure the availability of environmental cues, such as microhabitats or life histories. Two organisms in the same location may experience very different environmental conditions, potentially structured by their microhabitat, life history, trophic position, body size, or other factors. For example, the general findings of our model could potentially be applied to observed differences in phenological shifts correlated with phylogenetic groups (e.g., Parmesan 2007; Davis et al. 2010; Thackeray et al. 2010; Davies et al. 2013). Parmesan (2007) speculated that the particularly strong and variable phenological shifts of amphibians could be due to their particular reliance on precipitation-associated cues. Similarly, Davis et al. (2010) hypothesized that phylogenetic patterns in flowering time shifts could be caused by differences in cue use, potentially reflecting differences in the reliability of different cues in the evolutionary histories of different taxa. The results of our model are consistent with these hypotheses and the expectation that organisms exposed to different environments over their evolutionary history will evolve different phenological cueing strategies with consequences for their phenological responses to climate change.

#### *Conclusion*

The two key findings we report here are robust across a range of model parameters and appear to be rooted in fundamental mechanisms of multicue integration and the complexity of real-world climatic correlations. This suggests that similar mechanisms could potentially occur in a wide range of systems (e.g., Beshers and Fewell 2001; Wilczek et al. 2010; Seeholzer et al. 2018; Chmura et al. 2019) and that examining the reliability of cues in an organism's evolutionary history could provide a useful starting place for understanding current phenological cueing strategies. Understanding current phenological cueing strategies could potentially improve our ability to predict and respond to future phenological shifts. However, these results also suggest that the nature of cue integration may put fundamental limits on our ability to predict the responses and fitness outcomes of organisms living under novel climatic regimes.

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### Statement of Authorship

Both authors contributed equally to this work.

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