

Environmental variability shapes evolution, plasticity and biogeographic responses to climate change

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Abstract

Aim: We examine how environmental variability at seasonal and interannual time-scales influences evolutionary trajectories and the role of plasticity in response to recent and future climate change at biogeographic scales. We investigate the interplay of selection pressures at chronic (performance) and acute (thermal stress) time-scales.

Location: Colorado, USA.

Time period: 1950–2099.

Major taxa studied: A montane butterfly, clouded sulphur (*Colias eriphyle* W.H. Edwards, 1876).

Methods: We leverage field and laboratory data to construct phenotype-based models that predict fitness and evolutionary responses to recent and future climate change. Our focal phenotype, wing solar absorptivity, responds plastically to developmental (pupal) temperatures and determines adult fitness via its influence on body temperature.

Results: We project that phenology accelerates with decreasing elevation and climate change, but gradients in pupal and adult temperature with climate change are modest. Fitness of the first generation is predicted to decrease at low elevations and increase at high elevations with warming. Elevational clines in optimal wing absorptivity shift towards lower absorptivities with warming. We project that temporal shifts from selection for wing darkening (to extend flight time) to selection for wing lightening (to avoid overheating) in some cool, montane locations will ultimately impose fitness costs.

Main conclusions: Our analysis suggests that shifts in the balance of selection between acute and chronic responses to environmental variation will alter biogeographic responses to climate change. Evolutionary lags may ultimately confer greater sensitivity to climate change, but plasticity can reduce evolutionary lags by facilitating trait evolution.

KEYWORDS

butterfly, *Colias*, colouration, distribution, fitness, phenotype, selection, species distribution model

1 | INTRODUCTION

Many species have shifted their distributions across latitude and elevation in response to recent climate change (Scheffers et al., 2016). Species' traits are generally only weak predictors of the magnitude and even the direction of climate change responses within groups of species (Buckley & Kingsolver, 2013; MacLean & Beissinger, 2017). Range shifts likewise exhibit only limited phylogenetic conservatism (Diamond, 2018). This suggests that species with shared evolutionary history (and traits) respond similarly to climate change, but that mechanistic understanding of how species' traits and trait evolution influences their responses will be required to improve predictive capacity. Plasticity in thermal tolerance tends to reduce the magnitude of range shifts (Diamond, 2018), suggesting that plasticity in addition to evolution influences range shifts. Further, studies are increasingly demonstrating that intraspecific evolution and plasticity influence range shifts (Catullo, Ferrier, & Hoffmann, 2015; Cotto et al., 2017; Des Roches et al., 2018; Garzón, Alía, Robson, & Zavala, 2011; Peterson, Doak, & Morris, 2019).

Although rates of climate change are likely to exceed the capacity for evolutionary response for many species, evidence of evolutionary responses in phenology, morphology and physiology are gradually accumulating (Hoffmann & Sgrò, 2011; Merilä & Hendry, 2014; Scheffers et al., 2016). A key question investigated here is whether plasticity facilitates evolution by enabling persistence or hinders evolution by buffering selection (Hendry, 2015; Sgrò, Terblanche, & Hoffmann, 2016). Theoretical models indicate that the interaction of plasticity and evolution along environmental gradients will shape responses to climate change (Chevin, Lande, & Mace, 2010), but the models largely omit realistic environmental variability including seasonality (Chevin & Hoffmann, 2017). Correlative species distribution models (SDMs) provide detailed predictions of how organisms respond to spatial environmental variation, but they rely on statistical associations rather than the processes by which organisms respond to their environment (Buckley et al., 2010; Kearney & Porter, 2009). They thus tend to exhibit mixed performance at predicting distribution shifts, particularly when extrapolated into novel environments (Maguire, Nieto-Lugilde, Fitzpatrick, Williams, & Blois, 2015; Veloz et al., 2012).

SDMs are increasingly accounting for local adaptation (Peterson et al., 2019; Valladares et al., 2014) and frameworks for incorporating evolution in SDMs are emerging (Bush et al., 2016). However, evolutionary models generally require quantification of aggregate parameters related to selection and plasticity. These evolutionary parameters are likely to vary across distributions according to how phenotypes interact with environmental variability to shape performance and fitness. Mechanistic approaches incorporating these interactions may be necessary to understand how evolution and plasticity alter biogeographic responses to climate change (Chown et al., 2010). One mechanistic SDM suggests that the evolution of egg desiccation resistance (i.e. mortality) will substantially alter future

mosquito distributions across northern Australia (Kearney, Porter, Williams, Ritchie, & Hoffmann, 2009). We build upon this research by examining evolution of a phenotype determining fitness rather than a single fitness component.

Knowledge of how phenotypes interact with environmental conditions to determine fitness is lacking in many systems, but previous research integrating microclimate, heat balance, demographic and evolutionary models allows us to quantitatively relate phenotype to fitness for montane *Colias* butterflies (Buckley & Kingsolver, 2012; Kingsolver & Buckley, 2015, 2017, 2018). The research has focused on the phenotype of wing melanism, which determines the absorption of solar radiation and thus butterfly body temperature. Elevating body temperatures above ambient air temperatures is essential for achieving active flight (and subsequently many fitness-determining processes) in montane environments, resulting in darker wings at higher elevations (Eilers & Boggs, 2002, 2004a; Watt, 1968).

Wing absorptivity evolves in response to two opposing selection pressures: dark wings can increase flight time in cool, montane environments but absorbing excessive radiation risks overheating and declines in egg viability (Kingsolver & Watt, 1983; Watt, 1968). The phenotype thus provides insight into how responses to both chronic temperatures (via flight time) and acute thermal stress (via overheating) have shaped responses to recent climate change. Indeed, models for the high-elevation *Colias meadii* predict fitness declines at lower elevations and fitness increases at higher elevations (Buckley & Kingsolver, 2012). Incorporating phenotypic evolution suggests that environmental variation at higher elevations can cause large fluctuations in the direction of selection, dramatically slowing down evolutionary rates (Kingsolver & Buckley, 2015). The model estimates selection for wing lightening at low elevations and wing darkening at higher elevations over the last 60 years in Colorado (Kingsolver & Buckley, 2015).

Incorporating plasticity in wing absorptivity in response to developmental temperatures reveals that the relative importance of plasticity and evolution varies across environmental gradients in seasonal environments. In response to recent climate change, models for the lower elevation *Colias eriphyle* predict evolutionary declines in mean absorptivity (but little change in plasticity) at high elevations, and evolutionary increases in plasticity (but little change in mean absorptivity) at low elevations (Kingsolver & Buckley, 2017). Stronger evolutionary responses are predicted when the model includes plasticity. We estimate that phenological shifts have partially tracked recent climate change and altered selection and the adaptive value of phenotypic plasticity (Kingsolver & Buckley, 2018).

Our previous analyses suggest that the relative magnitudes of seasonality, interannual variability and climate change influence evolutionary trajectories and the role of plasticity. Here, we extend the analysis from several sites along an elevation gradient over recent decades to biogeographic scales (western Colorado, USA) and to future environments (using climate projections through 2099). These new analyses will allow us to evaluate the generality of our previous results across a single elevation gradient, and to assess spatial

heterogeneity in responses at different elevations. In addition, we can explore whether recent and future climate changes will elicit different phenotypic and evolutionary responses in this system.

Following our previous modelling results, we hypothesize that plasticity will facilitate evolution, especially at high elevations. We expect temporal shifts in the trade-off between warming increasing fitness by extending activity time and decreasing fitness by increasing overheating risk as warming proceeds. Over recent decades, fitness increases associated with extended activity have largely outweighed fitness losses due to overheating in alpine environments (Buckley & Kingsolver, 2012). Once warming reaches a sufficient magnitude, we hypothesize that fitness advantages associated with extending activity time will decline and overheating will increase in prominence. Butterflies in some montane areas are thus expected to shift from experiencing selection for wing darkening to experiencing selection for wing lightening, complicating phenotypic shifts through time.

2 | METHODS

We integrate microclimate, developmental, biophysical, demographic and evolutionary models to examine the fitness implications of phenological and morphological plasticity across a species' range (Figure 1). This modelling framework and description follows Kingsolver and Buckley (2017). We model evolutionary trajectories spanning 1950 to 2099. We estimate initial (1950) values of the focal trait, wing absorptivity (α), based on elevation (local adaptation, specified as α at 20°C, α_{20}) and plasticity (B) in response to developmental (pupal) temperatures. For each of the up to three

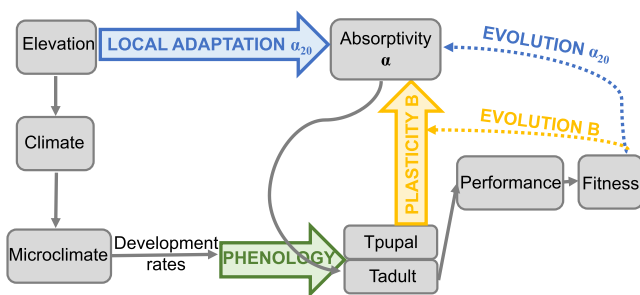


FIGURE 1 Flow diagram for the modelling framework. Climate and weather in each grid cell determine the microclimatic conditions experienced by larvae, pupae and adults. Microclimate determines developmental rates of larvae and pupae, which determine phenology. The focal trait, wing absorptivity, is initially determined by elevation differences among grid cells and is also influenced by microclimate due to the plastic effects of pupal temperatures (Tpupal). We model how wing absorptivity influences adult temperatures (Tadult) and ultimately performance in given microclimates and then use performance to estimate fitness. Fitness differences among individuals exhibiting variation in wing absorptivity can generate selection and cause evolutionary changes in the mean and plasticity of wing absorptivity in the next generation. Schematic based on Kingsolver and Buckley (2017) [Colour figure can be viewed at wileyonlinelibrary.com]

generations each year, we estimate fitness (net reproductive rate) associated with a sequence of wing absorptivities (α , spanning the possible range) based on environmental conditions. A microclimate model is used to translate environmental data at 2 m to the environmental conditions experienced by butterflies at plant height. We use larval and pupal temperatures to estimate developmental rates and subsequently phenology. Adult body temperatures are calculated using a biophysical model parameterized with thermoregulatory traits (including wing absorptivity) and microclimate data. Adult temperatures determine behaviour and performance (flight time and egg viability), which represent fecundity and are combined with survival to estimate fitness. Fitness estimates for the range of α values are used to estimate phenotypic selection on both the mean (α_{20}) and plasticity (B) of wing absorptivity. We incorporate these selection estimates in a quantitative genetic model to predict evolutionary changes in the next generation. We assume phenotypic variation and genetic variation remain constant through time and do not track population sizes. The following summaries of each model component are adapted from Kingsolver and Buckley (2017) (more details are given in the Supporting Information). We describe how the model is used to predict phenology, plasticity and fitness across grid cells. R code is available at github.com (<https://github.com/lbuckley/ColiasBiogeog>).

2.1 | Study system

We consider 1/8° latitude-longitude (c. 12 km by 12 km) grid cells within Colorado, USA, spanning elevations from 1,200 to 3,200 m, an elevation range slightly expanded from the observed distribution range of *C. eriphyle* (c. 1,400 to 3,000 m). *C. eriphyle* is the Rocky Mountain region member of the lowland *Colias* species complex (Watt, Han, & Tabashnik, 1979). Although *C. eriphyle* is found elsewhere in the Southern Rocky Mountains and eastern Great Basin (with spread facilitated by agricultural fields), we focus on Colorado where populations have been studied and data are available for model parameterization.

We analyse grid cells independently, assuming no migration among grid cells. Actual migration rates are low (c. 0.3 km dispersal distance, Watt et al., 1979; Tabashnik, 1980) because adults have short life spans and occupy grasslands isolated by forests or urbanization. Some gene flow likely results from long-distance migrants, but elevational clines in *Colias* wing absorptivity (Ellers & Boggs, 2004b) suggest selection can overcome gene flow [as also documented for *Colias* genetic polymorphism (Watt, Wheat, Meyer, & Martin, 2003)]. Larvae feed on hostplants in the legume family, including alfalfa, clover and vetch. Diapause is induced by larval photoperiod. We assumed that larvae overwintering as third instars could resume development once temperatures were permissive.

We model variation, plasticity and evolution of solar absorptivity (α) of the posterior ventral hindwings, the trait via which *Colias* populations and species (including *C. eriphyle*) are adapted to local climate (Ellers & Boggs, 2004b; Kingsolver, 1983b; Watt, 1968). Wing solar absorptivity (α = the fraction of incident solar radiative energy that

is absorbed by the wing surface) is determined by the relative proportions of pteridine (yellow or orange) and melanic (black) scales, and thus ranges between 0.4 (all pteridine scales) and 0.7 (all melanic scales) (Kingsolver, 1983b). Two other adult morphological traits also influence heat balance and body temperature: the length of setae on the thorax (fur thickness) and diameter of the thorax. We used values of fur thickness = 0.82 mm and thorax diameter = 3.6 mm in our analyses, based on measurements for *C. eriphyle* at several sites in Colorado (Kingsolver, 1983b). We focus on wing absorptivity due to its dominant influence on body temperature and pronounced elevational clines.

Increasing temperature during pupal development decreases wing melanin in *C. eriphyle* via phenotypic plasticity (MacLean et al., in review; Hoffman, 1978). We use two traits to characterize an individual's solar absorptivity (α): the slope of the reaction norm (B) relating α to the mean temperature during pupal development; and the mid-point absorptivity (α_{20}), the absorptivity at a reference pupal temperature of 20°C (Kingsolver & Buckley, 2017). The mean value of α_{20} increases with elevation (Ellers & Boggs, 2002, 2004b; Kingsolver, 1983b; Watt, 1968); based on data from Kingsolver (1983b), we used the initial mean starting value given by $\alpha_{20} = 0.4226 + 0.06517 * E$, where E is elevation in km. We estimated the mean reaction norm slope as $B = -0.00083 / ^\circ\text{C}$, based on data for *C. eriphyle* males at our low elevation site (Higgins, 2014). We assume slopes are constant across elevation for simplicity, but note that slopes are steeper (more negative) for populations at lower (1.5 km) than middle (2.1 km) elevations, and for males compared with females (MacLean, 2015). We explore scenarios with both fixed and evolving values of B and α_{20} (see below).

2.2 | Microclimate model and climate data

We used gridded projections of daily minimum and maximum air temperature ($^\circ\text{C}$, 2 m height) for 1950–2099 from the CMIP5 multi-model ensemble. The projections were statistically downscaled to $1/8^\circ$ latitude–longitude (c. 12 km by 12 km) resolution using daily bias correction and constructed analogues (bias correction constructed analogs (BCCA) method) 5 archive at http://gdo-dcp.ucllnl.org/downscaled_cmip_projections/). Our results are based on projections from the National Center for Atmospheric Research (NCAR) Community Climate System Model version 4 assuming representative concentration pathway (RCP) 6 (ccsm4.1.rcp60 experiment in the Coupled Model Intercomparison Project, CMIP5). The pathway is a mid-range scenario corresponding to a radiative forcing of $+6.0 \text{ W/m}^2$ in 2,100 relative to pre-industrial values. Mean temperature projections across our model region are presented in Supporting Information Figure S1. We ran additional simulations for two additional climate scenarios (bcc-csm1-1.1.rcp60 and gfdl-cm3.1.rcp60) to confirm the generality of our results. The temperature time series of the additional scenarios seemed less realistic (e.g. large temporal temperature jumps), so we chose to focus our results on the NCAR projections. We converted the daily minimum and maximum air temperatures to hourly temperatures using a diurnal temperature variation function with sine and exponential components (Parton & Logan, 1981). We

estimated butterfly body temperatures (see Section 2.4) additionally using hourly microclimate data from the microclim dataset (Kearney, Isaac, & Porter, 2014); we used monthly climate normals (1960–1990) at 15 km resolution for substrate temperatures in 0 and 100% shade ($^\circ\text{C}$), wind speed at the surface (1 cm, m/s) and solar zenith angle ($^\circ$). We thus assume these conditions do not shift over time.

Global horizontal solar radiation, a determinant of adult body temperature, was calculated as a function of elevation, latitude and longitude by discounting incoming global extraterrestrial radiation (Campbell & Norman, 2000). Radiation was then partitioned into direct and diffuse components as a function of the atmospheric transmissivity tau [ratio of global horizontal solar radiation at surface and calculated global extraterrestrial (top of atmosphere) horizontal solar radiation] using an empirical relationship (Erbs, Klein, & Duffie, 1982) modified for high-altitude sites in Colorado (Olyphant, 1984). We used kernel density estimation to select a tau value for each hour from distributions derived from several years of data from the National Renewable Energy Laboratory (NREL) Solar Radiation Research Laboratory Baseline Measurement System in Golden, Colorado (1,829 m, 39.74 N, 105.18 W http://www.nrel.gov/midc/srrl_bms/).

Our microclimate model (Mitchell, Beckman, Bailey, & Porter, 1975; Porter & James, 1979; Porter, Mitchell, Beckman, & DeWitt, 1973) uses finite-difference methods to solve heat balance equations describing soil temperatures at the surface and specified depths (Kingsolver & Buckley, 2015). We used temperature and wind speed profiles (Campbell & Norman, 2000) to scale microclimate variables to plant height (0.02 m, based on shaded substrate temperature). Profiles were derived from weather station data collected at heights spanning 0.05 to 1.5 m in a subalpine Colorado site during July 2011. We use mean wind speed (0.4 m/s at 0.5 m height) from the profile to parameterize our models.

2.3 | Developmental rates and phenological timing

We approximate the temperatures of *Colias* larvae and pupae, which typically occur on the shady undersides of hostplant leaves, as air temperatures in the shade at plant height (0.02 m). We used a single sine wave approximation (see http://www.ipm.ucdavis.edu/WEATH/ER/ddss_tbl.html) to calculate degree-days (G) based on daily maximum and minimum temperatures at each site. Thermal reaction norms for the rates of larval and pupal development are linear for *C. eriphyle* (Higgins, 2014; MacLean, 2015). We thus used lab rearing to estimate two parameters describing the reaction norm for development rate: the developmental zero temperature (D_0) below which $D = 0$; and the accumulated degree-days (G) above D_0 needed to complete development. We used three different sets of values of D_0 and G (Higgins, 2014; MacLean, 2015): for post-diapause (fourth and fifth instar) larval development ($D_0 = 9.22^\circ\text{C}$ and $G = 117.06^\circ\text{C days}$); for pupal development ($D_0 = 9.7^\circ\text{C}$ and $G = 101.9^\circ\text{C days}$); and for the entire period of (non-diapause) larval development ($D_0 = 11.5^\circ\text{C}$ and $G = 270.39^\circ\text{C days}$). Studies with two populations of *C. eriphyle* from different elevations yielded similar estimates, so we assumed that D_0 and G do not change with elevation in our model.

For the overwintering generation, we estimated the date when larval development resumes as well as the onset and completion of pupation. For each generation, we assumed a duration of 7 days from adult emergence to egg laying, and five additional days until larvae hatch (MacLean, Higgins, Buckley, & Kingsolver, 2016). We model three generations annually when we estimate they can be completed by the end of September; otherwise we model two generations annually. Field observations indicate that three generations can be completed before overwintering each year across most of the elevation distribution, but that two generations are completed above c. 3,000 m and four (sometimes more) generations are completed at low elevations (c. 1,800 m) (Tabashnik, 1980; Watt, Chew, Snyder, Watt, & Rothschild, 1977; Watt et al., 1979). Our estimates approximately align with these observations.

2.4 | Heat balance, performance and fitness

We use a steady-state heat flux model for *Colias* adults that was developed and field validated by Kingsolver (1983b) to predict thorax temperature (operative environmental temperature, T_e) based on thermoregulatory traits (body size, basal ventral hind wing solar absorptivity and thoracic fur thickness), behavioural posture (basking and heat avoidance) and environmental conditions (Buckley & Kingsolver, 2012). The model successfully predicts patterns of T_e , flight activity time and heat-avoidance in the field for *Colias* species including *C. eriphyle* along an elevational gradient in Colorado (Kingsolver, 1983b; Kingsolver & Watt, 1984). We predict T_e , and subsequently potential flight activity time and egg viability, at 10-min intervals.

Our performance estimates focus on the potential duration of active flight, which is temperature dependent and essential for fitness determining activities including courtship, mating, nectar-feeding and oviposition (Kingsolver, 1983a; Stanton, 1984). We use field flight data for *C. eriphyle* in Montrose (Kingsolver, 1981) to describe the dependence of flight on operative environmental temperatures, T_e : $P_{\text{flight}} = \exp(-0.5 \cdot (\text{abs}(T_e - 33.5))/5)^{3.5}$. Adults achieve body temperature required for flight via behavioural thermoregulating in the absence of endogenous heat production (Watt, 1968). We assumed that butterflies select the body temperature closest to their thermal optimum (35°C) within the available range corresponding to full sun (lateral basking posture with wings closed and the ventral hindwing surfaces orientated perpendicular to the sun) and full shade (no direct radiation).

Substantial microclimate variation at high elevations exposes *Colias* adults to short intervals of high body temperatures (>40°C) that are deleterious for survival and fecundity (Kingsolver & Watt, 1983). Lab experiments confirm that daily heat shocks at 45°C reduce adult life span and egg production (Kingsolver & Watt, 1983). We modelled egg viability as an exponentially decaying function of body temperature from 1 at 40°C to 0.75 at 50°C (Buckley & Kingsolver, 2012; Kingsolver & Buckley, 2015).

We then use a demographic model to translate these estimates of flight time and egg viability into the fecundity component of

fitness (net reproductive rate) based on 500 females per generation (Buckley & Kingsolver, 2012). We simulate a date of adult emergence for each individual using a normal distribution with a standard deviation of 2 days, truncated 7 days before and after our estimated date of adult emergence for the year and generation (Tabashnik, 1980; Watt et al., 1977, 1979). We calculate daily egg production for each female as the product of available flight time (assuming 50% of available time is spent ovipositing) and the rate of oviposition [0.73 eggs/min, as estimated for Colorado *Colias* (Stanton, 1984)]. We multiply daily egg production by the average of hourly viability estimates and average this quantity across the 500 females to estimate daily fecundity. We estimate λ as the product of survival (product of fixed, empirically derived estimates of survival to maturity and daily survival, see Supporting Information) and daily fecundity summed across days [until reaching either a duration of 5 days, reflecting the mean adult life span in the field (Watt et al., 1977, 1979), or a maximum fecundity of 700 eggs (Kingsolver, 1981)]. Because we average over 500 females that differ in emergence timing and sum fecundity across days, our model does not yield zero values for fitness that would represent local extinction.

2.5 | Selection and evolutionary response

We use a simple quantitative genetic model to predict selection and evolution of α_{20} and B based on the fitness λ of individuals with wing solar absorptivity (α). We used estimates of the phenotypic standard deviation of α for *C. eriphyle* in 1980 (0.062) (Kingsolver, 1983b). Ellers and Boggs (2002) used parent-offspring breeding experiments to estimate the narrow-sense heritability h^2 of wing absorptivity for *C. eriphyle*, yielding $h^2 = 0.43$ for males and 0.36 for females (Ellers & Boggs, 2002); we use a h^2 value of 0.40 for α_{20} in our simulations. We used data for full-sib families of *C. eriphyle* from a middle elevation population to estimate the phenotypic standard deviation of B as 0.0083 (Higgins, 2014). In the absence of information about heritability of B or about the phenotypic or genetic covariance between α_{20} and B , we assume that $h^2 = 0.4$ for B , and that α_{20} and B are uncorrelated. We also assume that selection is sufficiently weak so that the heritabilities and phenotypic and genetic variances do not change with time (Lynch & Lande, 1993). Sensitivity analyses suggest that our results are qualitatively robust to the precise values of h^2 and phenotypic variances. We estimate the (unstandardized) directional selection gradients β for both α_{20} and B , and use the heritability h^2 to predict the evolutionary responses to selection in the next generation (Lande & Arnold, 1983).

We explore different scenarios for phenology, plasticity and evolution across grid cells, and how the scenarios influence the geometric mean population fitness (across generations) for each year. We considered four scenarios relative to the scenario of α_{20} remaining constant (no plasticity or evolution) at its initial value:

1. "plast only": Plasticity occurs at its initial value, but neither α_{20} nor B evolves.

2. "evol only": α_{20} evolves, but there is neither plasticity nor evolution of plasticity.
3. "plast + evol": α_{20} evolves, and plasticity is fixed at its initial value.
4. "+ evol of plast": Both α_{20} and B evolve.

3 | RESULTS

Maps of Colorado reveal that the phenology of the first generation of adults delays and pupal temperatures decline with increasing elevation (Figure 2). We next examine how elevation clines in phenology and pupal and adult temperatures shift across generations and years (Figure 3). At higher elevation sites, butterflies develop later and experience cooler pupal and adult temperatures (Figure 3 top). Gradients in pupal and adult temperatures are stronger in the second and third generations. We predict advances in phenology, particularly at high elevations, as climate change has progressed since 1950–1980 (Figure 3 bottom). Advances in the phenology of the first generation across time tend to decrease pupal and adult temperatures. Changes in pupal and adult temperatures are more variable for subsequent generations, in part due to the temperature tracking associated with phenological shifts.

Optimal values for wing absorptivity vary across seasons and elevations in response to environmental conditions (Figure 4). During our baseline time period (1951–1980), high absorptivity generally confers higher fitness in the first generation, particularly at higher elevation sites. In subsequent generations, lower absorptivities have higher fitness at low elevation sites and higher absorptivities have higher fitness at high elevation sites (Figure 4). Optimal absorptivities have declined as temperatures warm due to climate change. Examining particular absorptivities across time indicates that fitness is projected to decrease between 1980 and 2070 at low elevation sites and to increase at high elevation sites.

Fitness shifts with climate warming are clarified by examining projections for absorptivities that are constant across time (i.e. the scenario without plasticity or evolution) but varying across elevation

(as initially parameterized, Figure 5). Butterflies in high elevation sites are generally projected to experience fitness increases with warming whereas butterflies in low elevation sites are generally projected to experience fitness declines with warming. For the first seasonal generation, the elevation above which fitness declines increases across years (Figure 5a loess smooths). For the second generation, fitness at low elevations declines across years (Figure 5c loess smooths). The elevation of highest fitness increases as warming proceeds and high-elevation butterflies are predicted to increase their flight activity time (Figure 5b,d). Note that spatial heterogeneity in fitness is greater at higher than lower elevations, for both past (Figure 5a) and future climate conditions (Figure 5c).

How can plasticity and evolution of wing absorptivity alter responses to climate change? We compare fitness patterns across elevation (y axis) and time (x axis) to the scenario of constant absorptivity (no plasticity or evolution, Figure 5b,d). Plasticity and evolution tend to increase fitness at high elevations relative to the case of no plasticity or evolution (Figure 6 top). At low elevations, plasticity and evolution can reduce fitness. Plasticity in response to cool early season conditions can reduce fitness if conditions rapidly warm. Warm years also result in low fitness. We estimate a shift from selection for wing darkening to capitalize on warming in recent decades to selection for wing lightening in response to projected future climate change. Consequently, values of wing absorptivity evolve to lower values over time after initial evolution towards darker wing absorptivity (Figure 6 bottom). Plasticity, and particularly the evolution of plasticity, facilitates the wing lightening. The scenarios including evolution increase fitness at lower elevations as wings lighten in response to future warming. At high elevations, plasticity tends to be more effective than evolution at increasing fitness through climate warming (Figure 6 top). The evolution of trait means and plasticity confers fitness advantages in future climates as wings lighten.

How will phenotypic plasticity and evolution alter geographic patterns of fitness and wing colouration through climate change? We focus on the period 2010–2040 when selection shifts from favouring wing darkening to favouring wing lightening (Figure 6). We chose this near future period to highlight differences among scenarios.

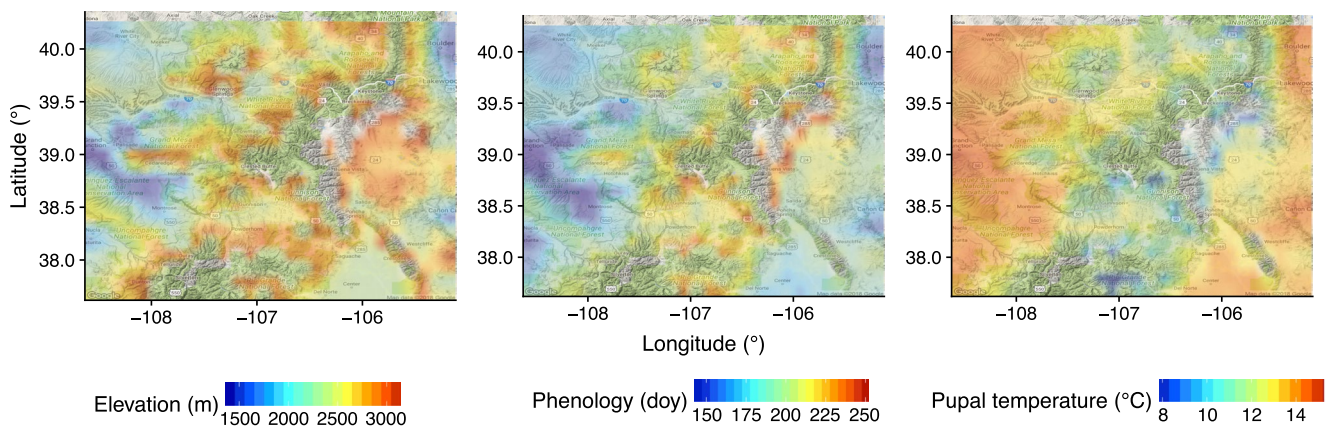


FIGURE 2 Spatial patterns across Colorado are shaped by elevation (left). For the first generation, adult phenology (doy: day of year, middle) delays and pupal temperatures ($^{\circ}\text{C}$, right) decline with increasing elevation [Colour figure can be viewed at wileyonlinelibrary.com]

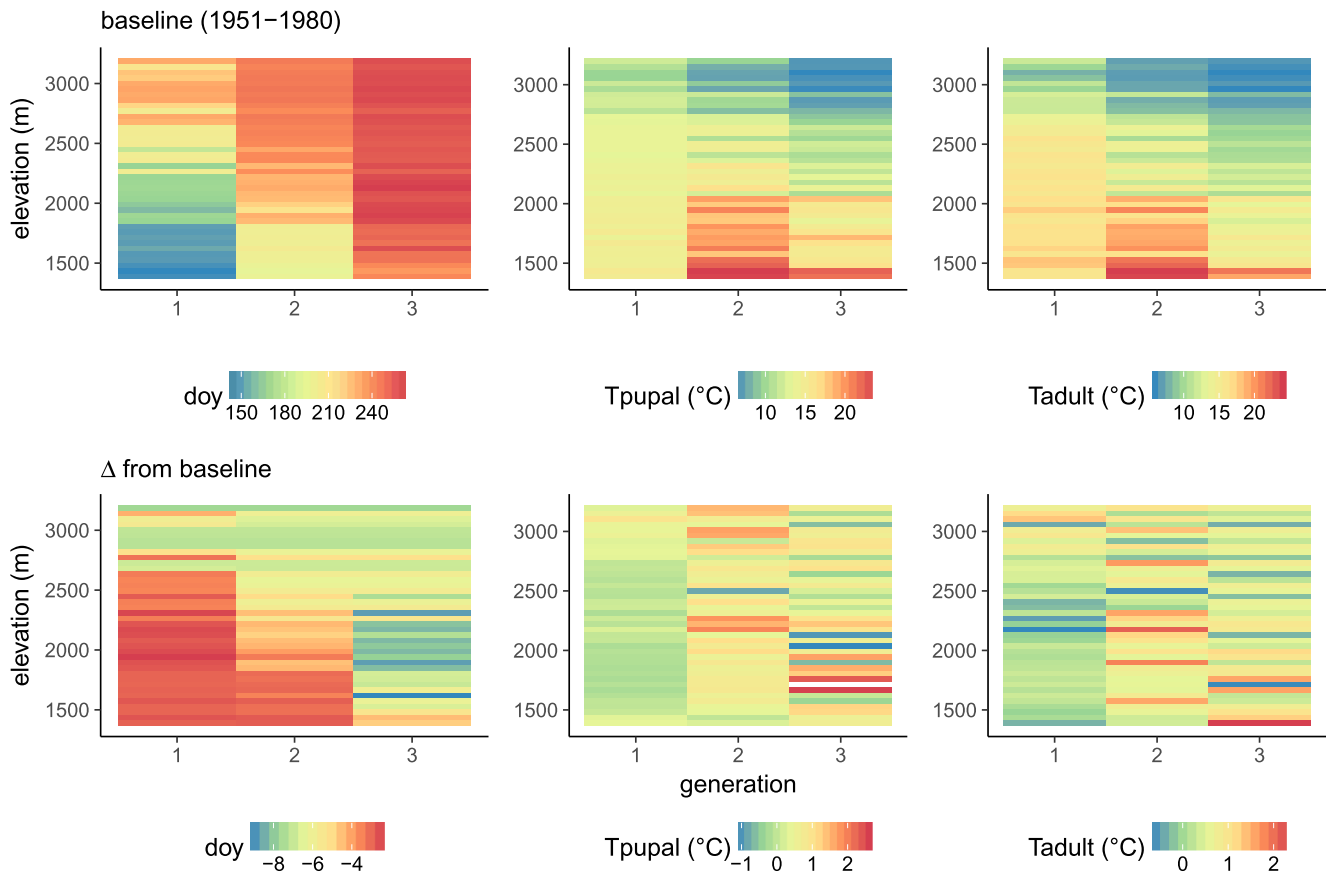


FIGURE 3 Adult phenology (doy: day of year), pupal temperatures (T_{pupal} , °C) and adult temperatures (T_{adult} , °C) vary as a function of elevation (m) and generation (1 to 3). We depict patterns for a baseline period (1951–1980, top row) and the difference (in 2011–2040) from the baseline period (bottom row). Values are interpolated across all grid cells at a given elevation using the `interp` function in the R package `akima` [Colour figure can be viewed at wileyonlinelibrary.com]

Evolutionary wing lightening in response to future warming is enhanced by plasticity, particularly the evolution of plasticity (Figure 7 top). Climate warming is generally predicted to increase fitness at high elevations and decrease fitness at low elevations across scenarios (Figure 7 bottom). Fitness declines at low elevation are exacerbated by an initial period of selection for wing darkening (Figure 6).

4 | DISCUSSION

Our analysis suggests that climate change will advance phenology across elevation gradients. We project that increases in pupal and adult temperatures over time will be most pronounced for the second and third generations. The fitness consequences of climate change will vary along the elevation gradient and across time. Fitness declines at low elevation will be countered by fitness increases at high elevation. Mean fitness will remain similar at intermediate elevations, but optimal absorptivities will decline over time. Although we do estimate variation in temperatures, phenology and fitness across geography within elevations, we find that elevation is a strong predictor of the fitness consequences of climate change in our system.

Climate change impacts on organisms are often determined by the balance of acute (e.g. stress responses to climate extremes) and chronic (e.g. energy balances in response to season warmth) responses. Responses at these different time-scales can be difficult to compare. However, our focal phenotype wing absorptivity is informative because a single phenotype influences fecundity due to both a chronic response (flight time) and acute stress response (declines in egg viability). Currently, in many locations and most seasons, thermal stress events resulting in egg viability declines are exceptionally rare, while darker wings allow butterflies to capitalize on warming. The potential to capitalize on warming is pronounced during cool, early and late diurnal and seasonal conditions that were too cool to be biologically relevant before warming. However, selection for wing darkening reverses once warming is sufficient to increase the risk of stressfully warm events that can dramatically decrease fecundity. Although differential chronic and acute responses to warming are less apparent when mediated by different phenotypes and mechanisms, the concept of differential selection pressures in response to chronic and acute warming conditions is likely to be general. Both chronic and acute responses influence fecundity in our system, but chronic responses will often influence fecundity whereas acute responses will often influence survival.

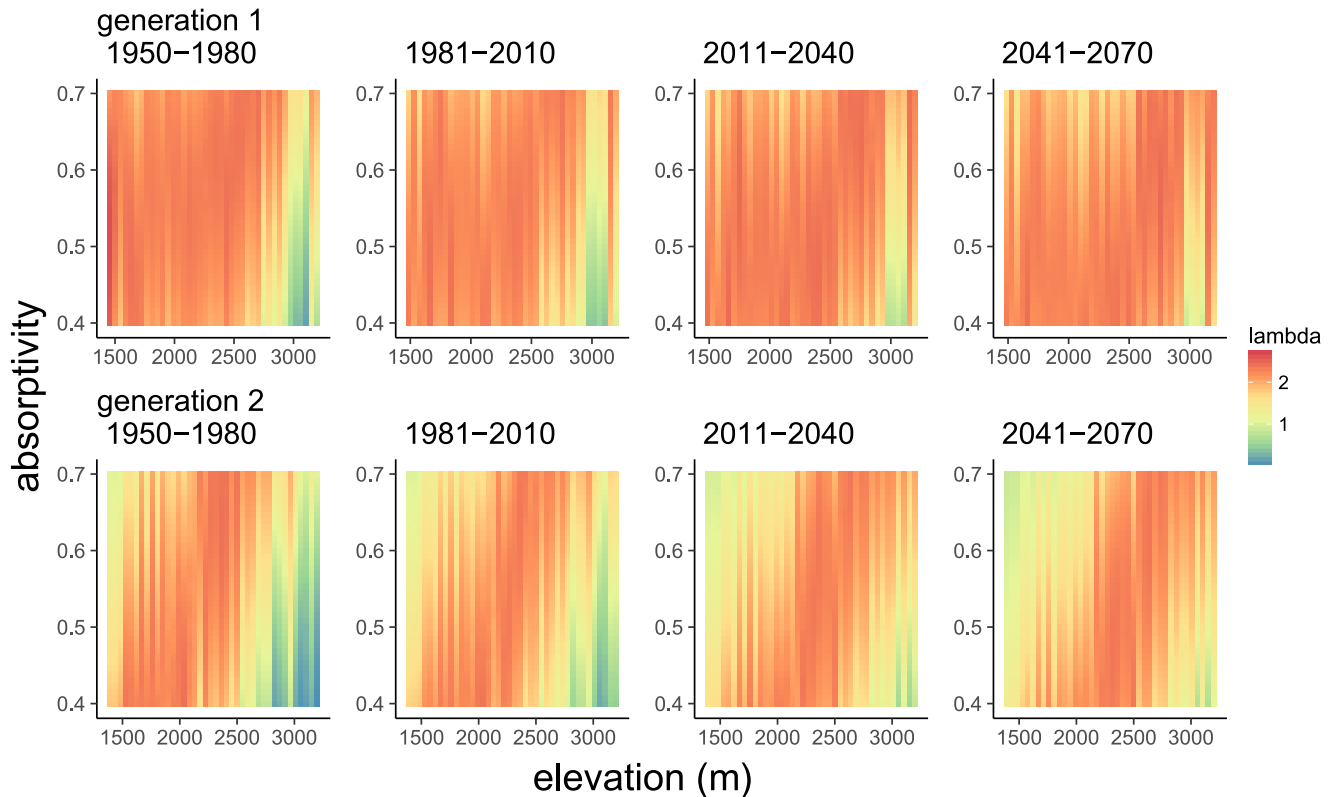


FIGURE 4 Fitness (λ) varies as a function of site elevation (m) and wing absorptivity for the first (top) and second (bottom) seasonal generation. Values are averaged across time periods (left to right): 1951–1980, 1981–2010, 2011–2040 and 2041–2070. Values are interpolated across all grid cells using the `interp` function in the R function `akima` [Colour figure can be viewed at wileyonlinelibrary.com]

Our findings complicate discussions over the role of evolution in responses to climate change. Our analysis suggests that evolution towards increased wing solar absorptivity will initially allow butterflies in cool, montane environments to capitalize on warming. However, once continued climate warming reverses the direction of selection towards declines in absorptivity, our analysis suggests that evolution will lag behind the decline in optimal absorptivity. Consequently, we predict that, in many regions, evolution will reduce fitness below that corresponding to the scenario of no evolution. The fitness advantages of evolution are limited in seasonal environments if selection fluctuates across generations (Kingsolver & Buckley, 2015).

We confirm at biogeographic scales that plasticity can facilitate evolution in seasonal environments. Our previous analysis for *C. eriphyle* for focal sites along an elevation gradient suggested that plasticity can facilitate evolution in seasonal environments by reducing shifts in the magnitude and direction of selection among generations (Kingsolver & Buckley, 2017). Our current analyses suggest that including the observed plasticity along with evolution leads to greater initial increases in wing absorptivity and subsequent greater declines in absorptivity. The subsequent decrease in absorptivity is further pronounced when plasticity itself can evolve. In both of these scenarios, the subsequent decrease in wing absorptivity is insufficient to counter fitness decreases associated with climate warming at low elevations. Thus, evolution and plasticity will ultimately exacerbate the fitness declines beyond those

in the absence of evolution and plasticity. Although we project that populations in most grid cells will remain viable through warming, projected fitness shifts suggest the importance of incorporating plasticity and evolution in SDMs (Buckley et al., 2010; Chown et al., 2010; Urban et al., 2016).

The fitness consequences of phenological shifts also depend on environmental context. Phenological advancements can increase fitness by enabling the completion of additional generations (Buckley, Arakaki, Cannistra, Kharouba, & Kingsolver, 2017), but cool, late-season temperatures can prevent the completion of the final generation or cause mortality (Hale, Morrongiello, & Swearer, 2016). Indeed, declines in butterfly populations were observed in regions where a greater proportion of individuals attempted an additional late season generation (Van Dyck, Bonte, Puls, Gotthard, & Maes, 2015).

Do empirical data for *Colias* butterflies support our projections that evolution will alter biogeographic responses to climate change? Recent empirical studies from one *C. eriphyle* population (2.4 km elevation) failed to detect changes in either mean absorptivity (α_{20}) or reaction norm slope between 1972 and 2012 (MacLean, 2015). Our models assume that α_{20} and slope are genetically uncorrelated (Scheiner & Lyman, 1991), but genetic correlations could slow evolutionary changes (Via & Lande, 1985). Many generations of directional selection may reduce genetic variation. Gene flow, which we omit, can also slow evolutionary shifts. Warming temperatures can increase gene flow via increased rates of butterfly dispersal (Kuussaari,

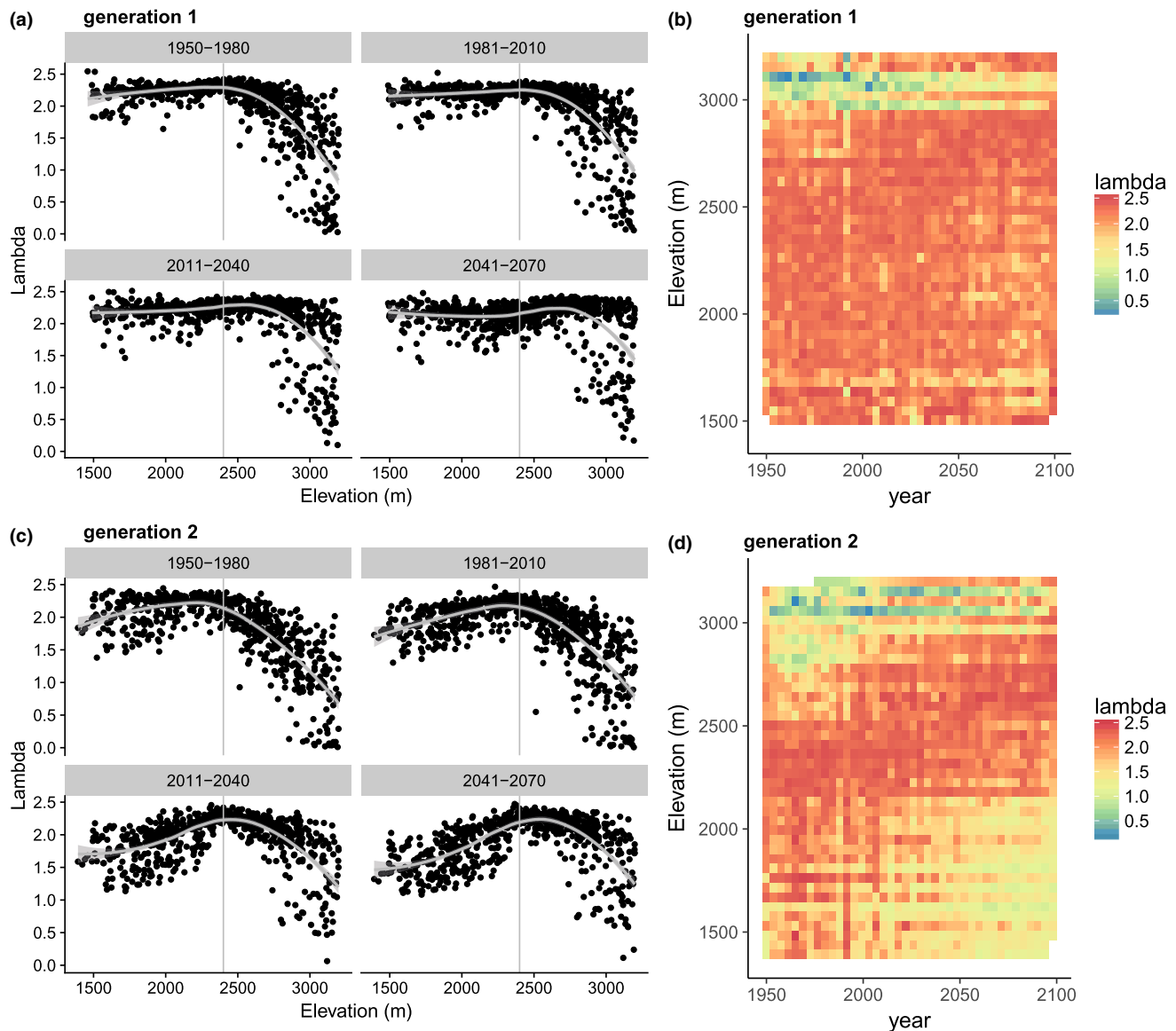


FIGURE 5 The elevation cline in fitness (lambda) shifts over four time periods for the (a) first and (c) second generations assuming constant wing absorptivity (i.e. scenario without plasticity or evolution). Points correspond to average values across the time period for each grid cell. Vertical lines at 2,400 m are intended to facilitate visualizing shifts in the elevation at which fitness declines. The grey line represents a loess smooth of the points. An alternative view shows how projected elevation clines (y axes) in fitness (lambda) shift over time (x axes) for the (b) first and (d) second seasonal generations. Values are interpolated across all grid cells using the `interp` function in the R function `akima` [Colour figure can be viewed at wileyonlinelibrary.com]

Rytteri, Heikkinen, Heliölä, & Bagh, 2016). A recent genetic analysis of low- and mid-elevation *C. eriphyle* populations in western Colorado suggests relatively low levels of genetic differentiation (MacLean et al., in review). Our model predicts mean fitness (net reproductive rate) rather than population dynamics. Changes in population size associated with warming could alter evolutionary trajectories and local extinctions may occur. Further empirical data are needed to incorporate these factors in our model predictions.

An examination of museum specimens of a closely related, high-elevation species, *C. meadii meadii*, documented shifts toward increased wing absorptivity between 1953–2012 in Colorado, consistent with our projections for *C. eriphyle* (MacLean, Kingsolver, &

Buckley, 2016). Analysis of collection dates suggests that phenological shifts may have extended the active season earlier at low elevations and later at high elevations. The shifts may have increased exposure to cool temperatures and selected for increases in thermoregulatory traits. Additionally, consistent with our models, fitness increases at higher elevations with warming could lead to shifts towards greater wing absorptivity. More broadly, a genetic study of a UK butterfly species documented evolution change associated with habitat use resulting from a range shift (Buckley, Butlin, & Bridle, 2012).

Interactions among phenotypes, phenological shifts and fitness are context dependent and difficult to predict, but several findings of our models are likely to be broadly applicable to ecological and

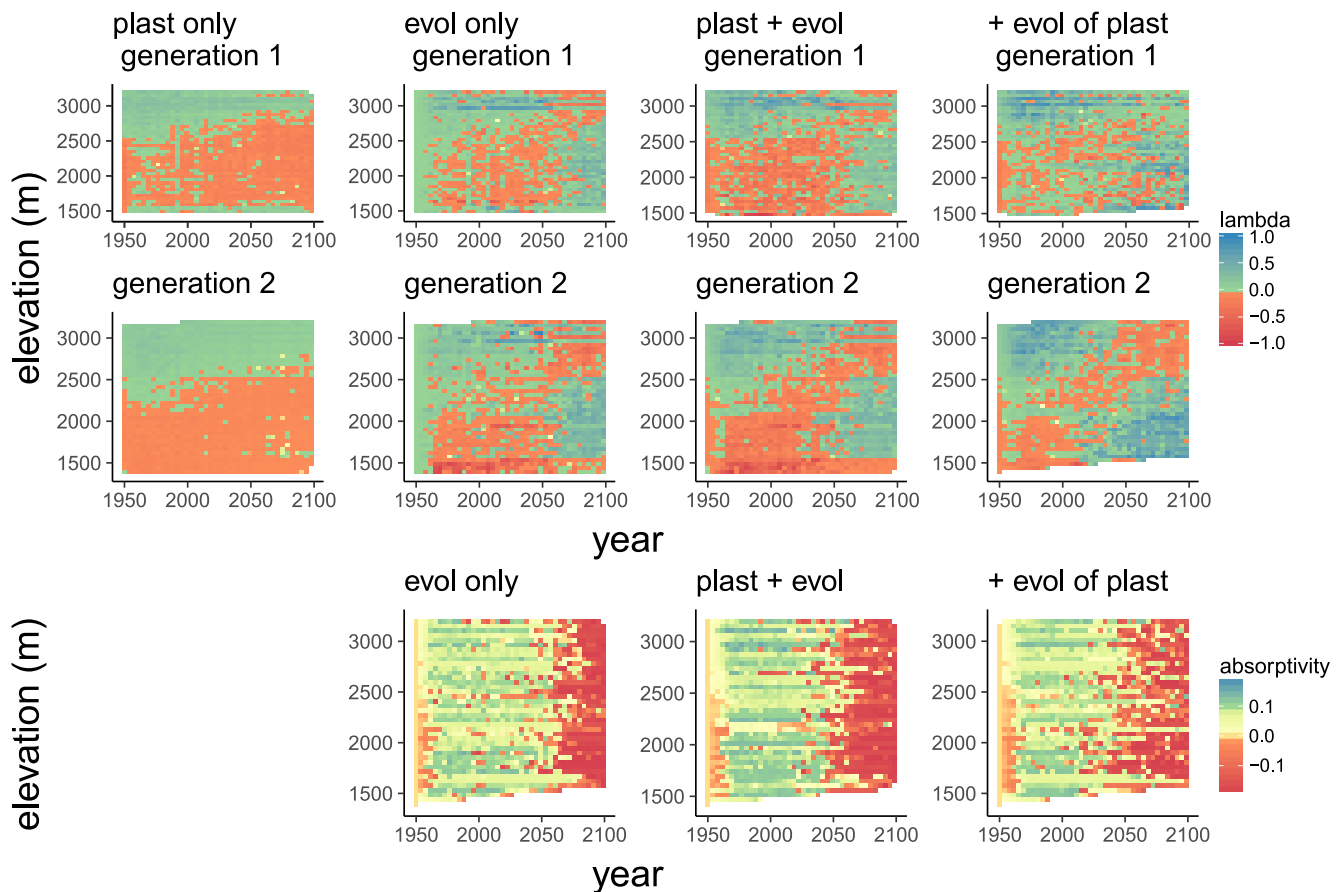


FIGURE 6 Fitness (λ , top: first generation, middle: second generation) and absorptivity (bottom: first generation) vary as a function of year and elevation (m). Absorptivity is depicted as α_{20} , so the value reflects the level of absorptivity that has evolved controlling for plasticity (by plotting values at 20°C). Metrics are depicted relative to the scenario of no plasticity or evolution for each time period. We depict the metrics for four scenarios (from left to right): plasticity (plast) only, evolution (evol) only, plasticity and evolution and evolution including of plasticity [Colour figure can be viewed at wileyonlinelibrary.com]

evolutionary responses to climate change. Our analysis suggests the viability of evolutionary responses, but that such responses may vary in direction as warming proceeds. Patterns of selection and shifts in response to warming are likely to vary across elevations with biogeographic implications. For multivoltine organisms, differences and shifts in selection along elevation gradients may be most pronounced for early season generations. Fluctuations in selection across generations may slow evolutionary responses (Kingsolver & Buckley, 2015), but plasticity can reduce variation in selection and facilitate evolution (Kingsolver & Buckley, 2017, 2018). As the fitness consequences of warming vary over time, evolution and plasticity may enhance fitness declines due to warming and alter biogeographic patterns.

Observed stasis in many traits that mediate the fitness consequences of environmental conditions is consistent with spatial and temporal variation in selection slowing evolution, as illustrated by the dynamics of our model. Related factors that slow selection include selection on correlated traits and environmental coupling of selection and genetic variation (Merilä, Sheldon, & Kruuk, 2001). In Soay sheep (*Ovis aries*), for example, harsh environmental conditions select for increased birthweight but reduce genetic variation

in birthweight, and the converse occurs when environmental conditions are favourable (Wilson et al., 2006). Additionally, our ability to detect genetic changes may be limited by environmental changes (Merilä et al., 2001).

Variation in the direction and strength of selection across both short (e.g. interannual) and long (e.g. decadal) time-scales is prominent across a variety of taxa and traits (Siepielski, DiBattista, & Carlson, 2009). An examination of whether the environment drives variation in selection attributed greater variation in selection to precipitation than temperature (Siepielski et al., 2017). However, the study's use of annual environmental conditions may obscure responses to intra- and inter-seasonal variation such as those explored here. Spatial variance in selection is roughly comparable to temporal variation, but spatial variance is concentrated in areas of weak selection and the variance is primarily in strength rather than direction (Siepielski et al., 2013). A long-term study of stick insects (*Timema cristinae*) highlights that environmental variation limits our ability to predict phenotypic evolution (Nosil et al., 2018). Both spatial and temporal variation in environmental conditions will shape plasticity and genetic adaptation in response to environmental change.

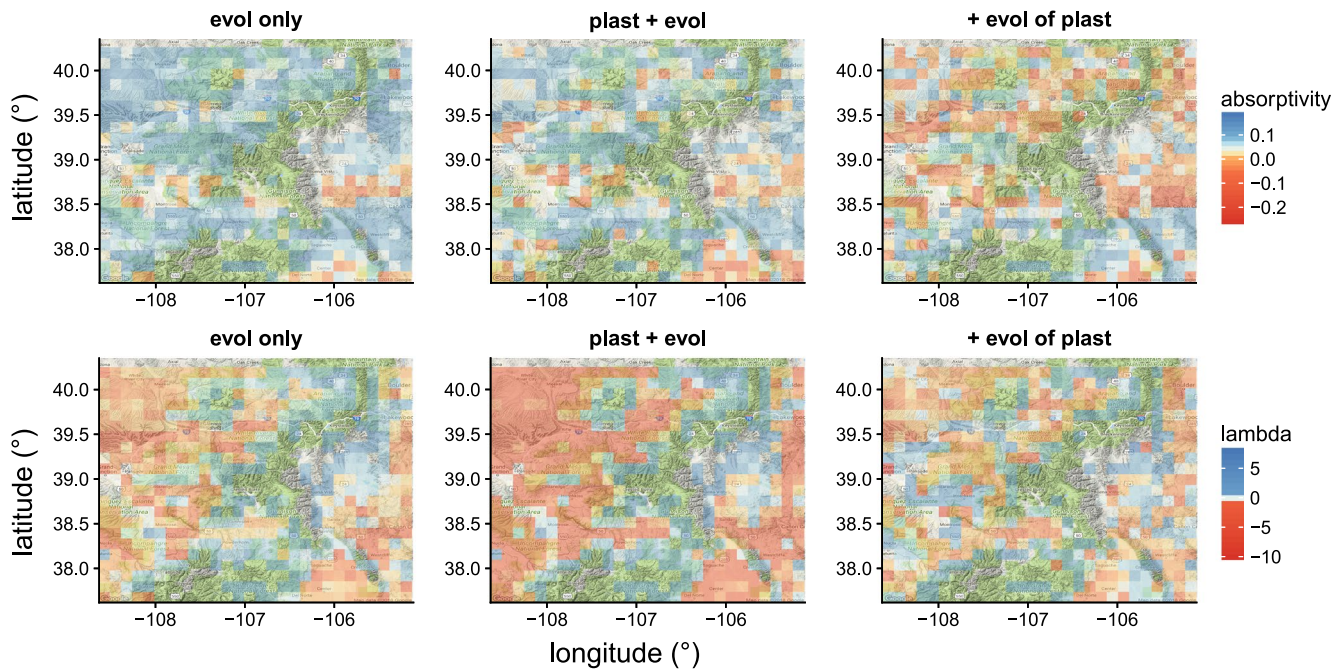


FIGURE 7 Maps of wing absorptivity (top) and fitness (bottom) for the first seasonal generation. Values are relative to absorptivities and lambdas predicted for the scenario without plasticity or evolution for 2010–2040. Blue colours indicate higher values and red colours indicate lower values than the no plasticity or evolution scenario (white = no difference in values). We depict the metrics for three scenarios (from left to right): evolution (evol) only, plasticity (plast) and evolution and evolution including of plasticity [Colour figure can be viewed at wileyonlinelibrary.com]

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DATA ACCESSIBILITY

Climate data are available from the BCCA 5 archive (http://gdcdcp.ucllnl.org/downscaled_cmip_projections/) and the NREL Solar Radiation Research Laboratory (http://www.nrel.gov/midc/srnl_bms/). R code for running the model is available at <https://github.com/lbuckley/ColiasBiogeog>.

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BIOSKETCH

Lauren Buckley, an Associate Professor at the University of Washington, and **Joel Kingsolver**, a Professor at the University of North Carolina, and their research groups have been repeating historic laboratory and field work and building models to understand *Colias* butterfly ecological and evolutionary responses to recent climate change. Having extensively modelled a single elevation gradient over recent climate change, they are happy to have progressed to modelling biogeographic scales and responses to future climate change.

SUPPORTING INFORMATION

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

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