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Evolution of plasticity and adaptive responses to climate change along climate gradients

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The relative contributions of phenotypic plasticity and adaptive evolution to the responses of species to recent and future climate change are poorly understood. We combine recent (1960–2010) climate and phenotypic data with microclimate, heat balance, demographic and evolutionary models to address this issue for a montane butterfly, *Colias eriphyle*, along an elevational gradient. Our focal phenotype, wing solar absorptivity, responds plastically to developmental (pupal) temperatures and plays a central role in thermoregulatory adaptation in adults. Here, we show that both the phenotypic and adaptive consequences of plasticity vary with elevation. Seasonal changes in weather generate seasonal variation in phenotypic selection on mean and plasticity of absorptivity, especially at lower elevations. In response to climate change in the past 60 years, our models predict evolutionary declines in mean absorptivity (but little change in plasticity) at high elevations, and evolutionary increases in plasticity (but little change in mean) at low elevation. The importance of plasticity depends on the magnitude of seasonal variation in climate relative to interannual variation. Our results suggest that selection and evolution of both trait means and plasticity can contribute to adaptive response to climate change in this system. They also illustrate how plasticity can facilitate rather than retard adaptive evolutionary responses to directional climate change in seasonal environments.

1. Introduction

Organisms have responded to recent and ongoing climate change through both phenotypic plasticity [1–3] and evolution [3,4]. However, the interaction between plasticity and evolution in determining adaptive responses of populations to climate change is unclear. Few studies have documented evolutionary changes in plasticity itself in response to climate change [5], but such changes seem likely given that climate change may increase environmental variability and generate novel climatic conditions [6].

Theoretical models predict that plasticity can slow adaptive evolution in response to sustained, directional environmental change by weakening selection, but that plasticity can enable population persistence and maintain genetic variance [2,7,8]. Alternatively, plasticity can enhance evolutionary responses in novel or fluctuating environments [9–11]. Empirical studies show that populations from more variable environments tend to be more plastic and to respond more rapidly to environmental change during experimental evolution [12]. In many organisms, plasticity is induced by environmental cues that influence subsequent trait development and phenotypic expression [13], and the evolution of adaptive plasticity will depend on the predictability of the environment across development [14,15]. As a result, patterns of environmental variation both within and between generations are important in determining how plasticity and its evolution will affect responses to environmental change [9–11].

Here, we leverage field and laboratory data with models [16,17] that link phenotypes to fitness as a function of the environment to investigate the interplay

between evolution and plasticity along realistic environmental clines. We ask: how does seasonal and inter-annual environmental variation influence the relative importance of phenotypic evolution and plasticity in adapting to climatic gradients and climate change? We focus on a butterfly species that has multiple generations per year, allowing us to parse selection in response to seasonal and inter-annual environmental variation, which vary along elevation gradients. Developmental plasticity enables phenotypes to respond to temperature seasonality [18] and can reduce differences in selection among generations, but theoretical models rarely include seasonality. We investigate the hypothesis that phenotypic plasticity and its evolution will contribute importantly to population responses to climate change in more seasonal environments.

The wing solar absorptivity of *Colias eriphyle* butterflies in the western USA exhibits adaptation to local climatic conditions along elevational and latitudinal gradients [19,20]. Wing absorptivity also responds plastically to developmental (pupal) temperatures [21], generating different wing phenotypes among seasonal generations [18,22]. Increasing wing absorptivity (due to a greater proportion of melanic wing scales [23,24]) can increase body temperature, flight time and reproductive success, but overheating reduces activity and egg viability [16,17]. Laboratory experiments with *C. eriphyle* show that mean wing absorptivity declines linearly with increasing temperatures during pupal development [21], so we can represent wing absorptivity of an individual (quantified as the solar absorptivity of the posterior ventral hindwing, α) in terms of two traits: α_{20} , the mid-point absorptivity at a mean pupal temperature of 20°C; and B, the slope of the reaction norm relating pupal temperature and wing absorptivity α . We combine climate data for three sites in Colorado (at 1.8, 2.4 and 3.0 km, approx. spanning the species' elevation range of 1.4–3.0 km) with microclimate, heat balance, demographic and quantitative genetic models to predict plastic and evolutionary changes in absorptivity across seasonal generations at each site from 1960 to 2010.

2. Material and methods

We first summarize and then detail our integration of microclimate, biophysical, demographic and evolutionary models to predict fitness as a function of thermoregulatory trait values and climatic data for 1960–2010 (figure 1). Details for each of the models are provided in the electronic supplementary material. Our approach follows Kingsolver & Buckley [17], but additionally incorporates both phenological shifts in seasonal timing, and developmental plasticity in adult traits. A microclimate model translates environmental data into temperature at plant height. We use laboratory-based estimates of developmental rate to predict average larval, pupal and adult phenology across the study period and the temperatures developmental stages experience each year. The focal trait, wing absorptivity, is influenced by microclimate due to the plastic effects of developmental (pupal) temperatures. We use a steady-state heat flux model for *Colias* adults [25] to predict thoracic body temperature and adult performance. We use a demographic model to relate adult performance to fitness, which we use to model evolution.

(a) Microclimate

Our high elevation site (3.0 km, 40.03 N, 105.55 W) is C1 of the Niwot Ridge LTER (<http://niwot.colorado.edu>) [26]. We also examined two National Weather Service Cooperative (COOP)

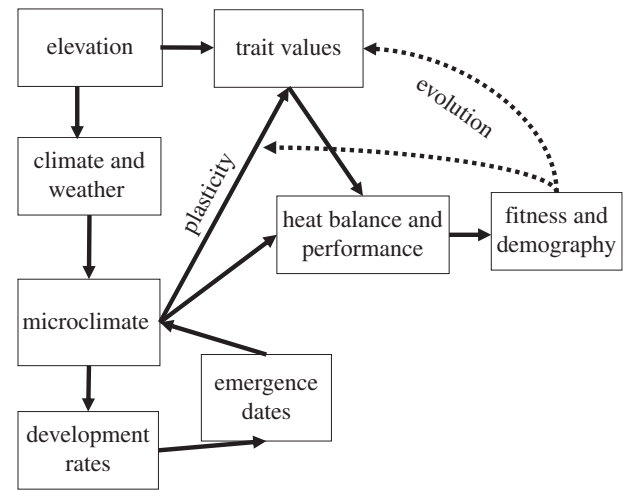


Figure 1. Flow diagram for the modelling framework. Climate and weather at each elevation determine the microclimatic conditions experienced by larvae, pupae and adults at each site. Microclimate determines developmental rates of larvae and pupae, which determine phenology. The focal trait, wing melanin, is initially determined by elevation differences among sites, and is also influenced by microclimate due to the plastic effects of developmental temperatures. We model how wing melanin influences heat balance and performance in given microclimates and then use performance to estimate fitness. Fitness differences among individuals exhibiting variation in wing melanin can generate selection and cause evolutionary changes in the mean and plasticity of wing melanin in the next generation.

Program sites: Cochetopa Creek (2.4 km, station 51713, 38.43 N, 106.75 W) and Montrose No. 2 (1.8 km, station 55722, 38.48 N, 107.88 W). Air temperatures at these sites differ in overall means, seasonal patterns and interannual variation in temperature (electronic supplementary material, figure S1). We estimated air temperatures (T_a) at 10 min intervals based on daily maximum and minimum temperatures from each site using a diurnal temperature variation function incorporating sine and exponential components [27]. Global horizontal solar radiation at the surface was calculated as a function of elevation, latitude and longitude, and the global extraterrestrial radiation [28]. Total radiation was then partitioned into direct and diffuse components as a function of the atmospheric transmissivity τ (=ratio of global horizontal solar radiation at surface and calculated global extraterrestrial (top of atmosphere) horizontal solar radiation). Distributions of τ were estimated hourly using several years of data from the NREL Solar Radiation Research Laboratory Baseline Measurement System in Golden, Colorado (1829 m, 39.74 N, 105.18 W, http://www.nrel.gov/midc/srrl_bms/). We used kernel density estimation to simulate a τ value for each time interval. Solar radiation was partitioned using an empirical relationship by Erb *et al.* [29], as modified for high-altitude sites in Colorado [30].

We implemented a microclimate model [31–33] using finite-difference methods to solve heat balance equations describing soil temperatures at the surface and specified depths [17,34]; predicted surface temperature is then used to compute air temperature profiles above the surface. We scaled microclimate variables to plant height by estimating temperature and wind-speed profiles [28] using data collected at heights spanning 0.05–1.5 m during 2–14 July 2012 at the subalpine site (see the electronic supplementary material). Based on weather station data from July 2011 at this site, the mean wind speed at 0.5 m height was 0.4 m s⁻¹.

(b) Developmental rates and phenological timing

We assumed that larvae diapausing over the winter as third instars could resume development once snow melted and

temperatures were permissive. We estimated snow-melt as Julian date, $J = 20$ at 1.8 km and $J = 105$ at 2.4 km (both 1961–1990 averages of data from the Western Regional Climate Center, <http://www.wrcc.dri.edu/>) and $J = 141$ at 3.0 km (averages of 1960–2010 data available from the Niwot Ridge LTER).

We used laboratory data [35,36] to characterize the reaction norm for development rate D with two parameters: the developmental zero temperature (D_0) below which no development occurs (i.e. $D = 0$); and the accumulated degree-days (G) above D_0 needed to complete development. For our models we used three different sets of values of D_0 and G based on recent data [35,36]: for post-diapause (fourth and fifth instar) larval development ($D_0 = 9.22^\circ\text{C}$ and $G = 117.06^\circ\text{C d}$); for pupal development ($D_0 = 9.7^\circ\text{C}$ and $G = 101.9^\circ\text{C d}$); and for the entire period of (non-diapause) larval development ($D_0 = 11.5^\circ\text{C}$ and $G = 270.39^\circ\text{C d}$). Studies with two populations of *C. eriphyle* from different elevations yielded similar estimates [35], so we assumed that D_0 and G do not change with elevation in our model.

Because *Colias* larvae and pupae typically occur on the shady undersides of leaves on the host plant, we assumed that larval and pupal temperatures were equal to air temperatures in the sun at plant height (1.8 km = 50 cm; 2.4 and 3.0 km: 20 cm; see the electronic supplementary material). We used a single sine wave approximation with data for daily maxima and minima temperatures for each site to calculate accumulated degree-days (G). For the overwintering generation, we estimated when larval development resumes as well as the onset and completion of pupation. For subsequent generations, we assumed a duration of 7 days from adult emergence to egg laying, and five additional days until larvae hatch [36]. Field observations indicate (and our simulations correctly predict) that two generations are completed before overwintering each year at 3.0 km, three generations at 2.4 km and four (sometimes more) generations at 1.8 km [37–39]. For comparative purposes we modelled two generations each year at 3.0 km and three generations at the other two sites.

(c) Heat balance, performance and fitness

We used a biophysical model to predict butterfly body temperature as a function of thermoregulatory traits [17]. Because *Colias* populations and species (including *C. eriphyle*) are adapted to local climate through differences in solar absorptivity (α) of the posterior ventral hindwings [20,24,25], our analyses here focus on variation, plasticity and evolution of this trait. Wing solar absorptivity (i.e. 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 spans possible values of 0.4 (all pteridine scales) to 0.7 (all melanic scales) [25]. Two other morphological traits also influence the heat balance and body temperature of a butterfly: the length of setae on the thorax (fur thickness), and diameter of the thorax. We used a fur thickness of 0.82 mm and thorax diameter of 3.6 mm in our analyses, based on measurements for *C. eriphyle* at several sites in Colorado [20,25].

Wing absorptivity in *C. eriphyle* is also phenotypically plastic: increasing temperature during pupal development decreases wing absorptivity [21,35]. We used the initial mean starting value $\alpha_{20} = 0.4226 + 0.06517 \times E$, where E = elevation in kilometres [25]. We estimated the mean reaction norm slope as $B = -0.083^\circ\text{C}^{-1}$, based on data for *C. eriphyle* males at our low elevation site [35]. In the absence of other information, we assumed that the slope does not vary with elevation, though we allow this value to evolve in our analyses (see below).

We used a steady-state heat flux model for *Colias* adults that was developed and field validated by Kingsolver [25] to predict thoracic body temperature (T_b) based on thermoregulatory traits (body size, basal ventral hind wing solar absorptivity and thoracic fur thickness), behavioural posture (basking and heat-avoidance) and

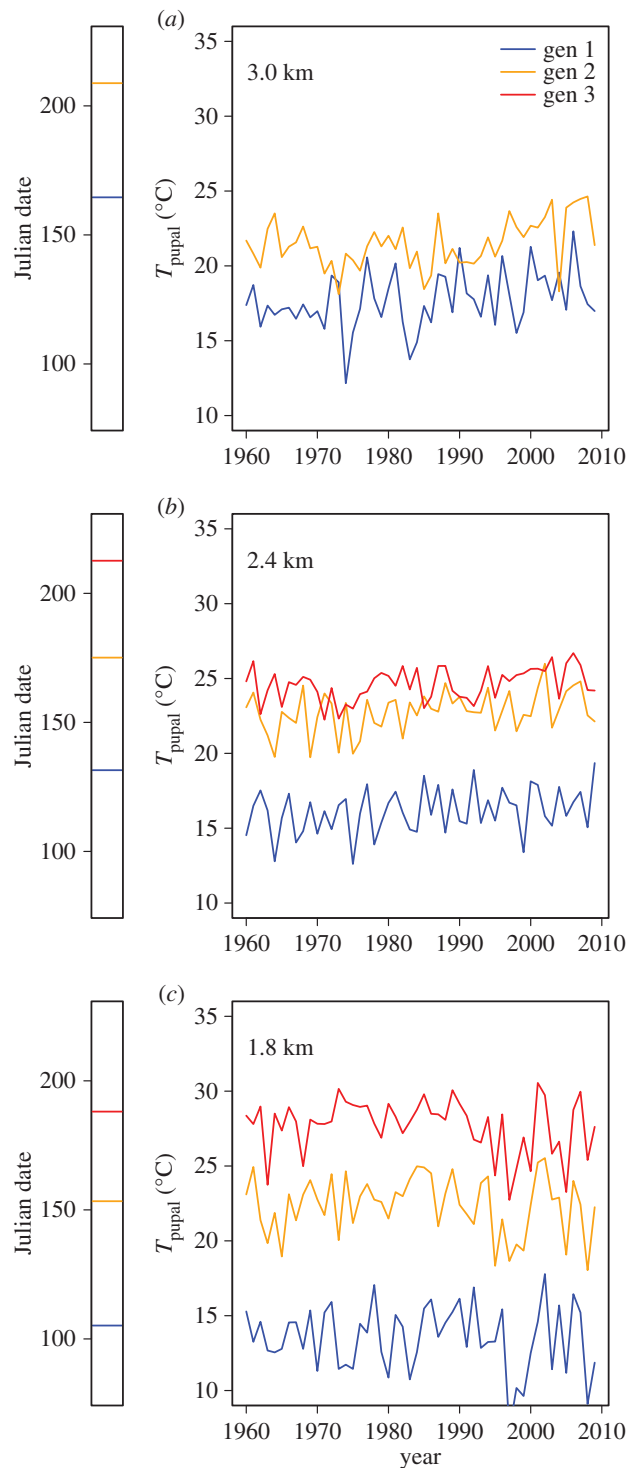


Figure 2. Predicted seasonal phenology and pupal temperatures across years. Climate and weather differences along the elevation gradient ((a) 3.0, (b) 2.4 and (c) 1.8 km) determine the Julian date of appearance for adults (left) and annual mean pupal temperatures (right, T_{pupal} in $^\circ\text{C}$) during the first (blue), second (orange) and third (red) generations (gen).

environmental conditions [16]. The model successfully predicts patterns of T_b , flight activity time and heat-avoidance in the field for *C. eriphyle* and other *Colias* species along an elevational gradient in Colorado [25,40]. Predictions of T_b are updated every 10 min. Adults behaviourally thermoregulate to achieve the body temperatures needed for flight, and do not use endogenous heat production to elevate body temperatures [24]. We assumed that butterflies select the body temperature closest to their thermal optima (35°C) with available body temperatures bracketed by those in full sun (lateral basking posture with wings closed and the ventral hindwing

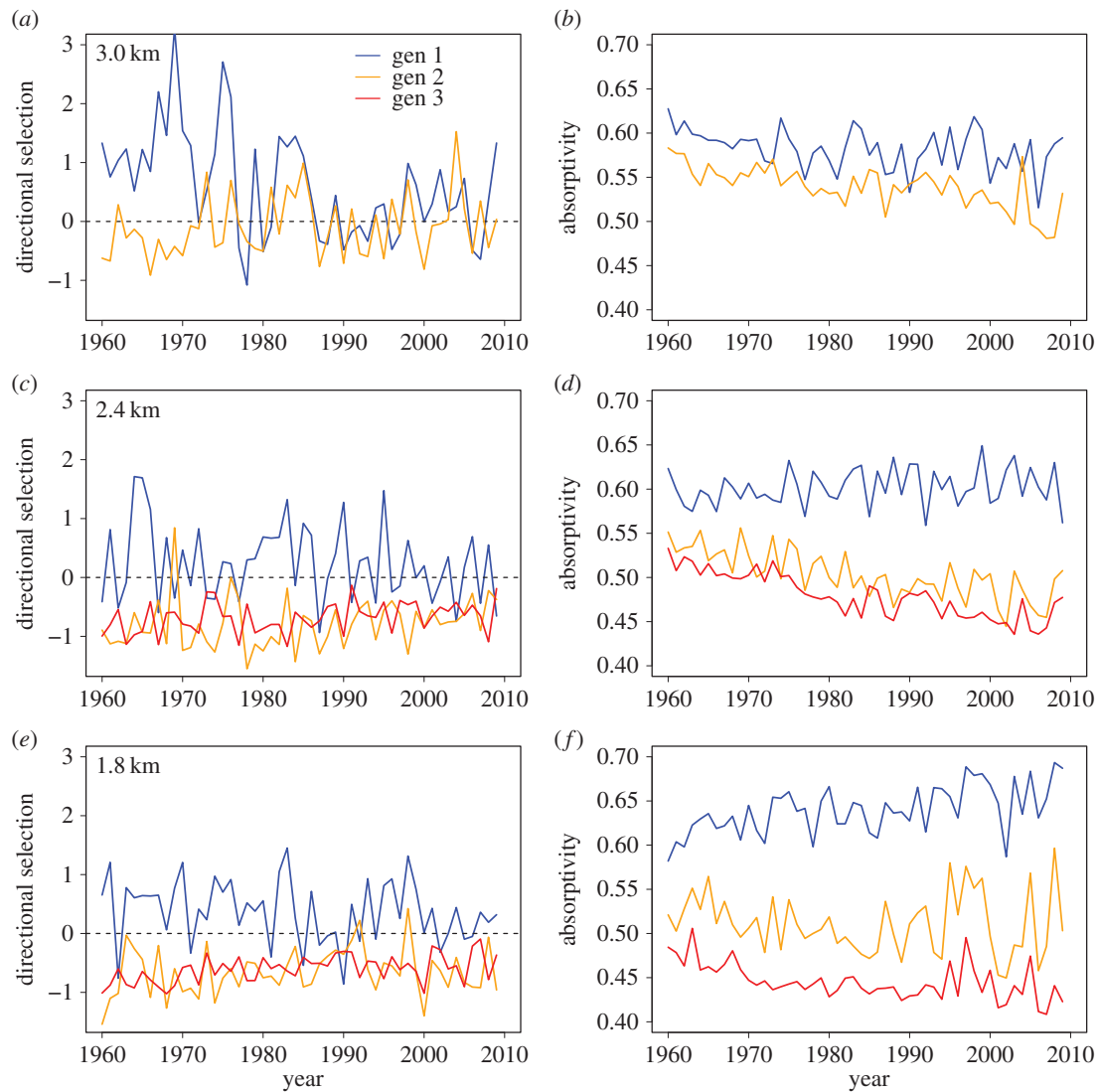


Figure 3. Predicted directional selection and mean absorptivity across years. We depict the directional selection gradient (β) on absorptivity (wing melanin, a, c, e) and mean absorptivity (b, d, f) across elevations as a function of year for each generation.

surfaces oriented perpendicular to the sun) and full shade (no direct radiation) [24,41].

We estimated fitness (λ , net reproductive rate) as the product of survival and the fitness-limiting process of egg deposition on host plants [17] (see the electronic supplementary material). We simulated fitness for 500 females per generation. We simulated 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 [37–39]. We calculated daily egg production for each female as the product of available flight time (where 50% of available flight time is spent ovipositing: [42]) and the rate of oviposition (0.73 eggs/min, as estimated for Colorado *Colias* [43]). We estimated the probability of flight for thermoregulating adults as a function of body temperature, T_b : $P_{\text{flight}} = \exp(-0.5 \times (\text{abs}(T_b - 33.5))/5)^{3.5}$ (based on field flight data for *C. eriphyle* in Montrose [25]). We multiplied daily egg production by the average of hourly egg viability estimates. Exposing *Colias* adults to even short intervals of deleteriously high body temperatures (greater than 40°C) reduces egg viability [44]. We modelled egg viability as an exponentially decaying function of body temperature from 1 at 40°C to 0.75 at 50°C [16,17]. We estimated λ by summing over days to either a duration of 5 days, reflecting the mean adult lifespan in the field [38,39] or reaching a maximum lifetime egg production of 700 [45] as the product of survival to maturity, daily survival and egg production

(averaged across the 500 females; see the electronic supplementary material for details).

(d) Evolution

Once we estimated the fitness λ of an individual *Colias* as a function of climate variables and solar absorptivity (α), we used a simple quantitative genetic model to predict selection and evolution of α_{20} and B. We used estimates of the phenotypic standard deviation of α for *C. eriphyle* in 1980 (0.062) [25]. Ellers & Boggs [19] used parent–offspring breeding experiments to estimate the narrow-sense heritability h^2 of wing melanin for *C. eriphyle*, yielding $h^2 = 0.43$ for males and 0.36 for females [19]; 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 0.083 [35]. In the absence of information about heritability of B or about the phenotypic or genetic covariance between α_{20} and B, we assumed that $h^2 = 0.4$ for B and that α_{20} and B are uncorrelated. We also assumed that selection is sufficiently weak so that the heritabilities and phenotypic and genetic variances do not change with time [7]. Additional simulations (not shown) suggested that the precise values of h^2 or phenotypic variances have little effect on our qualitative results. Because common garden experiments with *C. eriphyle* show that populations from higher elevations have greater wing absorptivity, we allowed mean absorptivity to

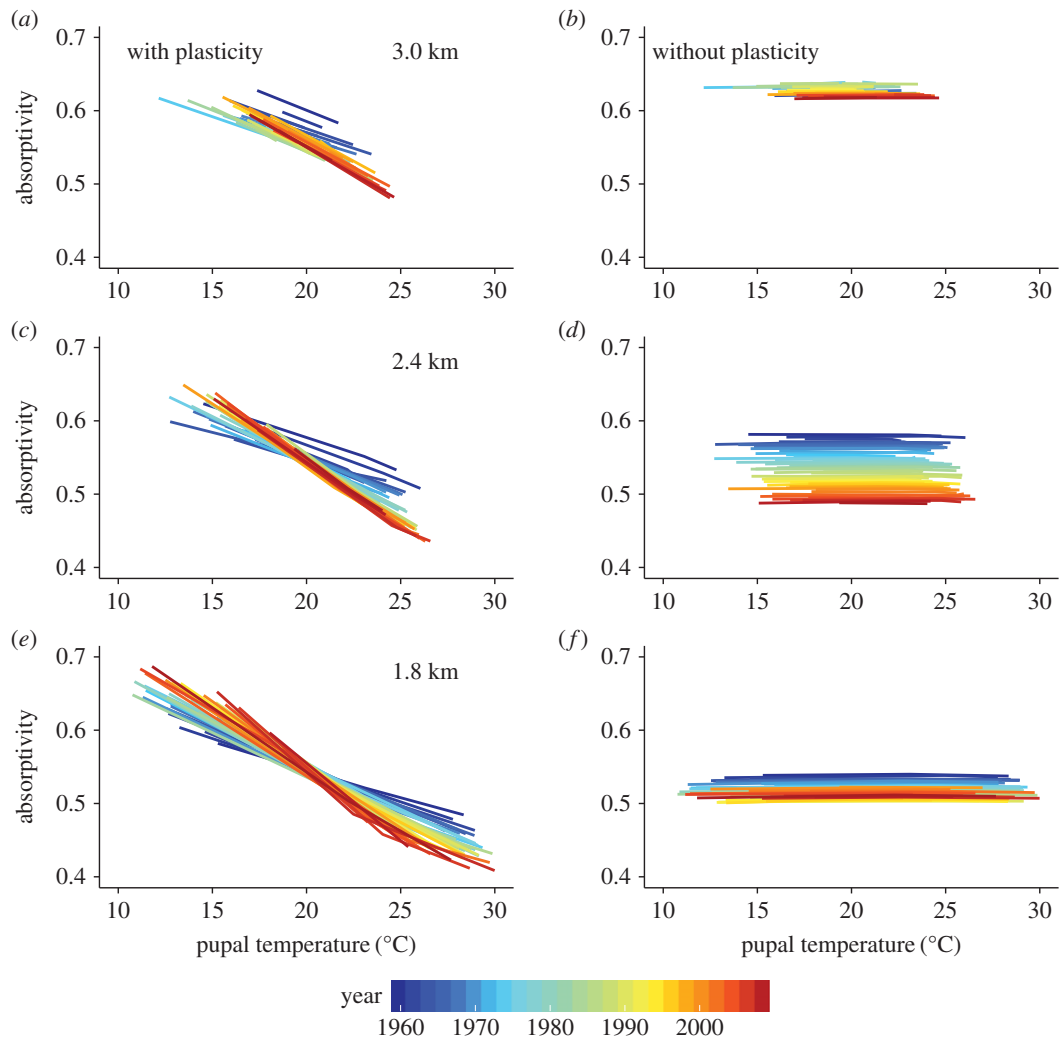


Figure 4. Plasticity facilitates evolution. The annual mean reaction norms (absorptivity as a function of mean pupal temperature) evolve differently over time (red to purple: 1960–2009) along the elevation gradient. Comparing mean absorptivity in the absence of plasticity reveals that plasticity facilitates evolution at the low and high elevation sites (*b,d,f*).

differ among the three sites at the start of the simulation (see the electronic supplementary material). Finally, we assumed no gene flow among populations. We estimated the (unstandardized) directional selection gradients β for both α_{20} and B , and used the heritability h^2 to predict the evolutionary responses to selection in the next generation [46].

We incorporated empirically estimated error or variability in several components of our models as described above. We account for trait variability by simulating individual butterflies with traits derived from a distribution based on empirical trait means and variability. We account for variability in development and emergence time by selecting from a phenological distribution centred on mean dates. We account for environmental variability by simulating radiation from a distribution across each time period. We also examined the sensitivity of our evolution models to heritability and phenotypic variance.

3. Results

As elevation increases, the predicted date of the first adult flight season and number of flight seasons decline (figure 2). Mean temperatures during the pupal stage are generally low during the first generation at all sites, but subsequent seasonal generations experience much higher mean pupal temperatures at lower elevations. As a result, the predicted range of seasonal

variation in pupal (and adult) temperatures decreases with increasing elevation (figure 2).

This elevational pattern has important consequences for seasonal patterns of wing absorptivity, selection and evolution. Developmental plasticity causes mean absorptivity to differ more among seasonal generations at lower than at higher elevation (figure 3). The predicted patterns of directional selection on absorptivity from 1960 to 2010 also vary with elevation. At the high (3.0 km) site (figure 3*a,b*), there has been positive selection (favouring increased absorptivity) during the first seasonal generation in most years from 1960 to 1985. Subsequently, the direction of selection has fluctuated about zero in both generations. By contrast at the low (1.8 km) site (figure 3*e,f*), there has been positive selection in the first generation and negative selection in the second and third generations in most years throughout the time period.

Historical shifts in wing absorptivity will reflect both changes in environmental temperatures (affecting phenotypic expression of plasticity) and evolutionary changes in mean and plasticity of absorptivity (figure 3). At the high site, predicted mean absorptivity in each generation declines over time, while the differences between generations remain similar. The predicted historical pattern at the low site is quite different: mean absorptivity increases with time in the first generation, but decreases with time

in the third generation. As a result, seasonal differences in absorptivity increase with time at low but not high elevation sites (figure 3).

These patterns can be understood in terms of predicted evolutionary changes in reaction norms, characterized by midpoint absorptivity (α_{20}) and the slope (B , figure 4). At the high site, α_{20} declines substantially over time, with a slight decrease in B ; at the low site, there is little change in α_{20} , but B becomes increasingly negative (steeper) over time (figure 4*a,c,e*).

4. Discussion

Our model results suggest that the contributions of plasticity and evolution to adaptation to climate change vary systematically along climatic (including elevation) gradients. At lower sites with longer growing seasons and the potential for more generations per year, recent and future climate change expands the seasonal range of environmental temperatures, and selects for greater developmental plasticity [12,14]. At higher sites with shorter growing seasons and fewer generations per year, the smaller seasonal range of environmental temperatures reduces the adaptive significance of plasticity, and climate warming selects for reductions in mean absorptivity. As shown by previous analyses of *C. meadii* in alpine and subalpine sites, stochastic environmental variation among years also reduces the evolutionary response of wing absorptivity to climate warming at higher elevations [17].

The importance of plasticity can be quantified by eliminating developmental plasticity from the model but allowing evolutionary responses in mean absorptivity (fixing $B = 0$). In the absence of plasticity, climate change results in little evolutionary change in α_{20} at the low and high sites, and a decline in α_{20} over time at the middle (2.4 km) site (figure 3*b,d,f*). Without plasticity, there is strong positive selection in the first generation and negative selection in later generations, resulting in little cumulative evolutionary change in mean absorptivity over time (at least at the low and high sites).

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 [35,47], in contrast to our model predictions (figure 3*c,d*). Our models assume that α_{20} and slope are genetically uncorrelated [48], as we lack empirical data for the covariance between these traits in *Colias*. Negative genetic correlations between α_{20} and slope would slow the rate of evolutionary change of these traits in response to climate warming [49]. Gene flow between populations along the elevational gradient could also retard evolutionary changes [50], and a recent genetic analysis of

low and mid-elevation *C. eriphyle* populations in western Colorado suggests relatively low levels of genetic differentiation (HJ MacLean, JK Higgins, GA Ragland 2016, unpublished results). Further empirical data are needed to incorporate these factors into our model predictions.

Our results highlight an important consequence of plasticity for adaptive responses to directional environmental change. In contrast to theoretical predictions [2,7], we find that developmental plasticity facilitates rather than retards evolutionary responses to directional climate change, by allowing adaptation to changing seasonal patterns of environmental variation [9,12]. This highlights the importance of incorporating realistic patterns of intra- and interannual environmental variation in modelling responses to directional environmental change [4,51]. Our results most directly apply to organisms with multiple annual generations in seasonal environments, but they are broadly relevant to the implications of plasticity for selection and evolution in temporally varying environments. For organisms that are only active during part of the year, considering realistic seasonality is essential to understanding the role of plasticity. We demonstrate how plastic responses to environmental cues in temporally variable environments can facilitate evolution by reducing temporal fluctuations in the direction of selection.

Our model results also illustrate that the contributions of developmental plasticity for adaptive responses to climate change are greater at lower elevations in seasonal environments. More generally, we predict that evolutionary changes in plasticity will be particularly important when climate change expands the seasonal range of environmental conditions, a pattern that is likely in many regions [1]. Our findings for elevation can be generalized geographically by considering latitudinal gradients in seasonality. Although seasonality increases with latitude, the length of the active growing season (and for many ectotherms, the number of generations per year) declines. As a result, realized seasonality and the evolutionary consequences of plasticity for climate change may be greatest at intermediate latitudes.

Data accessibility. Data are available from the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.72mr1>) [52].

Authors' contributions. J.G.K. and L.B.B. designed the study, built the model, performed the analyses and wrote the paper.

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Competing interests. We declare we have no competing interests.

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