

REVIEW

Shifts in the relative fitness contributions of fecundity and survival in variable and changing environments

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ABSTRACT

Organisms respond to shifts in climate means and variability via distinct mechanisms. Accounting for these differential responses and appropriately aggregating them is central to understanding and predicting responses to climate variability and change. Separately considering fitness components can clarify organismal responses: fecundity is primarily an integrated, additive response to chronic environmental conditions over time via mechanisms such as energy use and acquisition, whereas survival can be strongly influenced by short-term, extreme environmental conditions. In many systems, the relative importance of fecundity and survival constraints changes systematically along climate gradients, with fecundity constraints dominating at high latitudes or altitudes (i.e. leading range edges as climate warms), and survival constraints dominating at trailing range edges. Incorporating these systematic differences in models may improve predictions of responses to recent climate change over models that assume similar processes along environmental gradients. We explore how detecting and predicting shifts in fitness constraints can improve our ability to forecast responses to climate gradients and change.

KEY WORDS: Climate change, Climate extremes, Energy, Environmental gradient, Mechanistic model, Physiology

Introduction

Many approaches to predicting climate change responses rely on correlations with temporally and spatially averaged air temperatures (Nadeau et al., 2017; Potter et al., 2013). They often fail to predict what appear to be individualistic population and species responses (Maguire et al., 2015). One reason for predictive failure is that responses often result from the balance of different fitness components, which respond to environmental variation on different time scales. Fecundity tends to be an integrated response to environmental conditions over time via mechanisms such as energy use and acquisition, whereas survival is often influenced by exposure to short-term, extreme environmental conditions (Buckley and Huey, 2016; Dillon and Woods, 2016). Here we consider how fecundity and survival shift across environmental gradients and in response to environmental change. We argue that understanding systematic shifts in fecundity and survival, and how organism–environmental interactions produce these shifts can improve predictions of ecological and evolutionary responses.

We start by reviewing concepts relevant to detecting shifts in fitness components, including quantifying the thermal sensitivity of

fitness, aggregating fitness components over time, using physiological markers for fitness constraints, genotype by environment interactions, and demographic compensation, which refers to opposing shifts in fitness components. We then leverage empirical datasets to evaluate shifts in fitness components. We close by presenting examples of how shifts in fitness components can be modeled to predict responses to variable and changing environments.

Quantifying the thermal sensitivity of fitness

Thermal performance curves (TPCs) (Huey and Stevenson, 1979) describe how the environment influences performance and are often applied to integrate across time scales (Fig. 1). Fecundity varies across moderate body temperatures, as temperature restricts activity and thus energy gain, leading to some combination of slow growth and development, reduced energy stores, delayed phenology or extended generation times, and ultimately reduced fecundity outside of the optimal temperature range (Scranton and Amarasekare, 2017). Organisms tend to survive across a larger thermal range than they can reproduce within (although energetic and other chronic limitations certainly reduce survival) (Kingsolver et al., 2011). Mortality tends to occur when abiotic extremes approach or exceed physiological tolerances, activating biochemical damage-associated pathways (Dowd et al., 2015; Kingsolver and Buckley, 2017; Schaefer, 2014) and leading to losses in organismal performance and eventually death (Williams et al., 2016). Mortality itself can accumulate at elevated temperatures (not necessarily the extremes), and the cumulative effect of heightened temperature can then translate into a strong selective force on local populations (Rezende et al., 2020). Developing an appropriate modeling approach requires understanding the relative importance of fitness constraints and environmental drivers of the constraints (cumulative thermal units versus extreme events) (Amarasekare and Johnson, 2017). Applying TPCs for fitness components suggests that population dynamic and phenological shifts in response to warming depend on both increases in climate means and variability (Scranton and Amarasekare, 2017).

TPCs, or more simply thermal tolerances (Sunday et al., 2012, 2014), have gained prominence as a predictive approach accounting for physiology (Deutsch et al., 2008; Kingsolver et al., 2013; Tewksbury et al., 2008; Vasseur et al., 2014). However, their utility is generally limited by assumptions including that: acute (e.g. locomotion) TPCs can predict fitness (Kingsolver and Woods, 2016); TPCs are constant across fitness components and life stages (Kingsolver et al., 2011); time-dependent responses to thermal variability (e.g. compensatory responses) can be omitted (Huey et al., 2012; Sinclair et al., 2016; Williams et al., 2016, 2017); and body temperatures equal air temperatures (Huey et al., 2012). Considering shifts in the relative contributions of fecundity and survival to fitness along environmental gradients will help test these assumptions (Sinclair et al., 2016). Applying TPCs requires an assumption for how performance or fitness is integrated over time (Angilletta, 2009).

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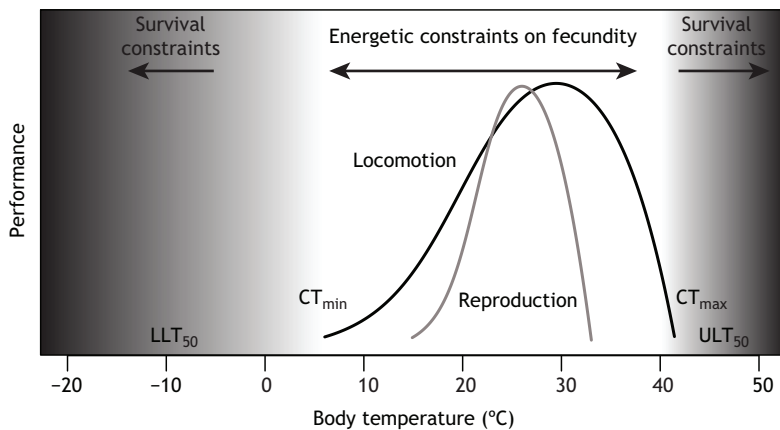


Fig. 1. A major challenge is to develop models that improve the predictive ability of thermal performance curves by integrating the temporal dependence of temperature and physiological mechanisms that vary along environmental gradients. Here, a thermal performance curve depicts the temperature dependence of locomotion (a proxy for energy acquisition, black line) and reproduction (measured as fertility) in *Drosophila melanogaster* (adapted from Williams et al., 2016). Survival constraints are expected to dominate when temperatures are outside the critical thermal limits (CT_{min} and CT_{max}, gray shading), whereas fecundity constraints are expected to dominate within critical thermal limits (unshaded portion). LLT₅₀ and ULT₅₀ denote upper and lower lethal temperatures for 50% survival.

Additive and multiplicative fitness components

The contributions of fecundity and survival to fitness have long been explored in evolutionary biology, assuming alternatively that fitness and fitness components aggregate additively or multiplicatively. Much of the work examines variable or changing environments and thus is relevant to climate change responses (Levins, 1968; Lewontin and Cohen, 1969). Integrating fitness multiplicatively across time periods and generations emphasizes survival as a fitness determinant. Multiplicative integration favors the evolution of thermal generalists (Lynch and Gabriel, 1987), and often leads to the maintenance of genetic polymorphism and/or the evolution of phenotypic plasticity (Williams et al., 2017). Integrating fitness additively minimizes the impact of mortality and favors the evolution of thermal specialists (Gilchrist, 1995, 2000). This often leads to local adaptation and can reduce genetic variation within populations (Kawecki and Ebert, 2004). The time scale of environmental variation relative to lifespan mediates the selective pressure posed by environmental variation (Levins, 1968). Environmental generalists are selected when environmental variation is predominantly across (rather than within) generations (Gilchrist, 1995).

A number of studies have focused on single fitness-determining processes or strategies, but fitness is determined by systematic shifts in both fecundity and survival along environmental gradients (Buckley and Kingsolver, 2012; Huey et al., 2012; Kellermann and van Heerwaarden, 2019; Overgaard et al., 2014; Sinclair et al., 2016). Combining additive (reproduction) and multiplicative (survival) components allows us to examine the relative contributions of fitness components. Such approaches indicate that rare, extreme environmental conditions can influence the evolution of TPCs (Buckley and Huey, 2016), but when selection acts to maximize fitness in response to average environmental conditions, the evolutionary significance of exceptionally rare extremes is minimized (Buckley and Kingsolver, 2012). Therefore, whether thermal stress causes short-term performance loss or mortality has major implications for the evolution of TPCs (Kingsolver and Woods, 2016).

Physiological markers of fitness constraints

Along latitudinal or elevational gradients, fecundity constraints intensify towards cooler poleward or upper elevational range boundaries, resulting in selection for high rates of growth and development (Conover et al., 2009; Hodkinson, 2005). Climate change is extending growing seasons, which is expected to relax fecundity constraints at poleward and upper elevational range limits (Buckley et al., 2015). Survival constraints operate more strongly at range edges that are set by abiotic factors (Sexton et al., 2009), and

the manner in which climate change will affect survival constraints will depend on the range-limiting factor, and the predicted direction of change. For example, at the southern range edge or lower elevational limit, heat stress may drive fitness (Buckley and Kingsolver, 2012; Kingsolver et al., 2013; Vasseur et al., 2014), and climate change will intensify this constraint (Bozinovic et al., 2011). Survival constraints at high latitudes or elevations can result from environmental variability, which climate change will probably increase (Buckley et al., 2013a; Kingsolver et al., 2013; Sheldon and Dillon, 2016; Vasseur et al., 2014). Exploring the role imposed by environmental constraints on individuals, populations, species and communities along a spatial environmental gradient can inform predictions of how environmental change leads to differential shifts in fecundity and survival.

Physiological assays can be used to detect strong fecundity constraints at high elevations and latitudes as well as strong survival constraints at low elevations and latitudes. At high elevations or latitudes, organisms grow more slowly, store less lipid, reach smaller body sizes (assuming constant development time) and produce fewer offspring (Hodkinson, 2005). At low elevations or latitudes, damage-associated molecular pathways will be upregulated (e.g. cellular stress response; Schaefer, 2014) and there may be high mortality, particularly after extreme heat events. To counter fecundity constraints, populations adapted to high elevations or latitudes frequently have higher metabolic rates and growth rates, and enhanced energy storage, underpinned by upregulation of pathways of aerobic metabolism (Conover et al., 2009; Schultz et al., 1996; Seebacher, 2018; Seebacher et al., 2015). Low elevation populations tend to mitigate survival constraints through increased thermal limits, leading to a differential cellular stress response and increased survival (Barua and Heckathorn, 2004; Tomanek, 2008).

Incorporating strong fecundity constraints at high elevations and latitudes and strong survival constraints at low elevations and latitudes may improve predictions of responses to recent climate change over models that assume similar processes along the environmental gradient. Natural history collections provide an underutilized resource for testing shifting constraints over time (MacLean et al., 2019). For populations under strong fecundity constraints, we predict that modern specimens will be larger or more lipid-dense and reach maturity earlier compared to historical specimens and there will be evidence of selection on genes or regulatory mechanisms of pathways involved in energy metabolism. For populations under strong survival constraints owing to increasing heat stress, body size and lipid reserve will have declined in modern compared to historical specimens, and heat-shock and damage-associated molecular pathways will be under selection.

Genotype and environment interactions

Determining how fecundity and survival constraints affect fitness requires an understanding of the evolutionary mechanisms that mediate these fitness responses through genotype and environment interactions. The fitness of genotypes might be expected to peak in the center of environmental gradients where both constraints are relaxed. However, populations may locally adapt to either fecundity or survival constraints at different positions on the gradient (Kawecki and Ebert, 2004; Somero, 2010). The propensity for local adaptation is influenced by the strength of selection, but also by ecological factors such as life history and dispersal ability (Kawecki and Ebert, 2004). Local adaptation to increase survival may result in fecundity trade-offs and vice versa (Angilletta et al., 2003; Gilchrist, 1995). Selection for genotypes and phenotypes that optimize energy balances can be particularly strong in highly seasonal environments, such as temperate mountains where species must complete their life cycle during the limited window when environmental conditions are permissive (Hodkinson, 2005; Williams et al., 2017). For example, if fecundity constraints are operating at high elevation, we anticipate selection on metabolic enzymes to upregulate rates of energy production to counter short growing seasons (Marden, 2013; Seebacher, 2018). If survival constraints are operating at low elevation, we expect extreme environmental conditions (such as heatwaves) to result in selection for enhanced thermal tolerance via mechanisms such as heat shock protein expression and resistance to oxidative stress (Dowd et al., 2015; MacMillan, 2019; Williams et al., 2016).

Phenotypic plasticity is expected to play a substantial role in mediating fecundity and survival constraints in response to environmental change (Sgrò et al., 2016). The timing of plasticity cues relative to environmental variation will shape the role of plasticity at both the acute time scales most relevant to survival constraints and the chronic time scales most relevant to fecundity constraints. Plasticity can buffer the selection on TPCs associated with environmental extremes, slowing evolution, but the extent of buffering depends on the consequences of thermal extremes (Williams et al., 2016).

Demographic compensation

Our expectation of opposing responses of vital rates including fecundity and survival to environmental gradients has been termed demographic compensation (Doak and Morris, 2010; Villellas et al., 2015). The concept has primarily been explored in plants, where numerous forms of vital rate opposition are plausible. For example, declines in both survival and recruitment of southern populations of tundra plants have been offset by higher growth of individual plants, potentially consistent with greater thermal opportunity (Doak and Morris, 2010). Some of the examined populations show opposing rates of survival and fecundity, but others show positive correlations between survival and fecundity (Doak and Morris, 2010; Villellas et al., 2015). A study of experimentally increased reproduction in boreal plants found that increased thermal opportunity (warmer temperatures or an extended growing season) decreased both the costs associated with survival and fecundity (Sletvold and Ågren, 2015). Even when demographic compensation does occur, it may be insufficient to prevent fitness declines at the trailing range edge (Sheth and Angert, 2018).

An analysis of plant demographic studies suggested that demographic compensation commonly occurs, driven by opposing trends in fitness components including fecundity, recruitment, survival and growth, with the outcome being a reduction in spatial variation in population growth (Villellas et al., 2015). Indeed, a subset of studies

demonstrate negative correlations among vital rates, more so than expected by chance. The mean and standard deviation of fitness in plant populations was more strongly influenced by survival than fecundity in peripheral populations, whereas fecundity influenced both central and peripheral populations (Villellas et al., 2013). Considerations of demographic compensation have focused on plants, probably owing to greater ease of performing reciprocal transplant and other experiments elucidating fitness components (Hargreaves et al., 2014).

Here we merge consideration of demographic compensation with a TPC framework. In contrast to the plant focus of demographic compensation research, TPCs have primarily been characterized for animals (but see Angert et al., 2011; Wooliver et al., 2020). One reason for this discrepancy is that animals often use behavior and movement to evade or alleviate environmental stress (Bradshaw, 1972; Huey et al., 2002). Bradshaw (1972) thus predicted that plants will be selected for enhanced physiological tolerance and phenotypic plasticity. Strong empirical tests of these predictions remain largely elusive owing to comparability challenges (Huey et al., 2002). However, empirical data are contrary to Bradshaw's (1972) prediction that plants should experience stronger selection: the strength of non-mortality selection is similar between plants and animals, and plants experience much weaker mortality selection than animals (Huey et al., 2002). The weaker mortality selection may result from many selection studies omitting sensitive early life stages in plants. Compilations of selection data for both plants and animals find that selection through fecundity differences is stronger and less temporally variable than selection through survival differences (Siepielski et al., 2011). The finding of weaker mortality selection in plants is consistent with analyses of plant density compensation revealing variable patterns in the contribution of survival to fecundity (Villellas et al., 2015).

Opposing trends in fitness components have also been considered in the context of species distributions (Pironon et al., 2018), including a demographic implementation of the Hutchinsonian niche considering reproduction and fecundity hypervolumes (Maguire, 1973). The niche concept led to the expectation that the optimal habitat, and thus the highest density, occurs in the center of a distribution. However, this 'abundant-center' hypothesis often fails to find empirical support (Pironon et al., 2015; Sexton et al., 2009). Our discussion of fecundity and survival constraints will generally assume that optimality occurs in the center of environmental gradients, but efforts to link microclimate to impacts on performance can refine the notion of optimal habitat (Woods et al., 2015).

Experimental insight into fitness constraints

We leverage previous studies and data compilations to examine trends in survival and fecundity across environmental gradients (using ANOVAs, see <https://github.com/lbuckley/FitnessJEB> for R code). Many of the data are from mountains, where multiple environmental attributes vary strongly over short geographic distances (Hodkinson, 2005). With increasing elevation, mean air temperatures decline while temperature variability and seasonality increase; clear-sky solar radiation increases, but so does cloudiness; and oxygen levels decrease (Cheviron and Brumfield, 2012). Extreme high temperatures at lower elevations can lead to stress responses and survival constraints. In contrast, cooler conditions and short active seasons at higher elevations can cause chronic energy balances to constrain fitness via fecundity. However, high environmental variability at high elevations may lead to survival and fecundity dually constraining fitness (Buckley et al., 2013a; Dillon et al., 2016).

Our analysis of a compilation of plant experimental warming studies (Anderson, 2016) reveals that experimental warming tends to decrease survival at low elevations and increase fecundity at high elevations and latitudes (Fig. 2). There is a non-significant tendency for experimental warming to decrease survival at low elevations ($F_{1,73}=3.2$, $P=0.08$), but the same pattern is not seen for latitudinal gradients ($F_{1,73}=0.0$, $P=0.88$). Survival decreases at intermediate elevations if a polynomial relationship is fitted ($F_{2,72}=4.9$, $P=0.01$), but again no latitudinal relationship is found. Fecundity shifts associated with experimental warming are positive at high elevations ($F_{1,49}=8.7$, $P<0.01$) and exhibit a tendency to be positive at high latitudes ($F_{1,49}=0.0$, $P=0.05$). The data are consistent with survival constraining lower elevations and fecundity constraining high elevations.

A compilation of transplant experiment data (primarily for plants; Hargreaves et al., 2014) reveals that transplanting beyond species' ranges tends to decrease fitness (Fig. 3), indicating that range limits often correspond to niche limits (see also Lee-Yaw et al., 2016). However, fecundity declines are more pronounced at cold range limits ($F_{1,40}=7.2$, $P<0.01$) and for elevation compared with latitudinal gradients ($F_{1,40}=4.3$, $P<0.05$). Survival declines do not differ between cold and warm range limits ($F_{1,73}=0.5$, $P=0.47$) but are more pronounced for latitudinal gradients than elevation gradients ($F_{1,73}=9.2$, $P<0.01$). These data are consistent with expectations that fecundity is more limiting at cold than at warm

range limits. Plants may face more severe survival constraints at cold limits than animals due to freezing risk (Huey et al., 2002).

Modeling fitness constraints along elevation gradients

Mechanistic and demographic models can be used to examine the mechanisms by which fecundity and survival components vary across the elevation gradient (Buckley and Kingsolver, 2019). Ideally, the models can be coupled with empirical data (as above) to test the mechanisms underlying fitness gradients. Phenotypes relevant to fecundity include metabolism, locomotion, feeding and digestion, energy storage, and egg production, whereas survival is primarily mediated by thermal tolerance. How these phenotypes vary across environmental gradients and plastically respond to environmental conditions may be central to elevation gradients in fitness. We present two case studies for montane insects in Colorado, USA, examining shifts in fitness components along elevational gradients.

Montane butterflies

Systems where one phenotype mediates both fecundity and survival are ideal for investigating responses to environmental variation. For montane *Colias* butterflies, the degree of wing melanization determines heating rates (Kingsolver, 1983; Watt, 1968). Wings must be sufficiently dark to allow the butterflies to reach a narrow range of temperatures that enable flight (and subsequently mating,

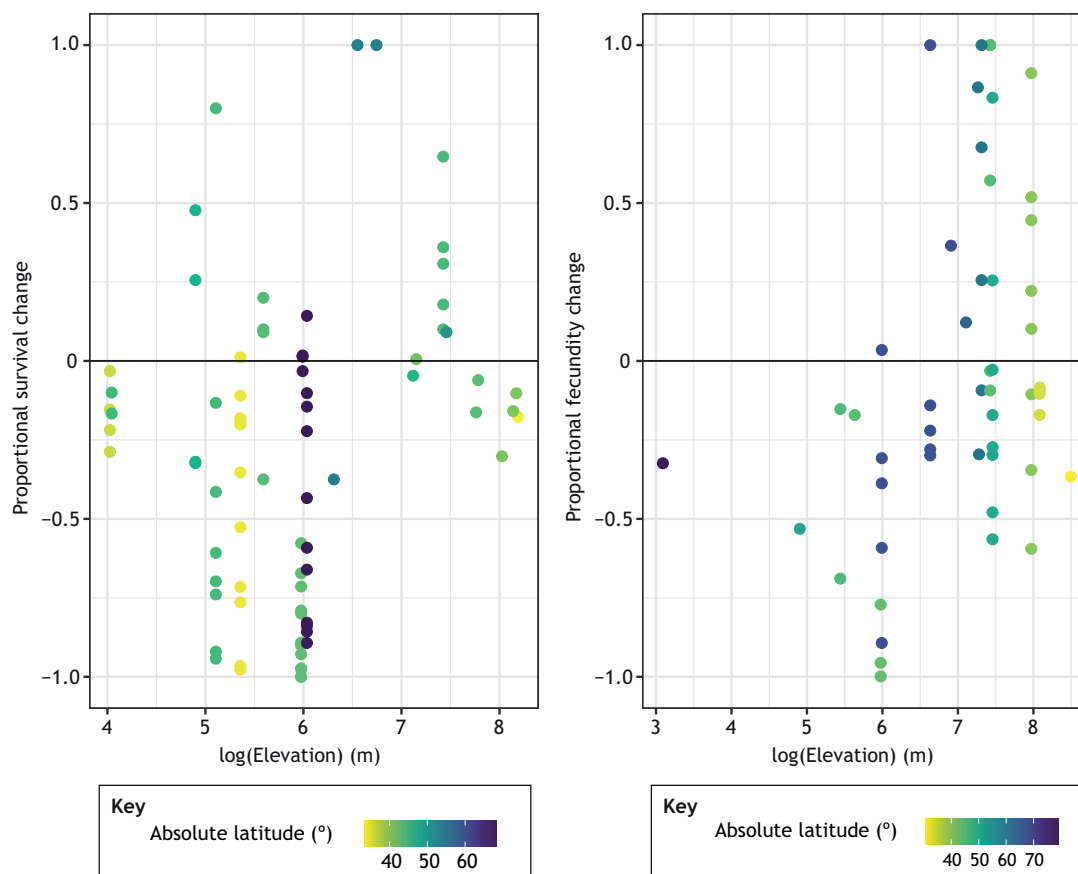


Fig. 2. The proportional survival and fecundity changes associated with experimental climate warming treatments as a function of study elevation and absolute latitude. Changes are calculated as $(F_{\text{experimental}} - F_{\text{control}}) / F_{\text{control}}$, where F is the fitness component in experimental and control plots. We bounded proportional fitness changes from -1 to 1 as several values >1 were identified statistically as outliers. We natural log transformed elevation, but not fitness change, to increase normality. Data are from Anderson (2016).

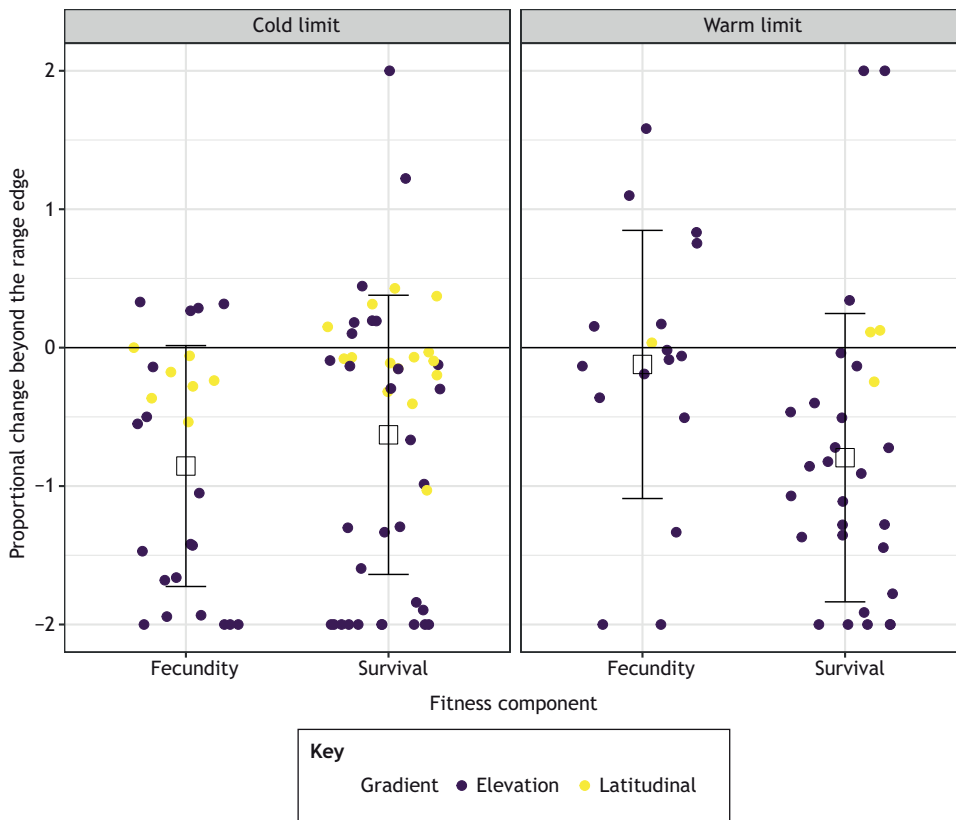


Fig. 3. The proportional changes in fecundity and survival when transplanting beyond the range edge differ between cold and warm range limits and between elevational and latitudinal gradients. Changes are calculated as $(F_{\text{beyond}} - F_{\text{within}}) / [0.5 \times (F_{\text{beyond}} + F_{\text{within}})]$, where F is the fitness component corresponding to planting a within-range population either beyond or within the range. Proportional changes are bounded -2 to $+2$, where -2 indicates positive fitness within the range but zero fitness beyond the range, and $+2$ indicates zero fitness within the range but positive fitness beyond the range. In addition to depicting fitness components for each population, we plot the mean and standard deviation for the fitness component. Data are from Hargreaves et al. (2014).

egg laying and other fecundity-determining processes). However, dark wings can also result in overheating, which decreases survival and egg viability. Models based on the performance implications of wing coloration suggest that fecundity peaks at low elevation (Buckley and Kingsolver, 2012). Butterflies risk overheating at both low elevations, where ambient temperatures are warm, and at high elevations, where radiation spikes can dramatically elevate body temperatures over air temperatures. Demographic analyses suggest that the fecundity benefit of increased flight opportunity associated with darker wings outweighs the survival detriment due to overheating in current environments (Buckley and Kingsolver, 2012), but fitness contributions are predicted to shift in future environments when warmer temperatures increase overheating risk (Buckley and Kingsolver, 2019). We use model output from a previous analysis (Buckley and Kingsolver, 2019) to illustrate elevation clines in primary determinants of fecundity (the duration of time that butterflies achieve body temperatures that enable flight) and survival (egg viability; Fig. 4). Fecundity peaks at mid-elevations, whereas survival declines are focused at low elevations. Projected future climate change (2099 projection of the CMIP5 multi-model ensemble representative concentration pathway 6) leads to fecundity peaking at higher elevations and to declines in survival. Shifts towards darker wings (higher wing absorptivity) in both time periods similarly results in fecundity peaking at higher elevations and survival declines being more pronounced and occurring at higher elevations. Most systems are more complex than a single phenotype mediating both survival and fecundity, but similar principles are likely to hold.

Montane grasshoppers

We leverage thermal sensitivity data for montane *Melanoplus boulderensis* grasshoppers to illustrate fitness responses to an

elevation gradient in Colorado, USA. We use the temperature dependence of performance (hopping distance) to approximate fecundity (Buckley and Nufio, 2014). Locomotion is a reasonable proxy for fecundity due to it being a strong determinant of rates of energy acquisition (Angilletta, 2009). We use thermal tolerance to approximate survival constraints (Buckley et al., 2013b) (see Appendix). We acknowledge that a limitation of this common approach to estimating survival is assuming that critical thermal limits represent loss of performance or mortality, as it is not always clear how to model declines in survival prior to critical thermal limits (Sinclair et al., 2016). To address this, we allow for survival to decline exponentially beyond 20–80% of TPC breadth (see Appendix). We omit adaptive and plastic differences in thermal sensitivity for simplicity and use phenotypic data measured for a population at 3048 m.

We use microclimate measurements for four sites along an elevation gradient but note that a more general approach is to apply a microclimate model to translate climate records into the environmental conditions experienced at the spatial and temporal scale of organisms (Kingsolver and Buckley, 2015). The sites are along the 40th parallel north in Boulder County, CO, USA: Eldorado Canyon (1740 m, 39.93°N, 105.29°W), A1 (2195 m, 40.01°N, 105.37°W), B1 (2591 m, 40.02°N, 105.43°W) and C1 (3048 m, 40.03°N, 105.55°W; niwot.colorado.edu). We measured (shaded) temperatures of the air and surface (Pace PT907 30 kΩ thermistor, $\pm 0.15^\circ\text{C}$), total global horizontal radiation (Pace SRS-100 Silicon Photodiode, 400–1100 nm, $\pm 5\%$ accuracy) and wind speed (anemometer, 0.9–78 m s⁻¹ range, $\pm 5\%$ accuracy) at 5 min intervals using a Pace XR5 datalogger (see Buckley et al., 2013a). We input the microclimate conditions into a biophysical model parameterized with morphological parameters (size, shape and solar absorptivity) to predict adult body temperatures (see Buckley and Nufio, 2014).

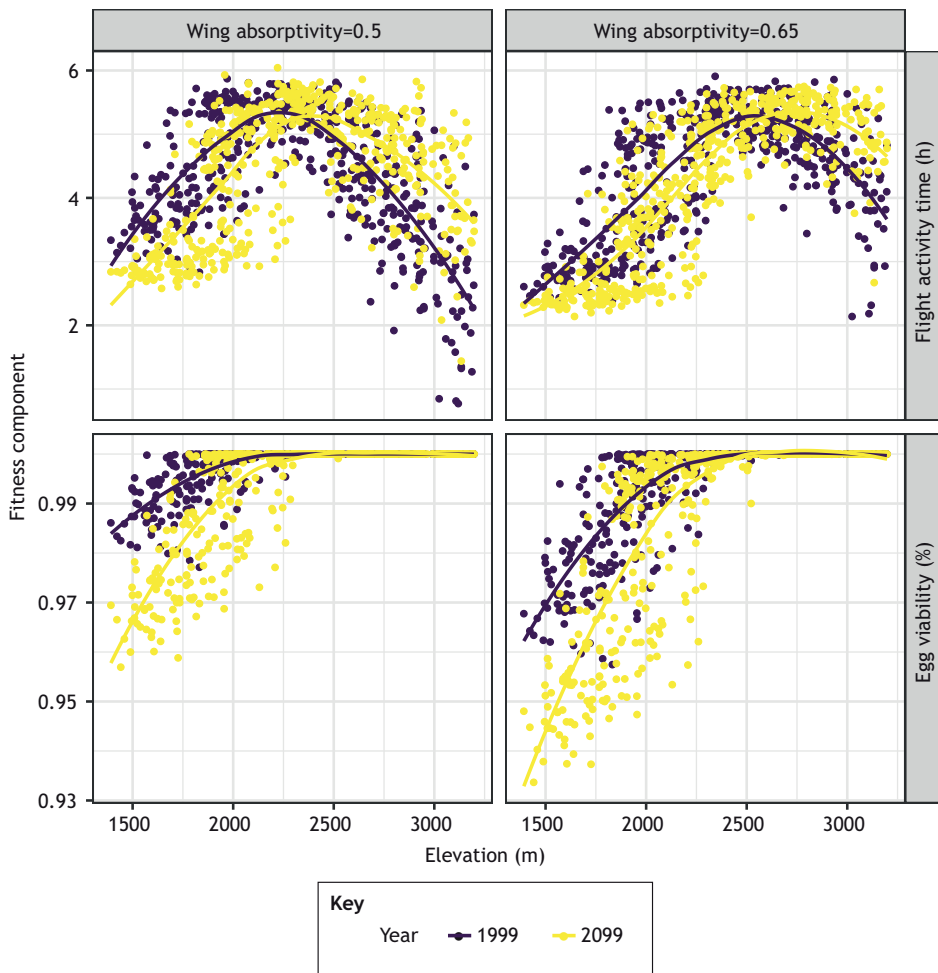


Fig. 4. *Colias* butterfly model predictions for fitness-determining processes vary across an elevation gradient. Each point corresponds to a 1/8° latitude–longitude grid cell in western Colorado, USA. Average daily flight activity time across the active season (top) is a primary determinant of fecundity and peaks at mid-elevations. Declines in egg viability (bottom) at low elevations are a primary determinant of survival. Darker (more absorptive) wings and the warmer temperatures projected for 2099 (CMIP5 multi-model ensemble representative concentration pathway 6) leads to fecundity peaking at higher elevations and to declines in survival. Data are model output from Buckley and Kingsolver (2019).

We assume that grasshoppers move between full shade and full sun to achieve the available temperature closest to their preferred body temperature (Buckley et al., 2013b). We incorporated

microclimate variation by simulating 500 individuals, randomly selecting microclimate values for each individual using a normal distribution centered at the temperature target of thermoregulation

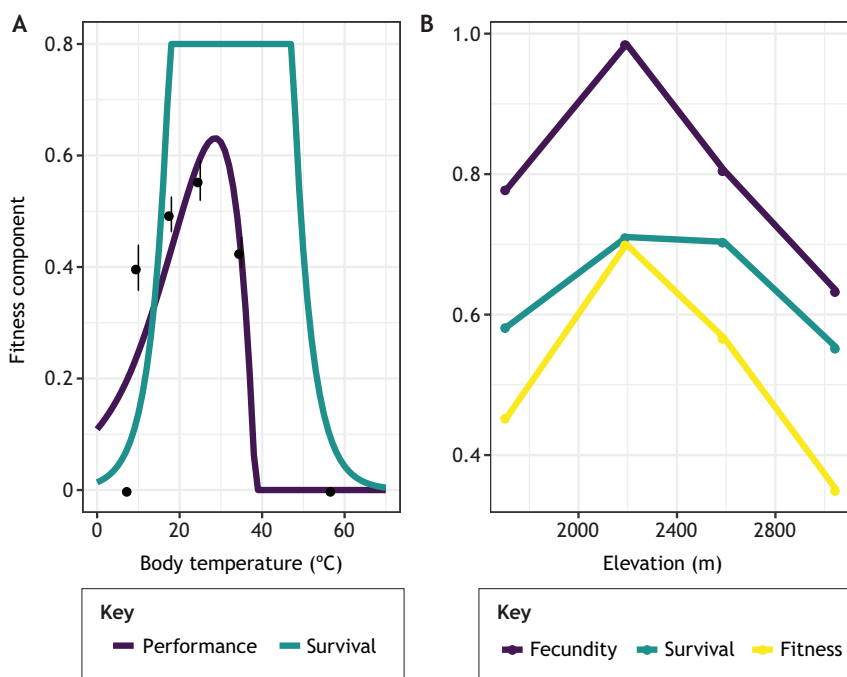


Fig. 5. The temperature dependence of grasshopper performance and survival can be used to predict fitness. (A) Temperature dependence varies between performance (hopping distance, m) and survival (%) for montane *M. boulderensis* grasshoppers. Points are means±s.e.m. of hopping data along with critical thermal limits. (B) We apply these fitness component functions to predict fecundity, survival and fitness as the product of survival and fecundity across the elevation gradient.

and with a standard deviation of 4°C. We bound the distribution by potential body temperatures in full shade and full sun. This allows us to estimate rates of fecundity (performance) and survival every 5 min during the daylight period, and then we scale fecundity estimates to a maximum of 1 and aggregate fecundity additively and survival multiplicatively across the period of available environmental data (6 July to 15 September). We estimate fitness as the product of fecundity and survival.

Survival and fecundity differentially shift across the elevation gradient (Fig. 5). We estimate performance and thus fecundity peaks at intermediate elevation. Survival is high at intermediate positions along the gradient but declines at low elevation due to high ambient temperatures and at high elevations due to high radiation levels that drive high body temperature extremes (Buckley et al., 2013a). These gradients in fecundity and survival combine to lead to steep declines in predicted fitness at low and high elevations.

Conclusions

Our simplified analyses serve to demonstrate how survival and fecundity can vary along environmental gradients. Separately considering survival and fecundity components serves to clarify responses to climate means and variability. Explicitly considering gradients in survival and fecundity, and detecting them using physiological metrics, can aid in predicting the fitness implications of climate change.

Appendix

Details of the montane grasshopper model

We assume critical thermal limits of 32.83 and 57.16°C and a preferred temperature of 7.78°C based on empirical measurements for *Melanoplus boulderensis* (Buckley et al., 2013b). We assume exponential declines in survival beyond 20 and 80% of the thermal tolerance range (T_{20} and T_{80} , respectively). Survival (S) below T_{20} and above T_{80} was modeled as a function of temperature T as follows: $S = \exp[-(T - T_{80})/4.34]$ and $S = \exp[-(T_{20} - T)/4.34]$, respectively. We used the R package rTPC to fit multiple forms of thermal performance curves to data (Buckley and Nufio, 2014) on the hopping distance of *M. boulderensis* grasshoppers from the 3048 m population as a function of temperature. We selected the curve from Rezende and Bozinovic (2019), where performance is modeled as:

$$C e^{T \ln Q_{10}/10}, \quad \text{if } T < T_{th},$$

$$\left(C e^{T \ln Q_{10}/10} \right) \times (1 - d(T - T_{th})^2), \quad \text{if } T > T_{th}, \quad (\text{A1})$$

where Q_{10} defines the fold-change in performance as a consequence of increasing temperature by 10°C, C is a constant describing shifts in the vertical axis that are independent of temperature, and d is a constant controlling the rate of decay from a threshold temperature T_{th} . We used the following parameters: $Q_{10}=2.27$, $C=0.109$, $T_{th}=9.02$ and $d=0.00116$.

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Competing interests

The authors declare no competing or financial interests.

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Data availability

Data and code are available from GitHub: <https://github.com/lbuckley/FitnessJEB>.

References

- Amarasekare, P. and Johnson, C. (2017). Evolution of thermal reaction norms in seasonally varying environments. *Am. Nat.* **189**, E31–E45. doi:10.1086/690293
- Anderson, J. T. (2016). Plant fitness in a rapidly changing world. *New Phytol.* **210**, 81–87. doi:10.1111/nph.13693
- Angert, A. L., Sheth, S. N. and Paul, J. R. (2011). Incorporating population-level variation in thermal performance into predictions of geographic range shifts. *Integr. Comp. Biol.* **51**, 733–750. doi:10.1093/icb/ict048
- Angilletta, M. J. (2009). *Thermal Adaptation: A Theoretical and Empirical Synthesis*. Oxford: Oxford University Press.
- Angilletta, M. J., Wilson, R. S., Navas, C. A. and James, R. S. (2003). Tradeoffs and the evolution of thermal reaction norms. *Trends Ecol. Evol.* **18**, 234–240. doi:10.1016/S0169-5347(03)00087-9
- Barua, D. and Heckathorn, S. A. (2004). Acclimation of the temperature set-points of the heat-shock response. *J. Therm. Biol.* **29**, 185–193. doi:10.1016/j.jtherbio.2004.01.004
- Bozinovic, F., Calosi, P. and Spicer, J. I. (2011). Physiological correlates of geographic range in animals. *Annual Rev. Ecol. Syst.* **42**, 155–179. doi:10.1146/annurev-ecolsys-102710-145055
- Bradshaw, A. D. (1972). Some of the evolutionary consequences of being a plant. *Evol. Biol.* **5**, 25–47. doi:10.1007/978-1-4757-0256-9_2
- Buckley, L. B. and Huey, R. B. (2016). How extreme temperatures impact organisms and the evolution of their thermal tolerance. *Integr. Comp. Biol.* **56**, 98–109. doi:10.1093/icb/icw004
- Buckley, L. B. and Kingsolver, J. G. (2012). The demographic impacts of shifts in climate means and extremes on alpine butterflies. *Funct. Ecol.* **26**, 969–977. doi:10.1111/j.1365-2435.2012.01969.x
- Buckley, L. B. and Kingsolver, J. G. (2019). Environmental variability shapes evolution, plasticity and biogeographic responses to climate change. *Glob. Ecol. Biogeogr.* **28**, 1456–1468. doi:10.1111/geb.12953
- Buckley, L. B. and Nufio, C. R. (2014). Elevational clines in the temperature dependence of insect performance and implications for ecological responses to climate change. *Conserv. Physiol.* **2**, cou035. doi:10.1093/conphys/cou035
- Buckley, L. B., Miller, E. F. and Kingsolver, J. G. (2013a). Ectotherm thermal stress and specialization across altitude and latitude. *Integr. Comp. Biol.* **53**, 571–581. doi:10.1093/icb/ict026
- Buckley, L. B., Nufio, C. R. and Kingsolver, J. G. (2013b). Phenotypic clines, energy balances, and ecological responses to climate change. *J. Anim. Ecol.* **83**, 41–50. doi:10.1111/1365-2656.12083
- Buckley, L. B., Nufio, C. R., Kirk, E. M. and Kingsolver, J. G. (2015). Elevational differences in developmental plasticity determine phenological responses of grasshoppers to recent climate warming. *Proc. R. Soc. Lond. B Biol. Sci.* **282**, 20150441. doi:10.1098/rspb.2015.0441
- Chevillon, Z. A. and Brumfield, R. T. (2012). Genomic insights into adaptation to high-altitude environments. *Heredity* **108**, 354–361. doi:10.1038/hdy.2011.85
- Conover, D. O., Duffy, T. A. and Hice, L. A. (2009). The covariance between genetic and environmental influences across ecological gradients: reassessing the evolutionary significance of countergradient and cogeographic variation. *Ann. N. Y. Acad. Sci.* **1168**, 100–129. doi:10.1111/j.1749-6632.2009.04575.x
- Deutsch, C. A., Tewksbury, J. J., Huey, R. B., Sheldon, K. S., Ghalambor, C. K., Haak, D. C. and Martin, P. R. (2008). Impacts of climate warming on terrestrial ectotherms across latitude. *Proc. Natl Acad. Sci. USA* **105**, 6668–6672. doi:10.1073/pnas.0709472105
- Dillon, M. E. and Woods, H. A. (2016). Introduction to the symposium: Beyond the mean: biological impacts of changing patterns of temperature variation. *Integr. Comp. Biol.* **56**, 11–13. doi:10.1093/icb/icw020
- Dillon, M. E., Woods, H. A., Wang, G., Fey, S. B., Vasseur, D. A., Telemeco, R. S., Marshall, K. and Pincebourde, S. (2016). Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. *Integr. Comp. Biol.* **56**, 14–30. doi:10.1093/icb/icw024
- Doak, D. F. and Morris, W. F. (2010). Demographic compensation and tipping points in climate-induced range shifts. *Nature* **467**, 959–962. doi:10.1038/nature09439
- Dowd, W. W., King, F. A. and Denny, M. W. (2015). Thermal variation, thermal extremes and the physiological performance of individuals. *J. Exp. Biol.* **218**, 1956–1967. doi:10.1242/jeb.114926
- Gilchrist, G. W. (1995). Specialists and generalists in changing environments. I. Fitness landscapes of thermal sensitivity. *Am. Nat.* **146**, 252–270. doi:10.1086/285797
- Gilchrist, G. W. (2000). The evolution of thermal sensitivity in changing environments. In *Environmental Stressors and Gene Responses* (ed. K. B. Storey and J. Storey), pp. 55–70. Amsterdam: Elsevier.
- Hargreaves, A. L., Samis, K. E. and Eckert, C. G. (2014). Are species' range limits simply niche limits writ large? A review of transplant experiments beyond the range. *Am. Nat.* **183**, 157–173. doi:10.1086/674525

- Hodkinson, I. D. (2005). Terrestrial insects along elevation gradients: species and community responses to altitude. *Biol. Rev.* **80**, 489–513. doi:10.1017/S1464793105006767
- Huey, R. B. and Stevenson, R. D. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *Am. Zool.* **19**, 357–366. doi:10.1093/icb/19.1.357
- Huey, R. B., Carlson, M., Crozier, L., Frazier, M., Hamilton, H., Harley, C., Hoang, A. and Kingsolver, J. G. (2002). Plants versus animals: do they deal with stress in different ways? *Integr. Comp. Biol.* **42**, 415–423. doi:10.1093/icb/42.3.415
- Huey, R. B., Kearney, M. R., Krockenberger, A., Holtum, J. A. M., Jess, M., Williams, S. E., Huey, R. B., Kearney, M. R., Krockenberger, A. and Holtum, J. A. M. (2012). Predicting organismal vulnerability to climate warming: roles of behaviour, physiology and adaptation. *Phil. Trans. R. Soc. B Biol. Sci.* **367**, 1665–1679. doi:10.1098/rstb.2012.0005
- Kawecki, T. J. and Ebert, D. (2004). Conceptual issues in local adaptation. *Ecol. Lett.* **7**, 1225–1241. doi:10.1111/j.1461-0248.2004.00684.x
- Kellermann, V. and van Heerwaarden, B. (2019). Terrestrial insects and climate change: adaptive responses in key traits. *Physiol. Entomol.* **44**, 99–115. doi:10.1111/phen.12282
- Kingsolver, J. G. (1983). Thermoregulation and flight in *Colias* butterflies – elevational patterns and mechanistic limitations. *Ecology* **64**, 534–545. doi:10.2307/1939973
- Kingsolver, J. G. and Buckley, L. B. (2015). Climate variability slows evolutionary responses of *Colias* butterflies to recent climate change. *Proc. R. Soc. B* **282**, 20142470. doi:10.1098/rspb.2014.2470
- Kingsolver, J. G. and Buckley, L. B. (2017). Quantifying thermal extremes and biological variation to predict evolutionary responses to changing climate. *Phil. Trans. R. Soc. B Biol. Sci.* **372**, 20160147. doi:10.1098/rstb.2016.0147
- Kingsolver, J. G. and Woods, H. A. (2016). Beyond thermal performance curves: modeling time-dependent effects of thermal stress on ectotherm growth rates. *Am. Nat.* **187**, 283–294. doi:10.1086/684786
- Kingsolver, J. G., Diamond, S. E. and Buckley, L. B. (2013). Heat stress and the fitness consequences of climate change for terrestrial ectotherms. *Funct. Ecol.* **27**, 1415–1423. doi:10.1111/1365-2435.12145
- Kingsolver, J. G., Woods, H. A., Buckley, L. B., Potter, K. A., MacLean, H. J. and Higgins, J. K. (2011). Complex life cycles and the responses of insects to climate change. *Integr. Comp. Biol.* **51**, 719–732. doi:10.1093/icb/icr015
- Lee-Yaw, J. A., Kharouba, H. M., Bontrager, M., Mahony, C., Csörgő, A. M., Noreen, A. M. E., Li, Q., Schuster, R. and Angert, A. L. (2016). A synthesis of transplant experiments and ecological niche models suggests that range limits are often niche limits. *Ecol. Lett.* **19**, 710–722. doi:10.1111/ele.12604
- Levins, R. (1968). *Evolution in Changing Environments*. Princeton: Princeton University Press.
- Lewontin, R. C. and Cohen, D. (1969). On population growth in a randomly varying environment. *Proc. Natl Acad. Sci. USA* **62**, 1056–1060. doi:10.1073/pnas.62.4.1056
- Lynch, M. J. and Gabriel, W. (1987). Environmental tolerance. *Am. Nat.* **129**, 283–303. doi:10.1086/284635
- MacLean, H. J., Nielsen, M. E., Kingsolver, J. G. and Buckley, L. B. (2019). Using museum specimens to track morphological shifts through climate change. *Philos. Trans. R. Soc. B Biol. Sci.* **374**, 20170404. doi:10.1098/rstb.2017.0404
- MacMillan, H. A. (2019). Dissecting cause from consequence: a systematic approach to thermal limits. *J. Exp. Biol.* **222**, jeb.191593. doi:10.1242/jeb.191593
- Maguire, B. (1973). Niche response structure and the analytical potentials of its relationship to the habitat. *Am. Nat.* **107**, 213–246. doi:10.1086/282827
- Maguire, K. C., Nieto-Lugilde, D., Fitzpatrick, M. C., Williams, J. W. and Blois, J. L. (2015). Modeling species and community responses to past, present, and future episodes of climatic and ecological change. *Ann. Rev. Ecol. Syst.* **46**, 343–368. doi:10.1146/annurev-ecolsys-112414-054441
- Marden, J. H. (2013). Nature's inordinate fondness for metabolic enzymes: why metabolic enzyme loci are so frequently targets of selection. *Mol. Ecol.* **22**, 5743–5764. doi:10.1111/mec.12534
- Nadeau, C. P., Urban, M. C. and Bridle, J. R. (2017). Coarse climate change projections for species living in a fine-scaled world. *Glob. Change Biol.* **23**, 12–24. doi:10.1111/gcb.13475
- Overgaard, J., Kearney, M. R. and Hoffmann, A. A. (2014). Sensitivity to thermal extremes in Australian *Drosophila* implies similar impacts of climate change on the distribution of widespread and tropical species. *Glob. Change Biol.* **20**, 1738–1750. doi:10.1111/gcb.12521
- Pironon, S., Villellas, J., Morris, W. F., Doak, D. F. and García, M. B. (2015). Do geographic, climatic or historical ranges differentiate the performance of central versus peripheral populations? *Glob. Ecol. Biogeogr.* **24**, 611–620. doi:10.1111/geb.12263
- Pironon, S., Villellas, J., Thuiller, W., Eckhart, V. M., Geber, M. A., Moeller, D. A. and García, M. B. (2018). The 'Hutchinsonian niche' as an assemblage of demographic niches: implications for species geographic ranges. *Ecography* **41**, 1103–1113. doi:10.1111/ecog.03414
- Potter, K. A., Woods, H. A. and Pincebourde, S. (2013). Microclimatic challenges in global change biology. *Glob. Change Biol.* **19**, 2932–2939. doi:10.1111/gcb.12257
- Rezende, E. L. and Bozinovic, F. (2019). Thermal performance across levels of biological organization. *Philos. Trans. R. Soc. B* **374**, 20180549. doi:10.1098/rstb.2018.0549
- Rezende, E. L., Bozinovic, F., Szilágyi, A. and Santos, M. (2020). Predicting temperature mortality and selection in natural *Drosophila* populations. *Science* **369**, 1242–1245. doi:10.1126/science.aba9287
- Schaefer, L. (2014). Complexity of danger: the diverse nature of damage-associated molecular patterns. *J. Biol. Chem.* **289**, 35237–35245. doi:10.1074/jbc.R114.619304
- Schultz, E. T., Reynolds, K. E. and Conover, D. O. (1996). Countergradient variation in growth among newly hatched *Fundulus heteroclitus*: geographic differences revealed by common-environment experiments. *Funct. Ecol.* **10**, 366–374. doi:10.2307/2390285
- Scranton, K. and Amarasekare, P. (2017). Predicting phenological shifts in a changing climate. *Proc. Natl Acad. Sci. USA* **114**, 13212–13217. doi:10.1073/pnas.1711221114
- Seebacher, F. (2018). The evolution of metabolic regulation in animals. *Comp. Biochem. Physiol. B Biochem. Mol. Biol.* **224**, 195–203. doi:10.1016/j.cbpb.2017.11.002
- Seebacher, F., White, C. R. and Franklin, C. E. (2015). Physiological plasticity increases resilience of ectothermic animals to climate change. *Nat. Clim. Change* **5**, 61–66. doi:10.1038/nclimate2457
- Sexton, J. P., McIntyre, P. J., Angert, A. L. and Rice, K. J. (2009). Evolution and ecology of species range limits. *Ann. Rev. Ecol. Syst.* **40**, 415–436. doi:10.1146/annurev-ecolsys.110308.120317
- Sgrò, C. M., Terblanche, J. S. and Hoffmann, A. A. (2016). What can plasticity contribute to insect responses to climate change? *Annu. Rev. Entomol.* **61**, 433–451. doi:10.1146/annurev-ento-010715-023859
- Sheldon, K. S. and Dillon, M. E. (2016). Beyond the mean: biological impacts of cryptic temperature change. *Integr. Comp. Biol.* **56**, 110–119. doi:10.1093/icb/icw005
- Sheth, S. N. and Angert, A. L. (2018). Demographic compensation does not rescue populations at a trailing range edge. *Proc. Natl. Acad. Sci. USA* **115**, 2413–2418. doi:10.1073/pnas.1715899115
- Siepielski, A. M., DiBattista, J. D., Evans, J. A. and Carlson, S. M. (2011). Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. *Proc. R. Soc. B* **278**, 1572–1580. doi:10.1098/rspb.2010.1973
- Sinclair, B. J., Marshall, K. E., Sewell, M. A., Levesque, D. L., Willett, C. S., Slotsbo, S., Dong, Y., Harley, C. D., Marshall, D. J., Helmuth, B. S. et al. (2016). Can we predict ectotherm responses to climate change using thermal performance curves and body temperatures? *Ecol. Lett.* **19**, 1372–1385. doi:10.1111/ele.12686
- Sletvold, N., Ågren, J. (2015). Climate-dependent costs of reproduction: survival and fecundity costs decline with length of the growing season and summer temperature. *Ecol. Lett.* **18**, 357–364. doi:10.1111/ele.12417
- Somero, G. N. (2010). The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *J. Exp. Biol.* **213**, 912–920. doi:10.1242/jeb.037473
- Sunday, J. M., Bates, A. E. and Dulvy, N. K. (2012). Thermal tolerance and the global redistribution of animals. *Nat. Clim. Change* **2**, 686–690. doi:10.1038/nclimate1539
- Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T. and Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proc. Natl Acad. Sci. USA* **111**, 5610–5615. doi:10.1073/pnas.1316145111
- Tewksbury, J. J., Huey, R. B. and Deutsch, C. A. (2008). Putting the heat on tropical animals. *Science* **320**, 1296–1297. doi:10.1126/science.1159328
- Tomanek, L. (2008). The importance of physiological limits in determining biogeographical range shifts due to global climate change: the heat-shock response. *Physiol. Biochem. Zool.* **81**, 709–717. doi:10.1086/590163
- Vasseur, D. A., DeLong, J. P., Gilbert, B., Greig, H. S., Harley, C. D., McCann, K. S., Savage, V., Tunney, T. D. and O'Connor, M. I. (2014). Increased temperature variation poses a greater risk to species than climate warming. *Proc. R. Soc. B* **281**, 20132612. doi:10.1098/rspb.2013.2612
- Villellas, J., Morris, W. F. and García, M. B. (2013). Variation in stochastic demography between and within central and peripheral regions in a widespread short-lived herb. *Ecology* **94**, 1378–1388. doi:10.1890/12-1163.1
- Villellas, J., Doak, D. F., García, M. B. and Morris, W. F. (2015). Demographic compensation among populations: what is it, how does it arise and what are its implications? *Ecol. Lett.* **18**, 1139–1152. doi:10.1111/ele.12505
- Watt, W. B. (1968). Adaptive significance of pigment polymorphisms in *Colias* butterflies. I. Variation of melanin pigment in relation to thermoregulation. *Evolution* **22**, 437–458. doi:10.1111/j.1558-5646.1968.tb03985.x
- Williams, C. M., Buckley, L. B., Sheldon, K. S., Vickers, M., Pörtner, H.-O., Dowd, W. W., Gunderson, A. R., Marshall, K. E. and Stillman, J. H. (2016). Biological impacts of thermal extremes: mechanisms and costs of functional responses matter. *Integr. Comp. Biol.* **56**, 73–84. doi:10.1093/icb/icw013
- Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K., Hereford, J., Humphries, M. M., Lisovski, S. and Marshall, K. E. (2017). Understanding evolutionary impacts of seasonality: an introduction to the symposium. *Integr. Comp. Biol.* **57**, 921–933. doi:10.1093/icb/icx122

Woods, H. A., Dillon, M. E. and Pincebourde, S. (2015). The roles of microclimatic diversity and of behavior in mediating the responses of ectotherms to climate change. *J. Therm. Biol.* **54**, 86-97. doi:10.1016/j.jtherbio.2014.10.002

Wooliver, R., Tittes, S. B. and Sheth, S. N. (2020). A resurrection study reveals limited evolution of thermal performance in response to recent climate change across the geographic range of the scarlet monkeyflower. *Evolution* **74**, 1699-1710. doi:10.1111/evo.14041