

LETTER

Fitness surfaces and local thermal adaptation in *Drosophila* along a latitudinal gradient

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Abstract

Local adaptation is commonly cited to explain species distribution, but how fitness varies along continuous geographical gradients is not well understood. Here, we combine thermal biology and life-history theory to demonstrate that *Drosophila* populations along a 2500 km latitudinal cline are adapted to local conditions. We measured how heat tolerance and viability rate across eight populations varied with temperature in the laboratory and then simulated their expected cumulative Darwinian fitness employing high-resolution temperature data from their eight collection sites. Simulations indicate a trade-off between annual survival and cumulative viability, as both mortality and the recruitment of new flies are predicted to increase in warmer regions. Importantly, populations are locally adapted and exhibit the optimal combination of both traits to maximize fitness where they live. In conclusion, our method is able to reconstruct fitness surfaces employing empirical life-history estimates and reconstructs peaks representing locally adapted populations, allowing us to study geographic adaptation in silico.

KEYWORDS

Darwinian fitness, geographical gradient, thermal death time curves, thermal performance curves, thermal tolerance, transplant experiment

José M. Alruiz and Ignacio Peralta-Maraver contributed equally to this study.

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INTRODUCTION

Adaptation to local environmental conditions, characterized by increased Darwinian fitness or reproductive potential of populations in their respective habitats as compared to other locations, is of paramount interest in the fields of ecology and evolution (Kawecki & Ebert, 2004; Whitlock, 2015). Local adaptation is considered a fundamental process underlying the generation and maintenance of biodiversity and is widely invoked to explain differences in distribution, abundance and resilience to change across populations and species (Blanquart et al., 2013; Savolainen et al., 2013). Assessing the adaptive variation across populations within species is essential for understanding its invasive potential, capacity to respond to selection and possible rates of response to ongoing anthropogenic impact (Bonnet et al., 2022; Hoffmann & Sgrò, 2011). However, such information is often neglected in studies that assume species-specific invariant responses across their geographical ranges (Bozinovic et al., 2011; O'Brien et al., 2017; Peterson et al., 2018).

Additionally, the mechanistic basis of local adaptation remains elusive, and the empirical evidence is highly fragmented for multiple reasons. From a mechanistic perspective, the environment involves variation across multiple dimensions—for example, temperature, humidity, salinity, productivity or the presence of competitors—that may impact fitness in a variety of ways (Angilletta, 2009; Kearney & Porter, 2009). Furthermore, numerous observed patterns, such as phenotypic or genetic differentiation across disparate populations, can be attributed to non-adaptive processes such as founder effects, genetic drift, local extinctions, trade-offs or extensive gene flow that may limit or hinder local adaptation (Blanquart et al., 2013; Hereford, 2009; Kawecki & Ebert, 2004; Whitlock, 2015). Local adaptation can be inferred when variation in a fitness trait surpasses genetic drift expectations or when it significantly correlates with pertinent environmental variables (Hancock et al., 2011; McKay & Latta, 2002). Nevertheless, such methods have limitations as they rely on few measurable fitness traits and may overlook the multifactorial nature of local adaptation stemming from unidentified phenotypic traits (Blanquart et al., 2013). Also, analysing how different molecular markers or chromosomal arrangements change with environmental conditions in time or space may be indicative of local adaptation, although trends may be confounded by gene flow and their phenotypic basis may not always be well understood (Balanyá et al., 2006, 2009). For these reasons, transplant experiments have been employed as the gold standard for assessing local adaptation across distinct populations. These experiments aim to systematically examine the ability of a given population or genotypic pool to survive and reproduce when relocated beyond their natural range (Lee-Yaw et al., 2016). When it is not feasible to

relocate the study species in natural habitats, researchers perform reciprocal transplants and compare key attributes under controlled settings or 'common garden' environments (Kawecki & Ebert, 2004).

In essence, empirically testing for local adaptation involves comparing fitness of multiple populations across various environments, which can be logistically challenging and expensive to implement (Kawecki & Ebert, 2004; Savolainen et al., 2013). These problems are exacerbated along geographical gradients, where both the environmental conditions and the genetic composition of the populations vary gradually. In these cases, adaptive responses may be counterbalanced by gene flow (Case & Taper, 2000), and transplant experiments become exponentially complex, costly and even infeasible. Given these challenges, most empirical research on local adaptation based on transplant experiments has been conducted on plants (e.g. Grassein et al., 2014; Hereford, 2009; Lee-Yaw et al., 2016), likely due to logistic constraints. Estimating fitness proxies, such as seedling survival and/or fruit or seed production, is easier in plants than in animals. Additionally, plants can be readily maintained in different common garden conditions as they are sessile, which also reduces the potential risk of invasion in case transplanted individuals are accidentally released. These studies have unveiled strong correlations between latitudinal and elevational clines of adaptive phenotypes and the temperature gradients of the population's origin. For example, temperate and boreal trees exhibit moderate-to-strong clines in phenology and growth along temperature gradients (reviewed in Aitken et al., 2008). Nonetheless, results vary across lineages and local adaptation seems to be negligible or absent in several species (Grassein et al., 2014).

In the animal literature, a substantial number of studies examine genetic and phenotypic gradients, but only a small fraction relies on transplant experiments (e.g. Crozier, 2004; O'Brien et al., 2017; Purcell & Avilés, 2008). Results are far from conclusive and are often contradictory. In *Drosophila*, for instance, egg, larval and adult life stages seem to be locally adapted to average temperatures in cosmopolitan *D. melanogaster*, although comparisons involve populations distributed worldwide (Austin & Moehring, 2019). Also, genetic work in species like *D. subobscura* provides overwhelming evidence of latitudinal adaptation in different continents (Rezende et al., 2010), significant adaptive capacity within few generations (Gilchrist et al., 2004; Santos et al., 2005) and rapid genetic responses to heat waves and warming temperatures (Balanyá et al., 2006; Kenig et al., 2015; Zivanovic et al., 2021). Nonetheless, the selective pressures, environmental variables and phenotypic attributes that might be under selection and that give rise to these genetic responses are not entirely understood (Balanyá et al., 2009; Rezende et al., 2010). In contrast, evidence of broad-scale climate adaptations is limited for *D. sukikii* (Lewald et al., 2021). On a similar note, in one of the few

cases of cage transplant experiments available, O'Brien et al. (2017) reported that non-native populations of the rainforest fruit fly *D. birchii* showed higher fitness than local counterparts along an altitude gradient, indicating maladaptation (see Hereford, 2009). These contrasting findings within *Drosophila* highlight the complexities in understanding the role of local adaptation, even among closely related lineages, in preserving genetic diversity, shaping distribution ranges and influencing invasive potential and resilience to environmental changes.

Even though local adaptation may seem contingent on many idiosyncratic factors such as past selection, the genetic architecture of populations, their connectivity and demographic processes, mechanistic models relating fitness to environmental variation can still provide crucial information for analytical and forecasting purposes (Peterson et al., 2018). Here, we focus on temperature effects and, by integrating thermal biology and life-history theory, examine whether populations of *Drosophila simulans* along a 2500 km latitudinal gradient in Chile are locally adapted to their thermal environment. With this purpose, we constructed fitness surfaces based on environmental temperature data and simulated transplant experiments in silico. Empirical estimates of viability and heat tolerance for *D. simulans* as a function of temperature were published elsewhere in detail (Alruiz et al., 2022, 2023), hence here we focus on how they can be combined to provide more realistic estimates

of fitness and employed to study local adaptation from an analytical perspective. We assessed two criteria posited as evidence of local adaptation *sensu strictu* in transplant experiments (Blanquart et al., 2013; Kawecki & Ebert, 2004): (i) that local populations demonstrate superior fitness in their native environment compared to foreign populations ('local vs. foreign' criterion), and (ii) that fitness in one's own locality surpasses fitness in other locations ('home vs. away' criterion). As explained in detail below, we not only obtained evidence of local adaptation but also identified a trade-off between annual survival and cumulative viability and that ultimately accounts for this result, illustrating how empirical data and theoretical analyses can be combined to study local adaptation when experimental procedures are not feasible.

MATERIALS AND METHODS

Samples collection and maintenance

Adult *D. simulans* were collected at eight locations along a latitudinal gradient (Figure 1; Table 1) spanning 2500 km between November 2018 and April 2019 during Austral summer. The collection period in each locality lasted between 5 and 6 days and adult flies were captured via traps of bananas or decomposing fruit. While variation in the collection dates may impact the genetic composition of

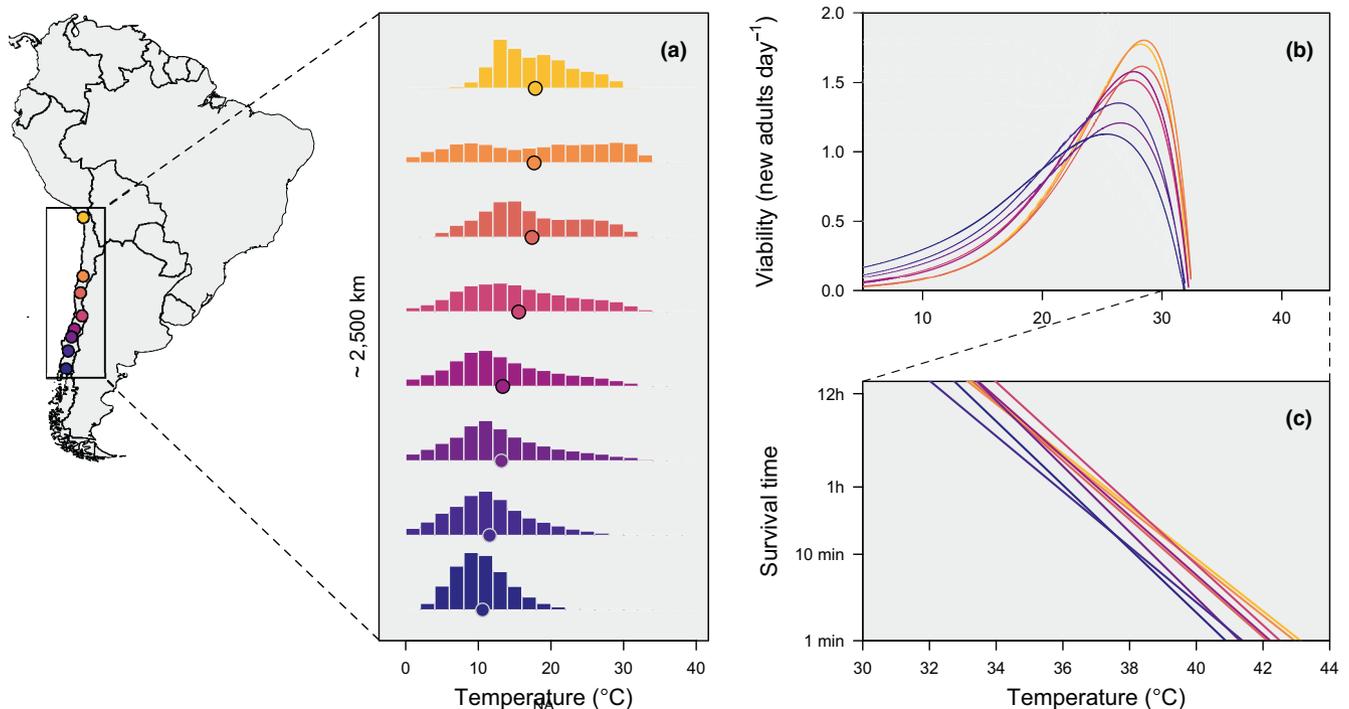


FIGURE 1 Life-history variation with latitude. (a) We collected *Drosophila* in eight localities in Chile and raised them under common conditions for multiple generations. The histograms display the distribution of temperature values recorded at a 1 h resolution and at a given temperature throughout the year (temporal trends for two populations are shown in Figure 2 and Figures S6 and S7). Dots represent the annual average temperature per locality. (b) Based on non-linear models, they exhibit gradual differences in their performance curves of egg-to-adult viability rate as a function of temperature. (c) According to thermal–death time curves, northern populations of *Drosophila* exhibit higher heat tolerance. For all curves, R^2 is between 0.83 and 0.99 ($mean=0.95$).

TABLE 1 Fitted parameters of viability rate $v(T)$ and heat tolerance $s(T)$.

Population (Lat)	Q_{10}	C (egg day ⁻¹)	T_{th} (°C)	d	R^2	T_{max} (°C)	z (°C)	R^2
Arica (18.47°S)	8.4	1.00 E-02	16.3	3.94 E-03	0.96	43.1	3.29	0.98
Copiapó (27.37°S)	8.5	9.31 E-03	16.1	3.73 E-03	0.97	42.9	3.27	0.96
La Serena (29.90°S)	7.6	1.11 E-02	16.8	4.04 E-03	0.97	42.1	2.94	0.98
Santiago (33.46°S)	5.5	2.65 E-02	17.4	4.53 E-03	0.94	42.5	2.84	0.96
Talca (35.43°S)	6.0	2.18 E-02	16.7	4.15 E-03	0.95	42.2	2.92	0.99
Chillán (36.61°S)	4.3	4.53 E-02	16.1	3.94 E-03	0.86	41.3	2.63	0.98
Temuco (38.74°S)	4.0	5.63 E-02	17.4	4.75 E-03	0.89	41.4	3.12	0.97
Puerto Montt (41.47°S)	3.1	9.38 E-02	16.2	4.10 E-03	0.83	40.9	2.71	0.99

Note: This table displays estimated parameters for both viability (Equation 1) and thermal tolerance curves (Equation 2), across sampled populations. For the egg-to-adult viability curves, the included parameters are as follows: Q_{10} , describing the fold increase in biological response for a 10°C rise in temperature; the constant C , indicating shifts in response independent of temperature; the threshold temperature T_{th} ; the rate of protein denaturation d ; and the R^2 coefficient of determination for each fit. Regarding the thermal tolerance curves, the parameters are as follows: the critical temperature T_{2max} for collapse after a standard 1-min challenge, the slope z estimating the decrease in temperature required for a tenfold increase in tolerance duration and the R^2 coefficient of determination for each fit.

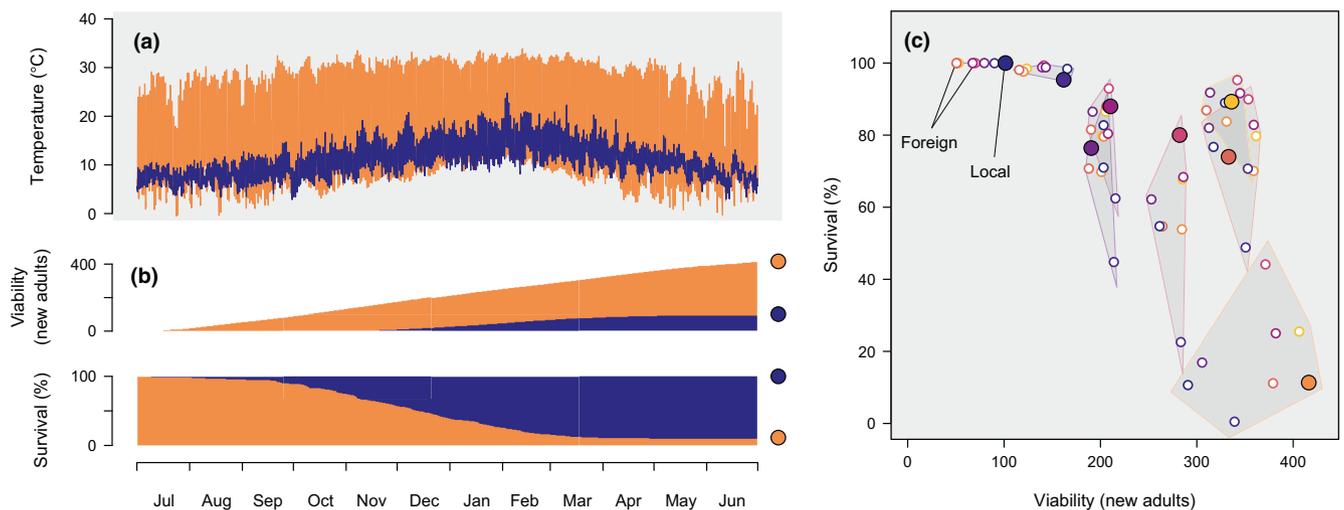


FIGURE 2 Annual cumulative viability and survival. We quantified how thermal effects on viability rate and survival translate into annual totals under field conditions along the distribution range. (a) Field temperatures in the warmest and coldest localities studied here (red and blue, respectively). (b) Cumulative number of new adults recruited over time based on egg-to-adult viability rates and survival predicted throughout the year for *Drosophila simulans* from these localities, and (c) trade-off between the cumulative number of adults recruited over the whole year and survival. Note that in panel (b), we are reporting the cumulative value of the viability rate. Data points correspond to 8 populations \times 8 localities. The polygons group the outcome by localities, with the south–north gradient shown from left to right. ‘Local’ populations tested in their native environment are shown in full symbols ($n=8$) as in (b), ‘Foreign’ populations in open symbols ($n=26$) and colours depict the population of origin (Figure 1).

the collected flies, this effect is expected to be small in comparison with the contrasting thermal profiles among the localities that ranged between diurnal mean maxima of 29.2°C in the north and 12.7°C in the south (Figures 1a and 2a). Individuals were brought to the laboratory for taxonomic identification and the subsequent establishment of laboratory lines. Flies were identified based on morphological characters to discriminate between *D. melanogaster* and *D. simulans*. Subsequently, separate laboratory lines from each of the eight locations were cultured employing a minimum of 50 to 60 wild females. Large and outbred populations were established from their offspring. Separate lines were then maintained in plexiglass cages ($27 \times 21 \times 16 \text{ cm}^3$) at 21°C on a non-overlapping discrete generation cycle, controlled larval crowded regime (c. 5 larvae mL^{-1} of medium) with a

LD=12:12 photoperiod. While it is true that several previous studies have demonstrated that more realistic conditions might involve the use of fluctuating temperatures throughout the day and night (e.g. Stazione et al., 2021), the aim of our experiment is to standardize environmental conditions, thereby eliminating any uncontrolled environmental effects. This standardized protocol allows us to isolate genetic sources of variation and more clearly interpret the effects of temperature, as confounding environmental effects of different photoperiods and larval crowding were controlled (Alruiz et al., 2022; Santos et al., 2005). Two replicate subcultures per line were maintained in separate cages, containing between 500 and 1500 breeding adult individuals. Replicates were pooled every generation to increase the effective population size and minimize genetic drift. Laboratory stocks

were maintained under these common garden conditions for at least three generations prior to experiments—range between three and six generations—to remove potential maternal and grand maternal effects.

Viability and heat tolerance estimation

To simulate fitness landscapes for different populations and localities, we combined measurements of birth versus death rates as a function of temperature, by quantifying egg-to-adult viability and heat tolerance. Note that these simulations are not, strictly speaking, models of population growth that require knowledge of age structure and fecundity that are virtually impossible to obtain across multiple temperatures and populations. To estimate egg-to-adult viability, clean food plates were placed in the maintenance cages allowing flies oviposition for 24 h. Afterwards, eggs were collected using a microscope Leica S6. From each plate, 20 eggs were transferred to vials with fresh culture medium, and 20 vials per population were assigned to climatic chambers at 12, 15, 20, 24, 27, 30 or 32°C (~22,400 eggs in 1119 vials in total, $n=20$ replicates per temperature and population with one vial excluded due to contamination). Hatching or the emergence of adults was followed every 24 h (between 9:00 AM and 11:00 AM) until the last egg hatched or alternatively after 60 days. We then defined egg-to-adult viability as the number of adult survivors divided by the average development time of survivors, which effectively provides a rate of new adult individuals that are recruited per unit of time (eggs h^{-1}). This measure is in line with the development time index by Vacek (1982). While it does not account for variation in fecundity across populations, which would be preferable for theoretical models quantifying fitness, it provides reliable estimates of egg-to-adult survival that are crucial at thermal extremes where bottlenecks are expected for a fraction of the labour (based on previous work from our group described in Cavieres et al. (2020)), fecundity estimates for eight populations across seven temperatures would require counting in the order of 3.5 million eggs.

We then expressed the egg-to-adult viability rate as a function of temperature $v(T)$ for each population applying the thermal performance curve proposed by Rezende and Bozinovic (2019). This curve includes, on the one hand, a thermodynamic component $t = Ce^{T \ln Q_{10}/10}$, where T corresponds to ambient temperature, Q_{10} describes the fold increase in performance following a 10°C increase in temperature and C is a constant describing sifs in the response that occurs independently of temperature (e.g. when examining the degradation rate of a substrate by a specific enzyme, C correlates with enzyme concentration). On the other hand, the equation includes a biochemical component $b = 1 - d(T - T_{\text{th}})^2$ representing loss of function due to denaturation occurring at a rate d above a given threshold temperature T_{th} . Viability $v(T)$ corresponds to $t \times b$ or, in its expanded form:

$$v(T) = \begin{cases} (Ce^{T \ln Q_{10}/10}) & \text{if } T < T_{\text{th}} \\ (Ce^{T \ln Q_{10}/10}) \times (1 - d(T - T_{\text{th}})^2) & \text{if } T > T_{\text{th}} \end{cases} \quad (1)$$

We fitted the non-linear model with the R function *boot.thermal.curve* written ad hoc to estimate parameters C , Q_{10} , T_{th} and d employing averages \pm SD measured empirically at each temperature ($n=7$ temperatures per population, with averages and SD estimated from 20 replicate vials per temperature). The bootstrap is necessary to ensure convergence of the non-linear model, and samples 100 times random values from a normal distribution with the empirical mean \pm SD for each temperature and the median from the distribution of fitted parameters is employed in subsequent calculations. To ensure that results were statistically robust, we replicated these analyses using three alternative thermal performance curves provided in the *rTPC* package (Padfield et al., 2021), namely *modifiedgaussian_2006*, *beta_2012* and *joehnk_2008*, which best fitted the viability data among the curves available in this package.

For heat tolerance assays, we transferred 50–100 eggs laid within a 24 h period into fresh bottles and monitored their development daily to obtain the experimental flies. We anaesthetized the adults that emerged with CO_2 for a brief period (<5 min) to separate males from females and transferred them to fresh medium vials for the subsequent estimation of thermal tolerance. Adult flies were assayed between 4 and 6 days post-eclosion to control for potential age differences in thermal tolerance. We placed flies in 5-mL glass vials and exposed them acutely to six constant stressful temperatures (35, 36, 37, 38, 39 and 40°C) in two pre-heated water baths. The temperatures of the water baths were randomized, and we measured 60 individuals simultaneously per assay—15 males and 15 females from each laboratory stock (i.e. 4 stocks were measured together in a single bath). Assays were recorded with a digital HD video camera (Logitech Carl Zeiss Tessar 1080 p) and we measured the knockdown time for each fly as the time elapsed until each individual lost righting ability and ceased to move.

We estimated heat tolerance in females, as their mortality will have direct impact on the predicted number of eggs laid in nature. We estimated the so-called ‘thermal tolerance landscape’ of each *Drosophila* population (Rezende et al., 2014), which describes how survival probability varies as a function of temperature and exposure time. For a fixed survival probability, the relationship between these variables follows the relationship:

$$\log_{10} t = (T_{\text{max}} - T) / z \quad (2)$$

which describes how exposure time t increases as ambient temperature T is less stressful and departs from T_{max} , or the critical temperature for collapse following a standard 1-min challenge. The slope z estimates the decrease in T required for a 10-fold increase in tolerance time (Peralta-Maraver & Rezende, 2021; Rezende et al., 2014). Parameters T_{max} and

z were calculated with the R function *tolerance.landscape* (Figure S3; Table 1), and showed that heat tolerance varies with latitude (Figure S4). We also fitted the survival probability function $s(T)$ required to predict heat mortality in variable temperatures (i.e. temperatures T that vary with time t), which shift the survival curve as a function of parameters T_{\max} and z in Equation (2) (Rezende et al., 2020):

$$\Delta S_{T(t)}(t) \approx \left. \frac{dS(t)}{dt} \right|_{T(t)} \Delta t \quad (3)$$

Detailed instructions on how to run these analyses automatically starting from empirical measurements are detailed in Rezende et al. (2020) and the R scripts to replicate all analyses reported here are available in DRYAD (<https://doi.org/10.5061/dryad.83bk3j9zk>).

Simulations with field temperatures

Having estimated how egg-to-adult viability $v(T)$ and survival $s(T)$ vary as a function of temperature for each *Drosophila* population (Equations 1–3), we then quantified how these variables should respond to more realistic thermal conditions in the field. We obtained hourly field temperature data from 2018, 2019 and 2020 from weather stations in the areas under study (the names of these eight stations can be found in Figure S4, with the .csv files available from the Chilean Agricultural Research Institute, INIA, at <https://agrometeorologia.cl/>). From these records, we calculated a vector T_f with the average temperature for each hour to minimize the impact of occasional extreme events in any given year, removing 29 February 2020 for simplicity. We then represented the annual cycle from July to June (i.e. winter to winter) to study how Austral summer temperatures are expected to affect viability and survival.

In the case of egg-to-adult viability and recruitment rate (expressed as new adults h^{-1}), we simply calculated $v(T_f)$ based on the vector T_f obtained from the field data on an hourly basis. Then, we added the estimated total viable eggs expected to have developed to adulthood throughout the year (cumulative egg-to-adult viability) (Figure 2). For these simulations, we assumed that flies only oviposit during the day and at temperatures above 12°C , where empirical value dropped to zero and deviated from the thermodynamic model that, due to its exponential nature, does not explicitly estimate a lower critical limit (Figure S1).

For relative survival, we replicated the analyses performed by Rezende et al. (2020) for *D. subobscura*, which combines the estimated thermal tolerance landscape with field temperatures to quantify thermal mortality in the field. This was accomplished by employing the *dynamic.landscape* function (Rezende et al., 2020), which combines the output of the *tolerance.landscape* function (see above) with T_f to predict daily mortality and

the resulting cumulative survival $s(T_f)$. This approach was validated against field abundance of *D. subobscura* monitored over 7 years in Santiago (one of the localities studied here) and successfully predicted the temporal course of population collapse due to heat stress (Rezende et al., 2020). Combining the eight thermal tolerance landscapes with T_f for the eight localities, we obtained the 8 populations \times 8 localities computerized transplant experiment. Detailed results for daily and cumulative viability and survival of the in silico transplanted populations are shown in Figures S5 and S6. Lastly, we combined estimates of viability and survival into a single estimate of Darwinian fitness to study local adaptation. For overall fitness expressed on a yearly basis (expressed as recruited new adults year^{-1}), we calculated:

$$x = \sum v(T_f(t)) \times s(T_f(t)) \quad (4)$$

where $v(T_f)$ corresponds to the egg-to-adult viability rate at time t and $s(T_f)$ the fraction of flies alive at that time, with t ranging between 1 h and 8760 h ($=24\text{h day}^{-1} \times 365\text{days}$). Shortly, viability is weighted by the fraction of survivors to obtain an annual fitness estimate that accounts for the effects of temperature on both life-history traits. Because egg-to-adult viability is being expressed as a rate of recruitment, its cumulative impact over a given period of time is expressed as the total number of adults recruited during that period because $v(T_f)$ is multiplied by t at each iteration until the completion of 1 year (Figure 2).

To make fitness comparable across localities, we calculated z -scores or $z_i = (x_i - \bar{x}) / \sigma$ that represent departures from the mean fitness of the locality \bar{x} expressed in units of standard deviation σ (Sokal & Rohlf, 2009). We employed a two-way ANOVA to partition the contribution of local conditions versus population of origin in the final dataset, which consisted of 64 predicted cumulative viability, heat mortality and overall fitness. We then used a regular t -test to test the ‘local versus foreign’ criterion (i.e. local populations are expected to exhibit higher fitness) and a linear regression between z -scores and the thermal mismatch between the tested locality and that of origin for the ‘home versus away’ criterion (i.e. the larger the mismatch between temperatures, the lower the expected fitness of the population). This procedure was replicated with different thermal performance curves from the *rTPC* package, as explained above, to ensure that results were robust.

RESULTS

The model's fit for viability measurements ranged between $R^2=0.828$ and 0.968 (Figure S1), and the viability curves exhibited discernible trends across populations along the latitudinal gradient. Cold-adapted populations exhibited higher viability in the cold at the cost of viability at warmer temperatures, resulting in performance

curves shifting towards lower temperatures and with lower thermal optima (Figure 1b). As a result, maximum egg-to-adult viability decreased from 1.90 to 1.10 new adults day⁻¹ with latitude, whereas thermal breadth where egg-to-adult viability surpasses 50% of the maximum increased from 9.0°C to 14.7°C (Figure S1). Thus, performance curves from populations from colder regions become both wider and lower, indicating a trade-off between thermal breadth and maximum performance, as discussed in detail in Alruiz et al. (2023).

Heat tolerance curves fitted with linear regressions exhibited R^2 between 0.96 and 0.99, with estimated T_{\max} ranging between 40.9 and 43.1°C and z between 2.6 and 3.3°C (Figure S2). Both T_{\max} and z vary predictably with latitude ($R^2 \geq 0.52$ and $p \leq 0.043$ in both cases) (Figure S3) and show that heat tolerance curves shift towards higher temperatures in warm-adapted populations (Figure 1c). The increase in T_{\max} with latitude results in curves displaced up to 2.25°C between cold- and warm-adapted populations, which implies that for an average $z = 2.97 \pm 0.09^\circ\text{C}$ (mean \pm SE), warm-adapted flies can tolerate 5.6 times more time at a given temperature than their cold-adapted counterparts (Figure 1c).

Trade-off and local adaptation

Simulated cumulative viability throughout the year was highly positively correlated with mean annual temperature ($r_{62} = 0.91$, $p = 2.0 \times 10^{-16}$), suggesting that most of its variation is determined by local thermal conditions. Indeed, according to a two-way ANOVA, locality accounted for 95.9% of the total sums of squares ($F_{7,49} = 216.9$, $p = 2.0 \times 10^{-16}$), whereas population of origin accounted for only 0.9% ($F_{7,49} = 2.1$, $p = 0.057$). In other words, viability is predicted to be higher in warmer localities regardless of the population origin. Despite the presence of adaptive differences in viability curves among *D. simulans* populations, these variations were unable to completely offset the thermodynamic constraints imposed by colder environmental temperatures (Figure 2b,c). Variation in cumulative survival was also determined primarily by local conditions, which account for 85.8% of the total variation ($F_{7,49} = 137.4$, $p < 2.0 \times 10^{-16}$) versus 9.8% due to origin ($F_{7,49} = 15.7$, $p < 1.4 \times 10^{-10}$). However, in contrast with viability, survival decreased with the mean temperature of each locality ($r_{62} = -0.79$, $p = 4.8 \times 10^{-15}$), which resulted in a general trade-off between the two variables and contrasting life-history strategies along the latitudinal gradient: in warmer localities, flies are exposed to higher mortality but also exhibit a higher rate of recruitment (i.e. new adults year⁻¹), whereas in colder localities, fewer flies die but recruitment is also impaired (Figure 2c).

Darwinian fitness generally diminished with increasing latitude, primarily due to thermodynamic constraints on viability. However, we also observed high

mortality at the warmest locality, situated at approximately 27°S (Figure 3a). Darwinian fitness was highly clustered within localities, with this factor explaining 91.2% of the total variation ($F_{7,49} = 116.3$, $p < 2.0 \times 10^{-16}$). Standardized fitness scores were significantly higher among local populations than foreign ones (Welch t -test, one-tailed $p = 0.023$) and decreased significantly with the mismatch between the mean temperature of the locality and the temperature of origin ($F_{1,62} = 18.5$, one-tailed $p = 3.03 \times 10^{-05}$) or the mismatch in latitude ($F_{1,62} = 4.6$, one-tailed $p = 0.018$), satisfying both criteria for local adaptation (Figure 3b,c). Results were similar when we employed other thermal performance curves in the analyses, even though the t -test in some instances only bordered statistical significance ($p < 0.07$ in all cases, Figure S5). These results are driven disproportionately by southern *Drosophila* populations, which consistently exhibited the highest or second-highest predicted fitness in their localities, and to a lesser degree, to northern populations where locals are often above average (Figure 3).

DISCUSSION

Here, we combined approaches from thermal biology (Angilletta, 2009) and life-history theory (Roff, 2002, 2010; Stearns, 1992), empirical data, high-resolution temperature records and computer simulations to demonstrate that populations of *D. simulans* distributed along a 2500 km latitudinal gradient in Chile are evolutionarily adapted to local thermal conditions along the latitudinal range in Chile. By integrating laboratory predictions of viability and survival (Figure 1) with field temperature records (Figure 2), we initially computed the expected cumulative viability and relative survival for each population on an annual basis (Figure 2b). We then combined both estimates to calculate a standard measure of annual Darwinian fitness that could be compared between populations and environmental conditions. Finally, we ran all permutations of population thermal responses against environmental conditions (Figures S6 and S7) to effectively simulate an 8 × 8 transplant experiment. This theoretical exercise suggests the existence of a trade-off between survival and reproduction, which is well-established in the life-history theory literature (Roff, 2002, 2010; Stearns, 1992) that is mediated by environmental temperature (Figure 2c). Our analyses then showed that local populations of *D. simulans* exhibit a combination of thermal responses in viability and survival that results in significantly higher fitness in their native environment than ‘transplanted’ populations, that is, evidence for local adaptation (Figure 3). In this sense, this constitutes a novel application of optimality models, commonly employed in evolutionary biology (Angilletta, 2009; Parker & Maynard-Smith, 1990; Roff, 2010), to study adaptation along an environmental gradient.

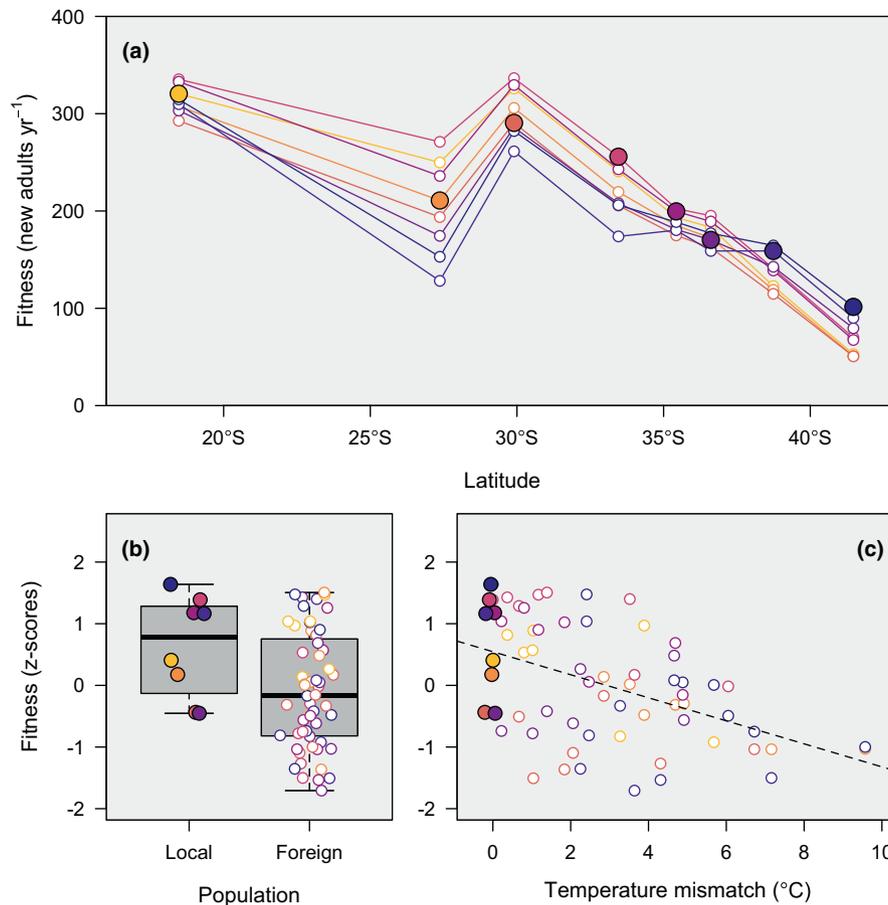


FIGURE 3 Local adaptation. (a) Fitness, estimated as the adults recruited at any given time multiplied by the fraction of survivors, summed over a whole year, varies predictably with latitude due to thermodynamic constraints in viability rate. (b) Testing the ‘local versus foreign’ criterion employing z -scores to control for fitness variation across localities and (c) the ‘home versus away’ criterion, where fitness should decrease as the thermal environment moves away from the local conditions in which each population evolved, estimated here as the mismatch between mean temperatures. ‘Local’ flies tested in their native environment in full symbols ($n=8$), ‘Foreign’ in open symbols ($n=26$) and colours depict the population of origin (Figure 1).

Whereas previous models have studied the role of local adaptation and the evolution of species ranges under climate change scenarios (Amarasekare & Coutinho, 2013), shifts in speciation rates (Doebeli & Dieckmann, 2003) and density-dependent survival (Atkins & Travis, 2010), most of them remain primarily theoretical. In contrast, here our theoretical analysis is able to reconstruct fitness surfaces based on empirical life-history data and how they are affected by temperature across eight *Drosophila* populations, and successfully puts to a test two alternative hypotheses of local adaptation along a geographic gradient. In doing so, we were able to bridge the gap between theoretical works focused on local adaptation (Case & Taper, 2000) and empirical experiments utilizing transplantation methods. We reconstructed how Darwinian fitness is expected to vary across an environmental gradient based on (i) empirical measurements of survival and reproductive performance as a function of temperature and (ii) high-resolution environmental data, and then employed the ‘local versus foreign’ and ‘home versus away’ criteria to test for local adaptation. Importantly, all outcomes or

pairwise transplants previously described in literature reviews of the subject (Blanquart et al., 2013; Kawecki & Ebert, 2004; Savolainen et al., 2013) are encapsulated in our results, illustrating how our approach provides a more general framework (Figure 4) and comprehensive understanding of the mechanisms driving local adaptation along geographical gradients.

In the specific case of our study, results show that Darwinian fitness decreases at higher latitudes (Figure 3). This is not in itself surprising, and the reconstructed surface not only supports the ‘hotter-is-better’ thermodynamic constraint hypothesis, which posits that evolutionary adaptation cannot entirely offset thermodynamic limitations (Alruiz et al., 2023; Huey & Kingsolver, 1989), but also illustrates how this constraint might translate into field conditions and quantifies *by how much* fitness is expected to decrease. Our approach can be combined with quantitative genetic analyses (Roff, 2002; Walsh & Lynch, 2018) to study rates of genetic and phenotypic adaptation to climate change. Nonetheless, we emphasize that our measures constitute relative fitness, which is adequate to compare

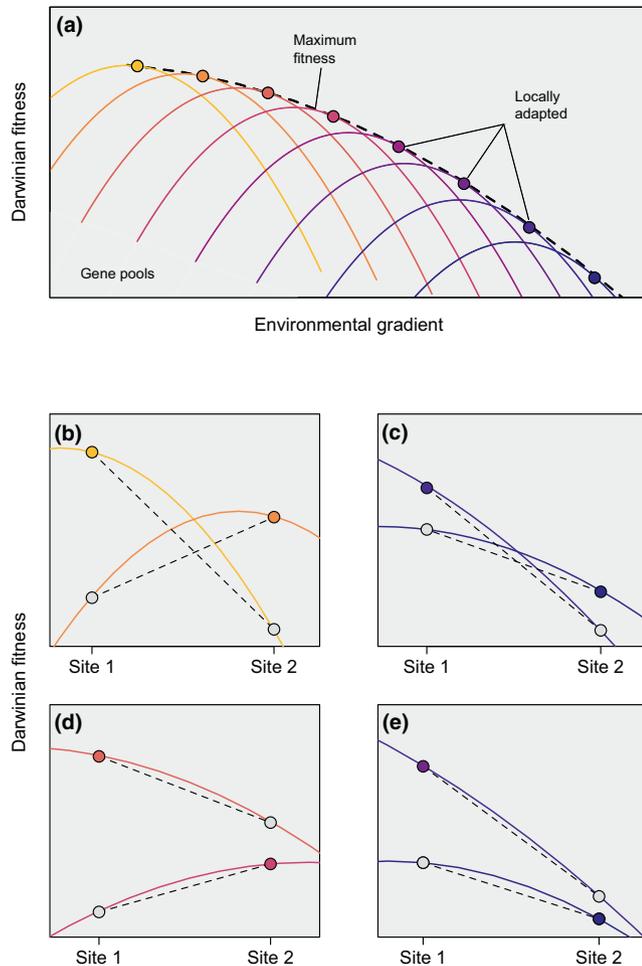


FIGURE 4 Surface of Darwinian fitness along the geographic gradient. (a) Geometric interpretation of ‘local adaptation’ and results conveyed here, generalizing the framework adopted for pairwise reciprocal transplants to a whole environmental gradient (Blanquart et al., 2013; Kawecki & Ebert, 2004; Savolainen et al., 2013). As explained in detail in these reviews, panels (b) and (c) satisfy the ‘local versus foreign’ criterion and panels (d) and (e) the ‘home versus away’ criterion. Note that all scenarios can be replicated by zooming in different regions of the fitness surface in (a). Importantly, this surface must be non-linear to allow for local adaptation along the whole gradient, which contrasts with the linear reaction norm depicted in the pairwise comparisons (dotted lines in panels b–e). Closed and open symbols represent local and transplanted populations.

populations everything else being equal, but do not necessarily translate into rates of increase in nature. Thus, while our results might be employed to predict how viability and survival might respond as temperatures increase along the cline, at present they cannot inform if populations will be resilient in the long term to warming conditions (i.e. the proposed methodology can reconstruct the fitness surfaces as shown in conceptual Figure 4, but we cannot identify where Darwinian fitness equals zero in the y -axis), particularly in the absence of more exhaustive measurements of fecundity. Moreover, our study at this point also does not consider reproductive traits that could affect the fitness landscape, such

as the ability to mate at different temperatures, which would be immensely beneficial for gaining greater accuracy in predictions.

Local *Drosophila* populations consistently outperformed their foreign counterparts (Figure 3b) given a thermal regime. Furthermore, as populations were exposed to thermal conditions distant from their native habitat, there was a gradual decline in fitness (Figures 3c and 4), satisfying both the ‘home versus away’ and ‘local versus foreign’ criteria. These findings hint at strong selective pressures that promote local adaptation despite potential gene flow across populations. Moreover, this study brings to light a compelling viability–survival trade-off, resulting in antagonistic pleiotropy within an environmental gradient (Hedrick, 1986; Hedrick et al., 1976) that favours the recruitment of new individuals in the population in warm environments at the expense of long-term survival and the opposite strategy in cold regions. This disjunction suggests no single genotype excels in both fitness traits across all habitats. Therefore, the thermal gradient, embodying spatial heterogeneity, supports the variety of genotypes and preserves *Drosophila* genetic polymorphism within the species distribution range. Such genotypic breadth allows for an array of adaptive strategies, albeit accompanied by inherent trade-offs (reviewed in Kawecki & Ebert, 2004). Ultimately, this viability–survival dichotomy not only supports the antagonistic pleiotropy paradigm along environmental gradient but also emphasizes the nuanced balance between genetics and environmental forces in dictating evolutionary pathways. While fecundity measurements would be highly desirable (Cavieres et al., 2020), it is also important to note that our method does not consider differences in activity period lengths among populations across latitudes (Hut et al., 2013), behavioural thermo-regulation (Castañeda et al., 2013) or sublethal effects on viability (Walsh et al., 2019), among others. However, it could be argued that adaptive variation across populations in any of these traits should exacerbate the difference in fitness between local versus foreign populations of *Drosophila* that we report.

Overall, our analyses illustrate the potential of combining empirical measurements and computer-intensive methods to study adaptive evolution to local conditions, as well as its mechanistic basis, in more detail. Our approach differs from the broader literature on clinal variation in functional, physiological and life-history traits (e.g. Cardillo, 2002; Sanford & Kelly, 2011) since the environmental impact in relative Darwinian fitness is modelled explicitly (Equations 1–4), which allowed us to simulate the transplant experiment in silico. Considering the logistical and ethical challenges of conducting transplant experiments on animals, and the limited examples in the literature focusing primarily on a few lineages of small invertebrate species (e.g. Blanquart et al., 2013; Crozier, 2004; Kawecki & Ebert, 2004; O’Brien et al., 2017; Purcell &

Avilés, 2008), the proposed approach should enhance our ability to predict how different organisms may cope with environmental conditions outside their distribution range or predict how they might respond to future climate change scenarios. Importantly, the analytical framework can be expanded to include other environmental factors, which may interact with heat stress and increase vulnerability to warming such as hypoxia (Verberk et al., 2023) or nutrient deficit (Koussoroplis et al., 2023). Furthermore, these analyses may take advantage of available published data to obtain comparable fitness metrics across lineages or environments, which may open the venue to quantify fitness surfaces in space or time, vulnerability to environmental change, invasive potential, coexistence or competitive displacement (see also Bellis et al., 2023). More generally, the present study highlights how empirical data and theoretical analyses can be combined to shed light on adaptive responses of different lineages to changing conditions in time and space and to study how local adaptation might contribute to the distribution and resilience of species with wide geographic ranges.

AUTHOR CONTRIBUTIONS

JMA, FB and ELR designed the study; JMA and GC collected the flies and performed the experiments; and IP-M and ELR performed the analyses and wrote a first draft. All authors contributed to the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no competing interest.

PEER REVIEW

The peer review history for this article is available at <https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14405>.

DATA AVAILABILITY STATEMENT

The R script used to conduct the data analysis and the datasets are available at the Dryad Digital Repository (<https://doi.org/10.5061/dryad.83bk3j9zk>).

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