

Heat stress and the fitness consequences of climate change for terrestrial ectotherms

Joel G. Kingsolver^{*,1}, Sarah E. Diamond² and Lauren B. Buckley¹

¹Department of Biology, University of North Carolina, Chapel Hill, North Carolina 27599-3280, USA; and ²Department of Biology, North Carolina State University, Raleigh, North Carolina 27695-7617, USA

Summary

1. Climate change will increase both average temperatures and extreme summer temperatures. Analyses of the fitness consequences of climate change have generally omitted negative fitness and population declines associated with heat stress.
2. Here, we examine how seasonal and interannual temperature variability will impact fitness shifts of ectotherms from the past (1961–1990) to future (2071–2100), by modelling thermal performance curves (TPCs) for insect species across latitudes.
3. In temperate regions, climate change increased the length of the growing season (increasing fitness) and increased the frequency of heat stress (decreasing fitness). Consequently, species at mid-latitudes (20–40°) showed pronounced but heterogeneous responses to climate change. Fitness decreases for these species were accompanied by greater interannual variation in fitness. An alternative TPC model and a larger data set gave qualitatively similar results.
4. How close maximum summer temperatures are to the critical thermal maximum of a species – the thermal buffer – is a good predictor of the change in mean fitness expected under climate change. Thermal buffers will decrease to near or below zero by 2100 for many tropical and mid-latitude species.
5. Our forecasts suggest that mid-latitude species will be particularly susceptible to heat stress associated with climate change due to temperature variation.

Key-words: climate change, ectotherms, fitness, heat stress, latitudinal gradients, thermal performance curves

Introduction

Climate changes during the past half-century have altered seasonal timing, geographic range and population abundance in many species around the world (Parmesan 2006). However, these shifts in phenology and distribution vary in both direction and magnitude among species (Williams & Jackson 2007; Williams, Jackson & Kutzbach 2007). As a result, predicting the responses of species to future anthropogenic climate change will require the integration of environmental information with data on the biological traits of different organisms. Choosing the appropriate level of biological detail needed to improve these predictions is a major challenge, given the need to forecast responses of diverse species from local and global scales (Williams *et al.* 2008; Buckley & Kingsolver 2012; Huey *et al.* 2012).

One approach to this challenge is to quantify the physiological sensitivities of organisms to temperature and other components of climate. For example, in ectotherms,

thermal responses of a genotype or species can be described in terms of a thermal performance curve (TPC) that relates organismic performance or fitness to environmental (or body) temperature (Huey & Stevenson 1979; Huey & Kingsolver 1989). Measurements of the thermal traits that characterize TPCs, including thermal breadth, optimal temperature (T_{opt}) and critical minimum (CT_{min}) and critical maximum (CT_{max}) temperatures for performance, reveal geographic patterns that are important for local adaptation and responses to climate change (Frazier, Huey & Berrigan 2006; Chown & Terblanche 2007). For example, terrestrial ectotherms at higher latitudes typically have wider thermal breadths and lower CT_{min} values than tropical ectotherms (Clusella-Trullas, Blackburn & Chown 2011; Sunday, Bates & Dulvy 2011).

What are the fitness consequences of these geographic patterns? In a landmark study, Deutsch *et al.* (2008) combined data on thermal traits for 38 insect species with observed climate data and future climate projections to model the fitness consequences of climate change from the late 20th to late 21st centuries. The results predict

*Correspondence author. E-mail: jgking@bio.unc.edu

decreased mean fitness in tropical species, but increased fitness at higher latitudes. This occurs because tropical species are thermally specialized and already experiencing mean annual environmental temperatures (T_{hab}) very close to their optimal temperatures (T_{opt}): their ‘thermal safety margins’ ($T_{\text{opt}} - T_{\text{hab}}$) are already only 1–4°C. Some mid-latitude desert species also have small safety margins (Huey *et al.* 2009). Thermal safety margins increase markedly with latitude, to 10°C or more at higher latitudes. As a result, many temperate ectotherms are expected to increase mean fitness in response to climate warming, despite the greater magnitude of warming at these latitudes (Deutsch *et al.* 2008). Several other recent analyses support the negative impacts of climate change for tropical ectotherms (Huey *et al.* 2009; Sinervo *et al.* 2010; Diamond *et al.* 2012; Bonebrake & Deutsch 2012; Thomas *et al.* 2012).

One limitation of these analyses is that they do not consider the negative fitness consequences of extreme temperatures: in these models, fitness (r) at temperatures below CT_{min} and above CT_{max} is bounded at $r = 0$ (replacement rate). Field studies suggest that even occasional ‘heat waves’ with environmental temperatures above CT_{max} can reduce population fitness below replacement rate, causing substantial population declines (McKechnie & Wolf 2009; Huey, Losos & Moritz 2010). Seasonal and interannual variation in temperature generally increases with latitude, particularly in continental regions. Climate projections suggest that extreme temperature and precipitation events will occur more frequently in the next 50–100 years; in many tropical and temperate areas, the hottest summers on record will represent the future norm (Battisti & Naylor 2009). Recent analyses with ectothermic reptiles show that geographic variation in CT_{max} is more closely related to temperature variation than to mean annual temperatures, implying more complex responses to climate change (Clusella-Trullas, Blackburn & Chown 2011). The fitness consequences of temperature variation and extremes under climate change have not been fully explored (Smith 2011).

In this study, we explore how seasonal and interannual variation in environmental temperatures affects the fitness consequences of climate change and the potential importance of population declines due to acute heat stress. We combine experimental data quantifying the thermal sensitivity of fitness in ectothermic insects with observed past and projected future climate data at multiple sites along a latitudinal gradient. Our analyses have two main goals. First, we quantify the predicted changes in mean and variation in fitness in response to climate change and how these vary with latitude. Secondly, we propose and apply two indicators that quantify the potential for heat stress due to high temperatures and identify which species and sites are most threatened by heat stress in current and future climate conditions. Our results suggest that climate change may negatively impact many tropical and temperate ectotherms as a result of temperature variation and

heat stress and that the potential for heat stress under future climate conditions may be greatest for species at middle latitudes.

Materials and methods

THERMAL PERFORMANCE CURVES FOR FITNESS

To predict the fitness consequences of past and future climates, we must first quantify the temperature dependence of fitness – the thermal performance curve (TPC) – for each species. Following Deutsch *et al.* (2008), we use the intrinsic rate of population increase (r) as the metric of fitness. We consider two different mathematical models for describing TPCs of r . The first model, called the RG model, is based on two key fitness components: net reproductive rate (R_0) and generation time (G). For this model, we used data from laboratory studies for 13 insect species that measured R_0 and G at a series of 3–7 constant rearing temperatures (see Kingsolver *et al.* (2011) for information about species, locations and data sources). For organisms (including most insects) with a relatively long juvenile (prereproductive) period compared with the reproductive period, the intrinsic rate of population increase (r) is given by

$$r = \ln(R_0)/G \quad \text{eqn 1}$$

For each species, we used a Gaussian function to model R_0 as a function of temperature (T).

$$R_0 = a \times \exp(-0.5 \times ((T - b)/c)^2) \quad \text{eqn 2}$$

Similarly, we used an asymptotic function to model G^{-1} as a function of temperature:

$$G^{-1} = d - e^{-T} \quad \text{eqn 3}$$

The parameters (a–d) in equations (2–3) were estimated for each species using nonlinear regression (R , nlme library). Combining these, we can use equation 1 to compute the thermal performance curve for r , which has the asymmetric shape characteristic of most biological rates (see Fig. S1, Supporting Information; Frazier, Huey & Berrigan 2006; Dell, Pawar & Savage 2011). Using this RG model for r (Equation 1), we can compute the optimal temperature (T_{opt}) and the maximum fitness ($r_{\text{max}} = r[T_{\text{opt}}]$). Note that when $R_0 < 1$ (equivalently, when $r < 0$), fitness is below replacement rate and the population will decline. For example, if $r = -0.25$ per month, then the population would decline by 22% in 1 month, and by 78% in 6 months. As a result, we define the critical thermal minimum (CT_{min}) and maximum (CT_{max}) as the lower and upper temperatures (respectively) at which $r = 0$: that is $r[CT_{\text{min}}] = 0$ and $r[CT_{\text{max}}] = 0$ (Deutsch *et al.* 2008). Note that CT_{min} and CT_{max} here refer to population fitness, not to survival or knock-down of individuals in response to acute temperature exposure (Angilletta 2009). At temperatures above CT_{max} , r declines asymptotically towards negative infinity. Because the goal in this study is to explore the fitness consequences of heat stress rather than cold stress, we assume that in cold, winter conditions, insects enter diapause (or the physiological equivalent) rather than die; thus, we define $r = 0$ for temperatures below CT_{min} (but see Discussion).

To evaluate whether the simulation results are sensitive to the specific model used for thermal performance, we also considered the TPC model of r (here labelled the GQ model, for Gaussian-quadratic) implemented by Deutsch *et al.* (2008) for 38 insect species across a wide range of latitudes (see Supporting Material in Deutsch *et al.* (2008) for information about species, locations and data sources). This piecewise model for r is a Gaussian function at

temperatures below T_{opt} , and a quadratic function above T_{opt} , allowing estimation of T_{opt} , r_{max} , CT_{min} and CT_{max} . Unlike Deutsch *et al.* (2008), here we allow $r < 0$ for temperatures above CT_{max} . Note that r declines quadratically at temperatures above T_{opt} and rapidly approaches negative infinity at temperatures above CT_{max} . To facilitate comparisons with the RG model, in the GQ model, we set an arbitrary minimum value of $r_{\text{min}} = -2r_{\text{max}}$. Additional simulations (not presented) suggest that our qualitative results are not sensitive to the choice of r_{min} .

CLIMATE DATA

Past climate data for the late 20th century (1961–1990) were obtained from high-resolution (0.5°) spatially interpolated global monthly surface air temperatures from the University of Delaware Center for Climatic Research (http://www.esrl.noaa.gov/psd/data/gridded/data.UDel_AirT_Precip.html). For future climate conditions for the late 21st century (2071–2100), we used monthly surface temperature anomalies (relative to baseline, 1961–1990) in a simulation from the Geophysical Fluid Dynamics Laboratory's CM2 global coupled climate models using greenhouse gas emissions scenario A2, a mid-range scenario for future emissions (Delworth *et al.* 2006). Climate warming in each month was added to the high-resolution (10') spatially interpolated baseline data (New *et al.* 2002). We used gridded data for our analysis as some populations lacked nearby weather stations.

We used monthly mean air temperatures (T_a), and did not include diurnal temperature variation, for two reasons. First, the empirical studies used here to estimate fitness are based on constant temperatures over the duration of the life cycle (i.e. the generation time). Over the full range of temperatures measured, the mean generation time for the species considered here was 38 days (SD = 26 days) with shorter times at higher temperatures (Kingsolver *et al.* 2011). At the highest temperatures measured in these studies, the mean generation time was 20 days (SD = 14 days). Thus, using monthly mean temperatures in our simulations reflects a time frame similar to that used during the fitness measurements at constant temperatures in the underlying empirical studies. Secondly, incorporating diurnal temperature fluctuations (e.g. based on daily minimum and maximum temperatures) would require assumptions about the diurnal pattern of temperature variation at each site and how this varies seasonally. At temperatures around and above T_{opt} , where thermal performances are strongly nonlinear, assumptions about diurnal patterns of variation may have important effects on model predictions (Savage 2004; see Discussion).

FITNESS PREDICTIONS

Using the thermal performance curve (TPC) for fitness (the RG model: equations 1–3) for each species, we determined r at monthly intervals for both past (1961–1990) and future (2071–2100) climate conditions. We then computed the (arithmetic) annual mean fitness at each site for the two cases considered by Deutsch *et al.* (2008): the 6-month 'growing season' each year (May–October in the northern hemisphere, November–April in the southern hemisphere); and the 12-month 'full-year'. Because most temperate and higher latitude insects overwinter in an inactive, diapause state, the growing season case allows us to focus on consequences of climate change during the active period (Deutsch *et al.* 2008); the full-year case also includes potential effects of climate change on altering the duration of the active period. To facilitate comparisons among species, we present all results in terms of relative r , defined as r/r_{max} , where r_{max} is the maximum fitness at the optimal temperature for each species.

THERMAL BUFFERS AND HEAT STRESS

We define and compute two related indices that quantify the potential for heat stress in past and future climate conditions. These indices reflect the magnitude and likelihood that organisms may experience deleteriously high mean monthly environmental temperatures (T_a) above CT_{max} . The thermal buffer (B) is defined as $B = \text{CT}_{\text{max}} - \max(T_a)$, where $\max(T_a)$ is the hottest mean monthly temperature in a given year. Similarly, the probability of heat stress (P_H) is defined as the probability that $B < 0$ in a given year. Thus, smaller (or negative) values of B indicate that populations are at greater risk of experiencing population declines; larger values of P_H indicate that a population is more likely to experience heat stress in a given time period. We used past and future climate data and estimates of CT_{max} (Frazier, Huey & Berrigan 2006) to compute B and P_H for 38 insect species at sites along a latitudinal gradient (Deutsch *et al.* 2008).

Results

ENVIRONMENTAL TEMPERATURE VARIATION, THERMAL TRAITS AND LATITUDE

We first chose four focal sites and species (Figs. 1–2) across different latitudes (6–41°N) that illustrate the variety of environmental variation and fitness responses that occur. Figure 1 shows the patterns of temporal variation in monthly environmental temperatures (T_a) for the four focal sites for both past (dark grey lines) and future (light grey lines) climate conditions. Values of CT_{min} and CT_{max} (solid black lines) and T_{opt} (dashed black lines) for the resident focal species at each site are also indicated. As expected, mean annual temperatures declined and seasonal temperature variation increased with increasing latitude; interannual variation in T_a was also greater at higher latitudes. During past climate conditions at three of the four sites (Fig. 1a–c), maximum summer temperatures frequently approached or exceeded T_{opt} , but did not exceed CT_{max} . These patterns suggest that in past climate conditions, many species may regularly experience mean monthly environmental temperatures close to their optimal temperatures during the hottest months of the year.

In future climate conditions (Fig. 1, light grey lines), focal sites at higher latitudes experienced larger increases in both mean annual temperatures and in seasonal and interannual variation. At all four focal sites, maximum summer temperatures frequently or always exceeded T_{opt} . Because of greater temporal variation, T_a sometimes approached or exceeded CT_{max} at the higher latitude sites (Fig. 1c,d). As a result, climate change at higher latitudes increased the frequency at which populations experienced environmental temperatures close to their optimal temperature, but may also increase the likelihood of occasional heat stress at those sites.

CLIMATE CHANGE AND FITNESS

Figure 2 shows the relative annual mean fitnesses (relative to r_{max} for each focal species) for the growing season case

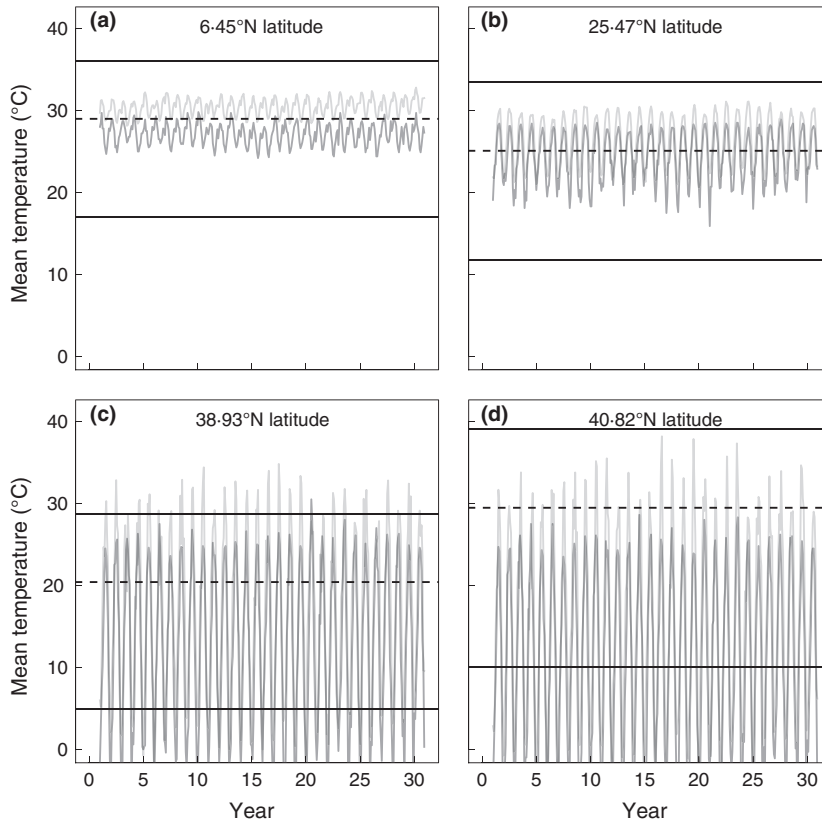


Fig. 1. Mean monthly temperatures under past (1961–1990: dark grey lines) and future (2071–2100: light grey lines) climate conditions for 4 focal species and sites. Values of CT_{\min} and CT_{\max} (solid black lines) and T_{opt} (dashed black line) are indicated for each species (RG model). (a) *Clavigralla shadabi*, 6-45°N latitude. (b) *Bemisia argentifolia*, 25-47°N latitude. (c) *Brevicoryne brassicae*, 38-93°N latitude. (d) *Muscidifurax raptorellus*, 40-82°N latitude.

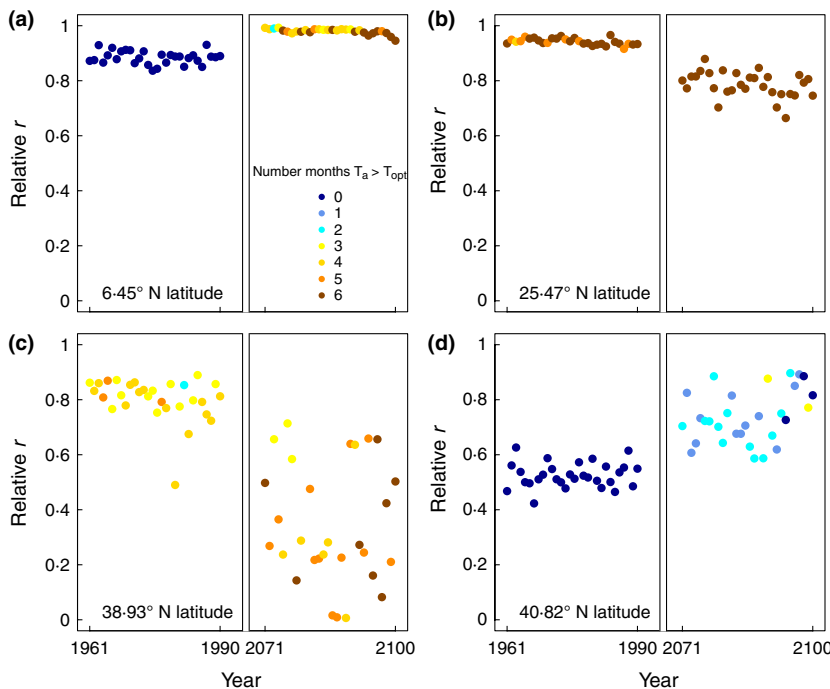


Fig. 2. Mean annual relative fitness (relative r) under past (1961–1990) and future (2071–2100) climate conditions for the four focal species, using the RG model. Species and sites are the same as in Fig. 1. Points represent mean relative r for each year for the growing season (6 months) case. The colour of each point indicates the number of growing season months (0–6) that year in which mean monthly temperature exceeded T_{opt} (see legend).

during past and future climate conditions. During past climate conditions, both mean fitness and interannual variation in fitness declined with increasing latitude across the four focal sites (also see below). However, the changes in mean fitness between past and future climates varied markedly among sites. For example, mean fitness increased

slightly between past and future climates for the low-latitude species (Fig. 2a). In contrast, at the two middle sites, future climate conditions decreased mean fitness and increased the variation in fitness (Fig. 2b,c), because species at these sites regularly experienced environmental temperatures well above T_{opt} (see Fig. 1 b,c). At the last

site, mean fitness increased in response to climate change (Fig. 2d), as this species more frequently experienced temperatures closer to its optimal temperature during the growing season (see Fig. 1d). Note that the different fitness responses of the two higher latitude (39–41°) sites (Fig. 2c, d) are largely due to the differences in T_{opt} and CT_{max} between these species, not the differences in environmental temperatures (Fig. 1c,d).

The full-season case (Fig. S2, Supporting information) gave qualitatively similar results, although the decline in mean fitness from past to future climate conditions at the two mid-latitude sites was smaller for the full-year (Fig. S2 b,c, Supporting information) than for the growing season (Fig. 2b,c) case. This pattern results from two opposing fitness effects of climate change at these sites: climate change increases the frequency of temperatures above T_{opt} and CT_{max} in the summer, but also increases the effective length of the growing season (months in which ambient temperatures exceed CT_{min}).

The results for these focal species suggest that interannual variation in mean fitness may be greater at higher latitudes, but do not indicate a monotonic relationship between fitness responses to climate change and latitude. Changes in the predicted mean and variation (SD) of fitness from the past to future climate conditions for all 13 species across the latitudinal gradient support this suggestion (Fig. 3). For the growing season case (Fig. 3a), 9 of 13 species (69%) showed decreased mean annual fitness in response to climate change. Responses of species at mid-latitudes (20–40°) were particularly heterogeneous, including the two largest increases and the four largest decreases in fitness; and all of the species with fitness declines were

at mid-latitudes. Climate change increased variation (SD) in annual fitness at 77% of the sites, especially at higher latitudes (Fig. 3b). Changes in the mean and SD of fitness were strongly negatively correlated ($r = -0.84$): species that had predicted declines in mean fitness also had increased interannual variation in fitness (Fig. 3). This pattern is due to the rapid decline in fitness at future environmental temperatures above T_{opt} , increasing the variation in fitness (Fig. 2).

Simulations for the full-year case (Fig. 3c) decreased the proportion of species (to 23%) that showed decreased mean fitness in response to climate change; again all of the species with fitness declines were at mid-latitudes. The highest latitude species (51°N) had the largest increase in mean fitness due to an extension of the growing season. Taken together, these results suggest that future increases in heat stress during hot summer months will reduce mean fitness, and increase fitness variation, in many mid-latitude species. Conversely, mid- and high-latitudes species will experience fitness benefits as growing seasons lengthen. The precise balance between these two effects, and thus overall effect of climate change on fitness, varied widely among sites, especially at mid-latitudes.

Note under past climate conditions, mean relative fitness declined significantly with increasing latitude for both the growing season case ($t = -2.53$, $P = 0.0279$, d.f. = 11) and the full-year case ($t = -4.034$, $P = 0.00197$, d.f. = 11). This latitudinal decline in mean fitness is associated with the increasing seasonal and interannual variation in environmental temperatures at higher latitudes (Fig. 1).

Simulations using the alternative GQ fitness model for 38 insect species showed qualitatively similar results

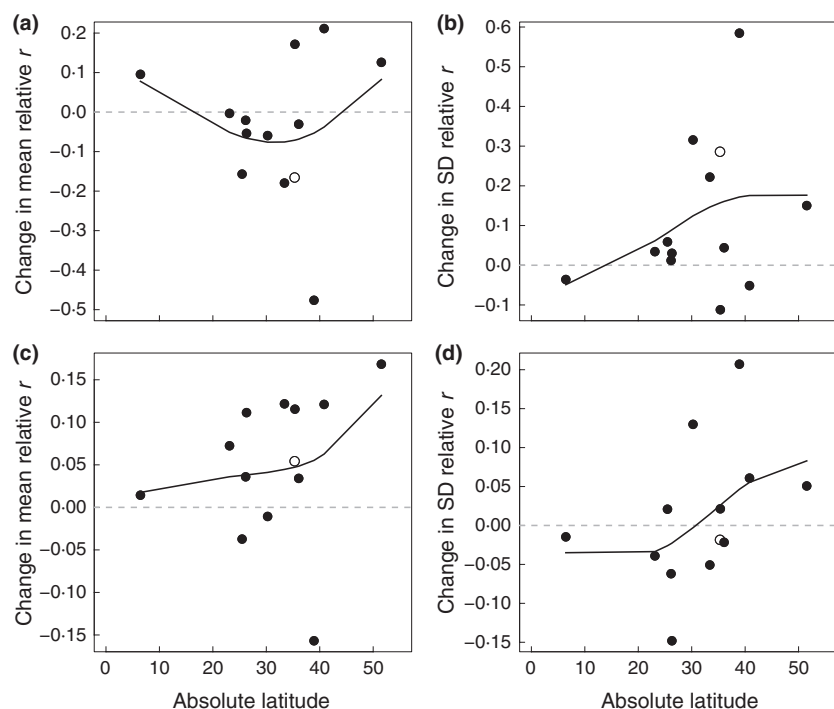


Fig. 3. Predictions using the RG model for the (a, b) growing season (6 months) case, and (c, d) full-year (12 months) case. Changes in the means (left panels, a and c) and standard deviations (right panels, b and d) of relative r in response to climate change as functions of absolute latitude. Circles represent values for each of the 13 species (solid circle, northern latitudes; open circle, southern latitudes). Lines indicate lowess curve fits.

for both the growing season and full-year cases (Fig. 4). We predict declines in mean fitness in response to climate change for both tropical and temperate species, including the majority of species at mid-latitudes. Again the predicted responses of mid-latitude species were strongly heterogeneous, including both the greatest increases and the greatest decreases in mean relative fitness.

THERMAL BUFFERS AND HEAT STRESS

Thermal buffer (B) – the difference between CT_{\max} and the maximum monthly temperature – showed a clear latitudinal pattern (Fig. 5). Median thermal buffers for past climate conditions ranged from 1 to 18 °C, with the largest values at the highest latitude sites. Lowess models showed that during both past and future climates, safety margins were smallest for sites between 10 and 40°N latitude. On average, median thermal buffers declined by 5–6°C in response to climate change; future thermal buffers for most species between $c.5$ –35°N latitude are close to zero. Climate change will eliminate the thermal buffer ($B < 0$) for 11 of 38 species across a range of latitudes.

Our metric of heat stress (P_H) indicates the probability that a species at a site will experience mean monthly temperatures exceeding CT_{\max} in a given year. Under past climate conditions, heat stress probabilities (per year) were low (Fig. 5): P_H was zero at 34 of the 38 sites and exceeded 0.1 at only two sites. However, P_H increased markedly under future climate conditions (Fig. 4): P_H exceeded 0.1 at 17 of the 39 sites and exceeded 0.5 at 10 sites. Strikingly, increases in heat stress in response to climate change were generally greater at mid-latitudes: for example, P_H increased in 12 of 17 species at sites between 20 and 40°N. These results suggest that ectotherms at mid-latitudes, particularly in the northern hemisphere, will be at greater risk for heat stress due to increases in the incidence of deleteriously high temperatures.

How do differences in thermal buffers among species and sites determine their responses to climate change? Past thermal buffer was a significant predictor of fitness change due to climate change, for both the growing season ($r^2 = 0.53$) and the full-year ($r^2 = 0.41$; linear regression). These results suggest that seasonal variability relative to

upper thermal limits is a major determinant of the fitness consequences of climate change for ectotherms.

Discussion

Three key components of climate vary predictably with latitude and impact fitness: mean annual temperature, seasonal variation and interannual variation. Higher latitudes experience greater thermal variation at both seasonal and annual time-scales, and ectotherms in these regions must adapt to these variable conditions. Although insects and other ectotherms have broader thermal performance curves at higher latitudes (Frazier, Huey & Berrigan 2006), greater environmental variation in higher latitudes can limit how well these species can adapt to local climates (Levins 1968; Moran 1992). For example, our simulations for past climate conditions indicate that mean relative fitness declines significantly with increasing latitude. Most insects and other ectotherms outside the tropics tolerate cold winter conditions by entering diapause or equivalent resting stages, but cannot readily escape from potentially stressful hot summer conditions (but see below). Our analyses focus on the fitness consequences of thermal variation and how they will change in response to future climate change.

Our results suggest that both tropical and temperate ectotherms may suffer declines in mean fitness during the growing season in response to climate change. As emphasized by previous analyses (Deutsch *et al.* 2008; Huey *et al.* 2009, 2012), many tropical ectotherms already experience environmental temperatures close to their optimal temperatures: future climate change will increase the frequency that tropical species experience temperatures above their optima, decreasing mean fitness (Deutsch *et al.* 2008). However, because thermal variability is limited in the tropics, our results suggest that heat stress (monthly temperatures exceeding CT_{\max}) may remain uncommon in many tropical species, even under future climate warming (Fig. 5). This tentative conclusion is tempered by the small number of tropical species in our analyses (Deutsch *et al.* 2008).

The consequences of climate change for ectotherms at middle (20–40°) latitudes are more complex. On the one

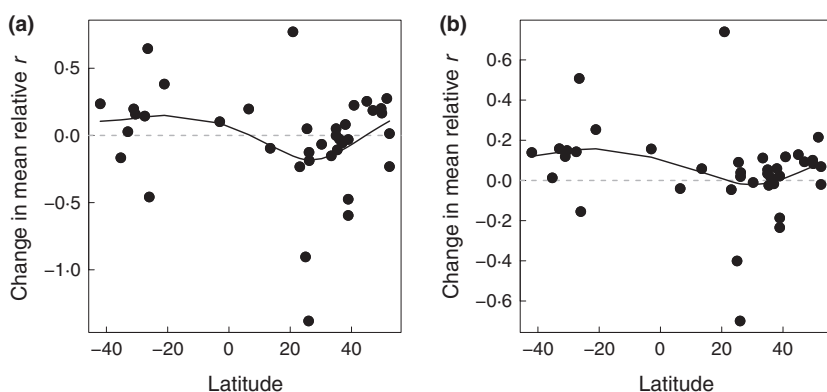


Fig. 4. Predictions using the Gaussian-quadratic (GQ) model (with parameter values from Deutsch *et al.* 2008) for the (a) growing season (6 months) case, and (b) full-year (12 months) case. Changes in mean relative r in response to climate change as a function of latitude. Circles represent values for each of the 38 species; lines indicate lowess curve fits.

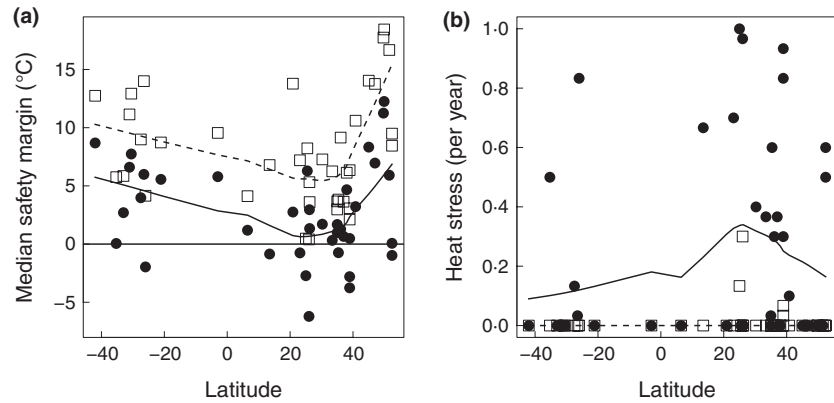


Fig. 5. Median thermal buffer (a) and annual probability of heat stress (b) as functions of latitude. Open squares represent values for past climate conditions, and filled circles represent future climate conditions. Lines indicate lowess curve fits for past (dashed) and future (solid) climates.

hand, climate warming will increase the length of the growing season, and increase the frequency with which species experience temperatures close to their optimal temperatures. On the other hand, climate change will also increase the frequency of high temperatures above CT_{max} , and the short-term negative fitness and population declines that follow. The fitness consequences of climate change will thus depend on the magnitude of temperature variation in relation to a species' optimal and critical maximum temperatures, which varies among mid-latitude sites (Figs 1–3). The striking heterogeneity in the predicted responses of mid-latitude species to climate change highlights the importance of incorporating physiological information about thermal sensitivity into ecological forecasts (Deutsch *et al.* 2008; Williams *et al.* 2008; Buckley & Kingsolver 2012; Huey *et al.* 2012). At higher latitudes ($>40^\circ$), climate change generally increases mean fitness, as warming will reduce the differences between environmental and optimal temperatures for most species.

Climate change will also affect temporal variation in fitness, with substantial increases and decreases in fitness variation in different sites. Importantly, changes in the mean and the variation in fitness are negatively correlated among sites. This pattern can be understood in terms of environmental temperatures in relation to the shape of thermal performance curves. If climate change at a thermally variable site increases the frequency that the species experiences environmental temperatures above T_{opt} (and above CT_{max}), this will both decrease mean fitness and increase fitness variation, because of the rapid decline in fitness at temperatures above T_{opt} . Increasing fitness variation should increase the variation in population size over time, making the population more susceptible to demographic stochasticity, environmental stochasticity and Allee effects that can increase the probability of extinction. In this sense, our predictions based on changes in mean fitness may underestimate the challenges of climate change for many temperate populations.

We focused on the RG model (equations 1–3) for the thermal sensitivity of fitness (r) in our analyses for two reasons. First, it highlights how the two distinct components, net reproductive rate (R_0) and generation time (G),

contribute to the thermal sensitivity of r (Fig. 1). Secondly, it provides a natural way to model fitness for temperatures at which fitness is below replacement rate ($R_0 < 1$; $r < 0$), since it approaches negative infinity asymptotically (rather than quadratically) as temperature approaches infinity. This model for fitness leads to somewhat different estimates of thermal traits, including T_{opt} and CT_{max} , than the Gaussian-quadratic (GQ) model used by Deutsch *et al.* (2008). However, our simulations suggest that the two models give qualitatively similar results in terms of latitudinal patterns of response to climate change (Figs 3–4). We emphasize that the scarcity of fitness data at higher temperatures, rather than the choice of specific functions, is the main limitation to modelling the fitness consequence of warming and heat stress. Parameter estimates are typically based on fitness measurements at 4–6 temperatures, and many studies do not include any data for high temperatures at which R_0 is below 1 (replacement rate): as a result, many estimates of CT_{max} represent extrapolation (Frazier, Huey & Berrigan 2006; Kingsolver *et al.* 2011).

Our analyses (and thus results) differ from those of Deutsch *et al.* (2008) in two important ways. First, we allow fitness values of $r < 0$ at high temperatures. This incorporates negative fitness consequences, and associated population declines, due to heat stress at high temperatures into our results. These effects are consequential for many mid-latitude populations. Secondly, we did not incorporate diurnal temperature variation into our model simulations, but instead used monthly mean temperatures. We chose this approach because the underlying data used to estimate thermal traits for each species were based on chronic (constant) rearing temperatures throughout the life cycle, and the generation times of these species are on the order of 0.5–3 months (see Methods). Modelling the effects of constant vs. diurnally fluctuating temperatures are particularly challenging at temperatures near and above T_{opt} , where thermal performance curves are strongly nonlinear (Fig. S1, Supporting information). Deutsch *et al.* (2008) incorporated diurnal variation by using a diurnal temperature range for each month at a site, computing fitness at both daily maximum and minimum temperatures and averaging

these two values to estimate mean monthly fitness. Mathematically, this is equivalent to assuming a square-wave pattern of diurnal temperature variation with a 12:12 h thermocycle that is identical among seasons, years and sites. This assumption likely contributed to the declines in mean fitness for many tropical species reported by Deutsch *et al.* (2008), relative to our results (Fig. 3 and Fig. S2, Supporting information). Fitness may decline more severely at daily maximum temperatures and be less affected at daily minimum temperatures relative to changes at daily mean temperatures due to TPC shape. Note that the magnitude of diurnal temperature fluctuations is higher at mid-latitudes (20–40°) than at either tropical or high-latitude sites. For example in summer, the mean diurnal temperature range is 13–14°C at 30° latitude, but only 9–10°C at the equator (Fig. S3, Supporting information). As a result, incorporating diurnal variation in our simulations would likely have greater effects on increasing the frequency of heat stress in mid-latitude than in tropical species. In any case, lack of data on the fitness consequences of diurnal fluctuations at higher temperatures is a major limitation on our ability to forecast heat stress and the fitness consequences of climate warming.

Because the main focus of our analyses was on heat rather than cold stress, we assumed that fitness does not fall below zero at temperatures below CT_{\min} during the winter. However, in some temperate insects, high winter temperatures can decrease survival of overwintering diapause stages (Han & Bauce 1997; Irwin & Lee 2003; Hahn & Denlinger 2011). Several experimental studies show that experimental warming during the winter increases metabolic costs, which can reduce survival, fat reserves and potential fecundity (Williams, Shorthouse & Lee 2003; Sorvari, Haatanen & Vesterlund 2011). Warmer and shorter winters may also increase other sources of mortality, including pathogen stress and freeze-thaw cycling (Leather, Walters & Bale 1993). The effects of increased winter temperatures on survival and other fitness components vary widely among temperate species, making generalizations difficult (Williams, Hellmann & Sinclair 2012). However, negative fitness consequences of increased winter temperatures could reduce or reverse the predicted fitness increases for higher latitude insect species reported here. Data on these overwintering effects for insects across a range of latitudes would be particularly valuable in improving future predictions of the ecological consequences of climate change (Regniere, St-Amant & Duval 2012).

Conversely, our models assume that populations do not use physiological or behavioural mechanisms to escape the negative fitness consequences of high environmental temperatures. Some insect species, especially in the tropics, do enter a diapause or dormancy stage during the summer or dry season, reducing the negative fitness consequences of high summer temperatures (Masaki 1980; Wolda 1988). In addition, many ectotherms, including lizards and snakes, use thermal refugia to avoid deleteriously high body

temperatures. In this case, high environmental temperatures typically reduce activity time and food intake, and indirectly reduce survival and reproduction (Sinervo *et al.* 2010).

For comparison with previous analyses (Deutsch *et al.* 2008), we considered both full-year (12 months per year) and growing season (6 months per year) cases. While the choice of 6 months is rather arbitrary, it allows us to focus on the fitness consequences of higher temperatures. Clearly, the length of the active growing season declines with increasing latitude, and at high latitudes and elevations season length may be much shorter than 6 months. Our results suggest climate change will increase the effective length of the growing season in temperate and higher-latitude regions, potentially increasing mean annual fitness. However, the effects of longer growing seasons (and shorter winters) on overwintering success are poorly understood for most insect species (Hahn & Denlinger 2011).

We have proposed a definition of thermal buffer ($B = CT_{\max} - \max(T_a)$) that quantifies how close hot summer temperatures are to the critical thermal maximum for a species. Our results show that in past climate conditions, thermal buffers were positive, and annual probabilities of heat stress (P_H) were zero or small, for all species and sites we considered. In contrast, under future climate conditions, thermal buffers were negative and heat stress probabilities were substantial for many species in both tropical and temperate regions (Fig. 4). Importantly, heat stress was most frequent at mid-latitude sites. This pattern results from the combination of two factors that increase with increasing (absolute) latitude: greater seasonal and annual variation in temperature, and larger increases in mean temperature due to climate change. Future climates will reduce median thermal buffers to near or below zero for most northern, mid-latitude species. In addition, our simulations suggest that the current thermal buffer for a species is a good predictor of the change in mean fitness resulting from future climate change. In summary, our results illustrate how climate change will increase the frequency of heat stress for many species outside of the tropics, reducing mean fitness and increasing fitness variation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Thermal performances curves for three aspects of fitness for *Brevicoryne brassicae*.

Fig. S2. Mean annual relative fitness (RG model) under past and future climate conditions for the 4 focal species.

Fig. S3. Diurnal temperature range across latitude.