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Increased temperature variation poses a greater risk to species than climate warming

David A. Vasseur[1], John P. DeLong[2], Benjamin Gilbert[3], Hamish S. Greig[4,5], Christopher D. G. Harley[6], Kevin S. McCann[7], Van Savage[8,9], Tyler D. Tunney[7] and Mary I. O'Connor[6]

[1]Department of Ecology and Evolutionary Biology, Yale University, New Haven, CT 06511, USA
[2]School of Biological Sciences, University of Nebraska Lincoln, Lincoln, NE 68588, USA
[3]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Ontario, Canada M5S 3G5
[4]School of Biological Sciences, University of Canterbury, Christchurch, New Zealand
[5]School of Biology and Ecology, University of Maine, Orono, ME 04469, USA
[6]Department of Zoology and Biodiversity Research Centre, University of British Columbia, Vancouver, British Columbia, Canada V6T 1Z4
[7]Department of Integrative Biology, University of Guelph, Guelph, Ontario, Canada N1G 2W1
[8]Department of Biomathematics, David Geffen School of Medicine at UCLA, Los Angeles, CA 90095, USA
[9]Santa Fe Institute, Santa Fe, NM 87501, USA

Increases in the frequency, severity and duration of temperature extremes are anticipated in the near future. Although recent work suggests that changes in temperature variation will have disproportionately greater effects on species than changes to the mean, much of climate change research in ecology has focused on the impacts of mean temperature change. Here, we couple fine-grained climate projections (2050–2059) to thermal performance data from 38 ectothermic invertebrate species and contrast projections with those of a simple model. We show that projections based on mean temperature change alone differ substantially from those incorporating changes to the variation, and to the mean and variation in concert. Although most species show increases in performance at greater mean temperatures, the effect of mean and variance change together yields a range of responses, with temperate species at greatest risk of performance declines. Our work highlights the importance of using fine-grained temporal data to incorporate the full extent of temperature variation when assessing and projecting performance.

1. Introduction

Over the past two decades, ecologists have widely recognized the potential for warming to alter species' distributions and phenology [1], the strength of species' interactions [2], community diversity and ecosystem functions and services [3]. More recently, ecologists have turned their attention towards climate variability, assessing how species are affected by the regime of temperature fluctuations that occur over a period of time at a particular location [4–11]. Given that global climate models predict changes to the frequency, intensity and duration of climate extremes [12–16], understanding the impact of climate variability on species' dynamics and distributions is a paramount task [4,12].

Recent models and experiments suggest that the impact of temperature fluctuations on fitness or other performance related traits may amplify the impact of warming on species [5,10,11,17,18]. However, temperature fluctuations can also impact performance independently of a changing mean owing to the nonlinearity of thermal reaction norms or thermal performance curves (TPCs). TPCs are typically constructed by fitting the measured performance or fitness of an individual or population across a range of constant rearing temperatures in the laboratory (for a review, see [19]). Generally, these curves are characterized by an exponential increase in performance at low temperatures, a transition to a peak at an
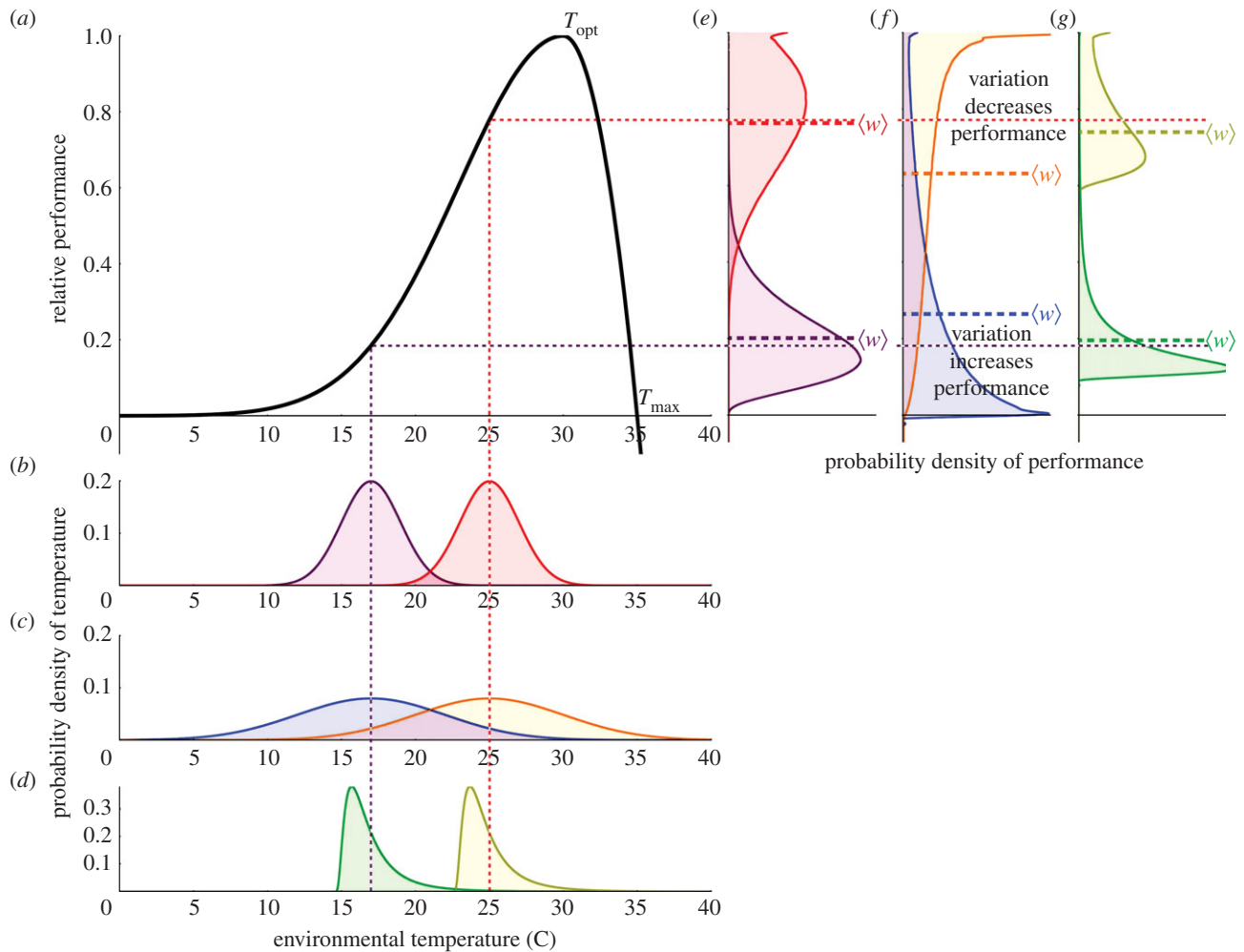
Figure 1. (a) A typical thermal performance curve (TPC) for relative performance (fitness or a proximate biological rate; black line) as a function of environmental temperature (equation (2.1)). T_{opt} marks the temperature at which performance is greatest and T_{max} marks the critical transition to negative values at high temperatures. Owing to the nonlinearity of this curve, species that experience temporal variation in temperature will have a mean long-term performance $\langle w \rangle$ that differs from the value predicted by the mean of their environment (owing to Jensen's inequality). The distribution of instantaneous performance and long-term performance means are shown for nominal 'cold' and 'warm' temperature distributions (b,e), distributions with increased variance (c,f) and distributions with positive skewness (d,g). In 'cold' conditions, increasing the variance leads to an increase in long-term performance, whereas positive skewness has little effect. In 'warm' conditions, increasing variances and positive skewness both lead to reductions in long-term performance. The mean temperatures of 'cold' and 'warm' distributions are equal [17,24] across (b) – (d); variance is equal for (b) and (d).

optimal temperature (T_{opt}), and a rapid decline above the optimal temperature through an upper critical threshold (T_{max}) beyond which performance is negative [20,21] (i.e. where the rate of mortality exceeds that of reproduction or development). In thermally fluctuating environments, the nonlinearity of these curves generates disproportionate effects of cool and warm events on performance (a relationship known as Jensen's inequality), even when the variation is symmetric about the mean [6,22,23]. Integrating performance measures over a period during which temperatures vary can increase or decrease performance relative to the value predicted by the mean temperature (figure 1). For instance, in a recent study with *Drosophila melanogaster*, temperature variability around a 17°C mean had a positive effect on the maximal population growth rate, whereas the same amount of variability around a 24°C mean had a negative effect [7]. Other studies have demonstrated varied effects of thermal variation on growth rates [9], development time [25] and fecundity [24,26], disease transmission [27,28] and stress resistance [29]. Given the ubiquity of nonlinearity of TPCs, the relationship between thermal variation and biological performance undoubtedly plays a key role in many aspects of a species' ecology.

Previous studies have used TPCs to predict how performance will be impacted by thermal fluctuations [5,7,11,18]. In a recent survey of 38 species of terrestrial invertebrate ectotherms, Deutsch *et al.* [5] projected future change in performance by integrating across climate regimes constructed of warmed seasonal cycles coupled to a fixed diurnal range. They projected an increase in performance in temperate regions and a decrease in performance in tropical regions, suggesting that tropical species, but not temperate species, were likely to experience detrimental effects of climate change because the differences between their optimal temperature and the mean environmental temperature (their thermal safety margins) are much smaller than for species in temperate regions. However, this result may hinge on the assumption of an invariant daily thermal range; including variation in the daily thermal fluctuations experienced by individuals may increase the frequency of extreme temperatures, depress thermal safety margins and exacerbate the potentially detrimental effects of climate change [10]. Furthermore, the sharpness of the decline in performance above the optimal temperature (the declining phase of the TPC) is more closely related to the magnitude of temperature variation than the

mean temperature experienced by a species [11,18]. This suggests that the critical parameters underlying TPCs may be more closely tuned to historical climate variability than climate mean, and thus performance itself may be more responsive to changes in the variability, throwing into question conclusions based solely on changes in mean temperature.

A great challenge underlying the estimation of biological impacts to changes in temperature is to determine the temporal grain over which temperature variation most strongly influences performance [30]. In any system, organisms experience variation at multiple temporal resolutions, with effects on performance varying among grains. For example, temperate ectotherms may benefit from an increase in mean annual temperature, because current means tend to be well below performance optima and far from critical upper tolerances [5,17,30]. Increasing temperature variability may generate larger amplitudes of seasonal and/or diel cycles in temperature, leading to prolonged periods of time at temperatures far from their optima and potentially beyond critical limits. Behaviour may allow organisms to avoid daily extremes [31], whereas acclimation may improve performance at seasonal extremes [32]. Most experiments and theory have modified thermal variation by changing temperatures on a daily basis [5,10,27,28,33,34]. Using 26 species of ectothermic insects, Liu *et al.* [33] concluded that the method of 'rate summation', whereby performance is calculated as the integral of the TPC-derived rate of performance with respect to time, accurately accounted for the impact of a diel sinusoidal temperature variation on development time. However, their analysis restricted temperature variation to the range of temperatures over which development is possible under constant conditions. In cases where temperatures surpass critical limits, acute and chronic exposure may yield different effects on performance [35]. Understanding how rate-summation projections of performance are impacted by thermal variability at different resolutions is critical for understanding the range of potential species responses.

There is compelling evidence that thermal variability will change over the next century. Although most studies have cited changes to the duration, frequency and extent of extreme events (e.g. droughts, heat-waves) [12–14,16,36], such changes will manifest in the higher statistical moments (e.g. variance, skewness, etc.) of the frequency distribution of temperatures accrued over time at any particular location [37,38]. For instance, projected changes in the variance of daily minimum and maximum temperatures are spatially heterogeneous, but may increase as much as $3°C^2$ in some north-temperate regions [37]. Positive skewness is also projected to increase across nearly all regions [37], making extreme cold events rarer and extreme warm events more frequent. Understanding how these moments will independently and interactively impact species' performance is an important next step in establishing general predictions for the impact of climate change.

Herein, we demonstrate the independent and interactive effects of mean temperature and temperature variability on performance using a rate-summation approach and by independently altering the statistical moments of the distribution of temperature. We then combine previously published TPCs for 38 globally distributed ectothermic invertebrates [5] with fine-grained, site-specific historical temperature data, and we show how changes to the mean, variance and positive skewness of historical temperatures impact these species. We also incorporate a moving-average filter of environmental temperature to better assess how the temporal grain of our dataset impacts performance. Our results show that performance tends to decline or remain the same under a future climate scenario, with larger declines occurring at mid-latitudes, and that changes in performance are well-explained by the interactive effects of the changing mean and standard deviation of temperature.

2. Methods

(a) Model

The responses of many biological rates (including metabolism, growth, development and a variety of other performance related quantities) to ambient temperature are well-described by curves that rise to a maximum at some optimal temperature and then fall steeply once this optimal temperature is surpassed (figure 1a) [5,20,39]. Although a variety of mathematical formulae have been proposed in the literature [20,39], there is no general consensus for a common model form. For convenience, we describe the dependence of performance on environmental temperature using the function parametrized in Deutsch *et al.* [5] where the 'rise' is given by a Gaussian curve and the 'fall' by a parabolic function,

$$w(T) = \begin{cases} \text{Exp}[-((T - T_{\text{opt}})/2\sigma_p)^2], & T < T_{\text{opt}} \\ 1 - [(T - T_{\text{opt}})/(T_{\text{opt}} - T_{\text{max}})]^2, & T \geq T_{\text{opt}}, \end{cases} \quad (2.1)$$

where w is a performance metric (e.g. fitness), T is body temperature of the organism, σ_{p} is a shape parameter determining the steepness of the 'rising' portion of the curve, T_{opt} is the temperature that maximizes performance and T_{max} is the upper critical temperature beyond which performance is negative. Negative performance values correspond to situations where the negative contributions of adult mortality to performance exceed the positive contributions of reproduction and development [39].

The mean performance of a population, averaged over a sufficient time, is given by $\langle w \rangle = E[w(T)]$, where $E[\cdot]$ represents the expectation of $w(T)$. For a constant temperature T_c, $\langle w \rangle = w(T_c)$; however, when temperature varies over time, $\langle w \rangle$ depends on the distribution of T. In this case

$$\langle w \rangle = \int [w(T) \cdot \text{PDF}(D, T)] dT, \quad (2.2)$$

where $\text{PDF}(D,T)$ represents the probability density function of the distribution D, evaluated at T. For a small set of distributions (e.g. the normal), equation (2.2) can be analytically solved. However, when analytical solutions are not available $\langle w \rangle$ can be approximated using numerical integration of equation (2.2), or by solving

$$\langle w \rangle = \int_{t=1}^{\tau} w[T(t)] dt, \quad (2.3)$$

where $T(t)$ is an interpolated sequence of τ temperatures in time, drawn from D, and τ is sufficiently large to ensure the distributional properties of T are well-represented. Moreover, equation (2.3) can be used to incorporate empirical time-series of temperature into estimates of performance.

To investigate the impact of mean temperature, variance and positive skewness on a population with the TPC given in figure 1, we used the following distributional transformation to ensure that mean, variance and skewness could be independently controlled:

$$D = \begin{cases} x, & \gamma = 1 \\ \mu + \sigma(\gamma^x - e^{\text{Ln}(\gamma)^2/2})/[e^{\text{Ln}(\gamma)^2}(e^{\text{Ln}(\gamma)^2} - 1)]^{1/2}, & \gamma > 1, \end{cases} \quad (2.4)$$

where x represents a normal distribution $N[\mu,\sigma]$, where μ is the mean, σ is the standard deviation and where γ represents a
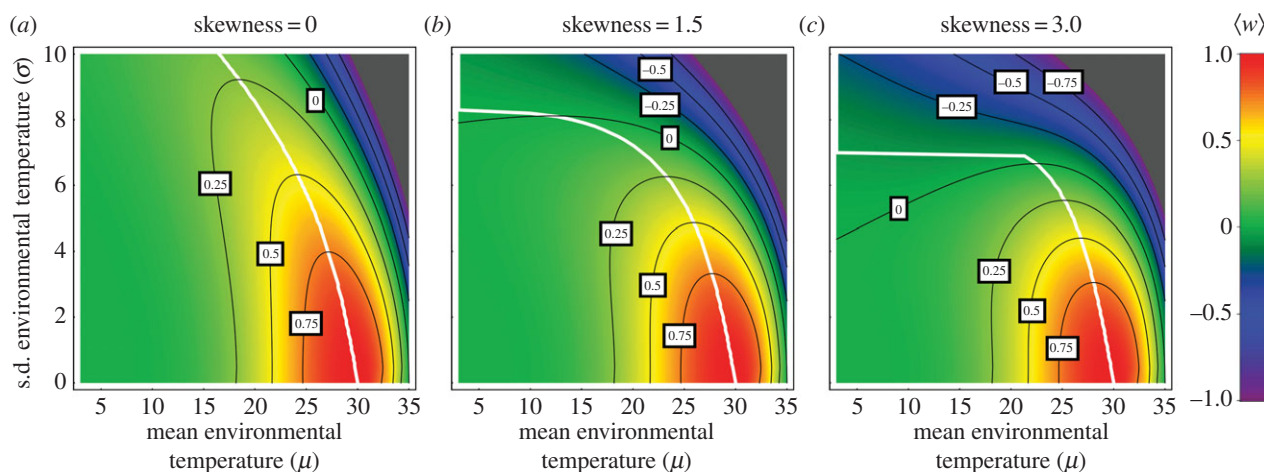
Figure 2. Relative long-term performance $\langle w \rangle$ of a species with thermal performance curve shown in figure 1 as a function of the mean, standard deviation and skewness (a–c) of a normal distribution environmental temperature. Relative performance values below −1 are shaded in dark grey and are not resolved as they decrease quickly beyond this point. Along $\sigma = 0$, where no environmental variation is present, contours are given exactly by the TPC. In regions to the left of the white lines, an increase in the mean temperature yields an increase in performance; to the right of the white line, an increase in mean temperature yields a decrease in performance. Exact values of $\langle w \rangle$ are given by $\int w(T) \cdot \text{PDF}[D(\mu, \sigma, \gamma), T] dT$.

factor influencing the symmetry of the distribution. This basis of this transformation is the inverse of a logarithmic transformation, but it is normalized to have constant first and second moments. The actual skewness produced by this distribution is dependent on both σ and γ (see the electronic supplementary material).

(b) Empirical data and climate change scenarios

We incorporated TPCs of 38 populations for which Deutsch *et al.* [5] estimated the three parameters of equation (2.1). These populations included a variety of invertebrate ectotherms across a $100°$ latitudinal range and were originally collected from other published studies (the electronic supplementary material). For each population, we obtained the sampling location from Deutsch *et al.* [5] and collected 10 years of recorded daily temperature maxima and minima from the nearest monitoring site using the KNMI Climate Explorer (http://climexp.knmi.nl/) to access data from the Global Historical Climatology Network-Daily database. In order that our historical climate data best reflected the conditions experienced by study populations, our 10-year collection window began 12 years prior to publication of the source paper in which the TPC was measured (which allowed for a 2 year lag between collection of organisms, experimental determination of the TPC and the publication of results). We used equation (2.3) and the TPC parameters for each species to estimate the long-term performance of each population in its local, historical thermal conditions, by linearly interpolating between daily maxima and minima (assuming 12 h intervals between) and smoothing temperature over the previous m days using an untapered moving average. Because performance is measured relative to each species' optimum value, we can directly compare performance of species that existed in historically different environments. Linear interpolation reduces the impact of extremes relative to higher-order interpolations, because these spend more time near local extrema. Furthermore, using a moving average reduces the impact of any single extreme event while retaining the impact of longer-duration extreme events. We analysed our results across the range $0 \le m \le 10$, but present only the case for $m = 2.5$ in the main paper; a moving average of 2.5 days eliminated any strong effects of short-term exposure (see the electronic supplementary material, figure S1), whereas larger values had very little effect on our results. We used the function *NIntegrate* in MATHEMATICA v. 9.0 to numerically compute the integral in equation (2.3). Each of the 38 TPCs, along with histograms of historical and future

climatic conditions, are shown in the electronic supplementary material, figure S3.

We then addressed the response of each population to changes in the temperature distribution by independently varying the mean, variance and skewness using the following transformations of the historical temperature series T_t:

$$
\left.
\begin{aligned}
T'_t &= T_t + c, \\
T'_t &= (T_t - \bar{T})\varepsilon + \bar{T} \\
\text{and} \quad T'_t &= \bar{T} + \sigma_T(\gamma^{T_t} - e^{\text{Ln}(\gamma)^2/2}) / [e^{\text{Ln}(\gamma)^2}(e^{\text{Ln}(\gamma)^2} - 1)]^{1/2}.
\end{aligned}
\right\} \quad (2.5)
$$

where $\bar{T}$ and σ_T represent the sample mean and standard deviation and c is an additive change to the mean, ε is a multiplicative change to the standard deviation, and γ (>1) increases the positive skewness. We examined relative performance under an additive change in mean temperature ($c = -2$ to $+5°C$), a multiplicative change in standard deviation ($\varepsilon = 0.5$–2.0), and a range of γ generating positive skewness values from 1 to 3 (see the electronic supplementary material, figure S2). We calculated the rate of change of relative performance with respect to each moment at the historical climate conditions ($c = 0$; $\varepsilon = \gamma = 1$).

Finally, we obtained site-specific climate projections of the daily maxima and minima of near-surface air temperature for the period 2050–2059 from the third-generation coupled global climate model of the Canadian Centre for Climate Modelling and Analysis (CGCM3.1/T47) using the Intergovernmental Panel on Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A2 scenario [40]. This simulation has a surface grid with spatial resolution of approximately 3.75°, thereby providing reasonable site-specificity for each of our samples. For each scenario, long-term performance was estimated in the manner described above. We then estimated the change in each moment relative to historic daily maxima and minima and partitioned the effect of each moment on the change in performance using a residual sums of squares analysis.

3. Results

Using the parameters of the TPC shown in figure 1, we demonstrate how independent changes in the mean, variance and positive skewness of an (initially) normally distributed temperature distribution affect long-term relative performance (figure 2). As variance is increased independently of the mean, performance at T_{opt} is reduced and peak performance
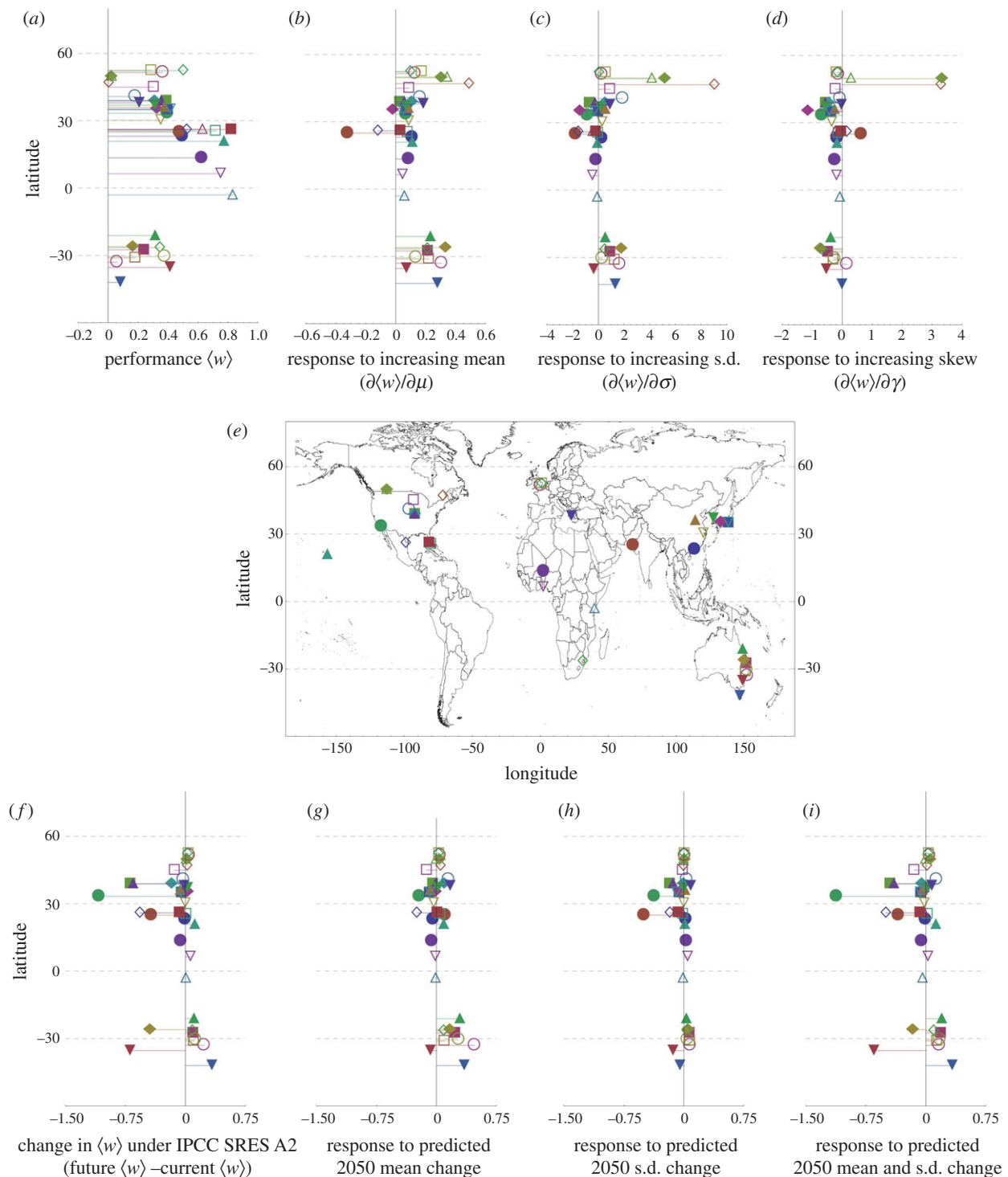
Figure 3. Estimated performance over 10 years of historical local thermal variation (a) for each of the 38 ectothermic invertebrates collected at the locations shown in (e). (b–d) The change in performance as the mean, s.d. and positive skewness of historical local climates are independently increased. (f) The projected change in performance using a decade (2050–2059) of simulated site-specific daily maximum and minimum surface air temperatures (see Methods). (g–i) The change in performance observed when only the mean (a), s.d. (b) or both mean and s.d. (c) of historical climates are altered to match future predictions. In (a), performance is estimated relative to performance at the optimum (T_{opt}). The mean change alone accounts for 32% of the predicted change in (f), the s.d. change alone for 54%, but interactively they account for 93%.

occurs at a lower mean temperature and with a reduced magnitude (figure 2). Skewness interacts with variance to further reduce performance and shift peak performance to lower mean temperatures (figure 2). As variance and skewness increase, it becomes increasingly likely that an increase in the mean temperature will negatively impact performance.

Using 38 ectothermic invertebrates for which TPCs were previously described [5], and a decade of local historical temperature data, we found that relative performance tends to be lesser at temperate latitudes (figure 3a), because thermal variability incurs a cost to performance (as demonstrated in figure 2). By independently modifying the statistical moments of the historical climate distribution experienced by each of these species, we measured the rate of change of performance as the statistical moment is increased (figure 3b–d). We find predominantly positive effects of increasing mean temperature

on performance in temperate regions and weaker/negative effects on performance at lower latitudes (figure 3b). Increasing variance yielded more negative effects on performance across a wider range of latitudes (figure 3c). The transition from positive to negative effects when considering temperate or tropical regions shows evidence of the differential effect of nonlinear averaging in cold and warm environments, as described in figure 1, although there is substantial variation across TPCs (see electronic supplementary material). Increasing positive skewness had a nearly ubiquitously negative, albeit weak effect on performance (figure 3d).

To determine how the mean, variance and skewness of the temperature distribution interactively impact performance in a changing climate requires a forecast of their coupled changes. We calculated the performance of the 38 invertebrate populations using site-specific projected daily extrema from a global climate model (CGCM3.1 [40]) for the decade 2050–2059. These projections show substantial reductions in performance (less than 90% of historical performance) in 14 species, small reductions (90–100%) in five, small increases (100–110%) in six and substantial increases (greater than 110%) in 13. The most substantial reductions occurred at subtropical latitudes ($\pm 30°$) and the most substantial increases occurred south of $-30°$ (figure 3f). For each projection, we quantified how well changes to the mean and variance of the temperature distribution explain the overall change in species' performance. In particular, we determined the change in mean and variance at each site by comparing CGCM projections against historical climate and incorporated these changes independently and concurrently into the historical climate data (see Methods; figure 3g–i). Changes in mean temperature alone explain only 32% of the variation in species' performances (figure 3g), suggesting that our ability to predict future performance based upon mean temperature change is extremely limited. Incorporating the change in variance alone is better (54% explained); however, when the mean and variance are simultaneously included, 93% of the change in species' performance is predicted (figure 3i). The synergistic effect of the mean and variance is much larger than their additive effects because their interaction is highly nonlinear, as portrayed in figures 1 and 2. Accounting for changes in skewness and even higher-moments of the temperature distribution explains only a small fraction of the remaining changes in performance, consistent with the relatively weak effects of skewness shown in figure 3d, and the expectation that projected changes in skewness are fairly moderate [37].

4. Discussion

Our results demonstrate that the risks imposed on performance by climate change are best understood by considering changes in the mean and variance of temperature concurrently. Because the impact of increasing variance can be either positive or negative, depending on the mean temperature relative to the curvature of the species' TPC, manipulating the mean and variance independently will yield contrasting results. For instance, Deutsch et al. [5] predicted the impact of climate change on this set of species by linking historical diurnal temperature ranges (averaged per-season) to the seasonal variation and anticipated mean of future climate. They found that tropical species were more likely to show reduced performance in future climates, owing to the higher likelihood that these species will experience temperatures greater than their critical thermal tolerances. In contrast, we incorporated diurnal temperature fluctuations that varied through time (in both the historical and climate change GCM data), enhancing our resolution of thermal extremes over previous work. The differences among our projections highlight the importance of considering mean and variance change together and reiterate a clear need for improved fine-scale model output or downscaled data for assessing climate change impacts on populations [4].

Our results suggest that species at mid-latitudes are most susceptible to large performance declines under a future climate scenario. Recently, Kingsolver et al. [11] demonstrated a similar result and also showed strong heterogeneity in performance changes at these latitudes. They suggested that the consequences of climate changes are most complex for species inhabiting the middle latitudes (20–40°), because the positive influence of increased mean temperature (e.g. by creating a longer growing season) can be counteracted by the negative influence of increased magnitudes and durations of heat stress during summer [11]. Our model analysis (figure 2) shows that counteracting effects of increasing mean and increasing variance can also yield changes to performance that differ in sign. This counteracting effect is echoed in our projections for ectothermic invertebrates, whereas anticipated changes to the mean temperature have mainly positive effects on performance (figure 3g) and anticipated changes to the variance of temperature have mainly negative or null effect on performance (figure 3h). It is only when considered together that the mean and variance of temperature can appreciably predict the response to climate change (figure 3i). Although positive skew magnifies the impact of variance on performance, the values shown in figure 2 are larger than those projected by climate models (which range from 0 to 0.4 over much of the planet) and currently exhibit only a small amount of positive skew [37], suggesting that changing skewness will only be important in areas with high thermal variance.

Our simple metric of performance does not explicitly allow individuals to avoid thermal stress and/or maximize their use of optimal environments. Although the body temperature of small-bodied ectotherms is expected to equilibrate quickly to ambient conditions [41], a variety of mechanisms, including differentiation of the thermal tolerance of development from that of mortality [39], incorporating the phenology of ontogenetic development [30,42] and behavioural thermoregulation via microhabitat use [31] can buffer the detrimental effects of stressful temperatures. Furthermore, while chronic exposure may have detrimental effects on performance, acute exposure to temperatures above T_{max} may benefit organisms by allowing for short bursts of increased activity [35,43]. To better deal with this mismatch, we averaged environmental temperatures over the previous 2.5 days. This weakened the impact of short-lived thermal extremes, but retained the detrimental effects of stressful conditions lasting multiple days (see the electronic supplementary material, figure S3). Although this is not a biologically motivated solution, it ensures that our results are conservative and not simply reflective of short-lived thermal anomalies which organisms could easily avoid through behaviour or other means. In addition to behaviour and phenological regulation, an organism's physiology can filter the environment by acclimation through physiological plasticity [44,45] and evolutionary responses may alter the TPC itself [46–49], yielding deviations from our predictions. Understanding the constraints and trade-offs that shape adaptation of the TPC and the

potential for temperature variation to drive selection is an important area deserving further research [49,50].

A recent analysis of temperature–performance relationships in squamate reptiles found that the parameters governing high-temperature performance (herein T_{opt} and T_{max}) were closely related to both the mean diurnal temperature range and precipitation and that low-temperature performance was closely related to mean temperature [18]. These results suggest that current TPCs may reflect selection on species to both the historical mean and variation of the temperature regime encountered over evolutionary time. Provided that TPCs are well-suited to the conditions in which species have historically evolved, it is unlikely that changing means and variances of temperature could yield appreciable increases in performance. The wealth of positive responses of performance shown in our analysis may be evidence for the complex interaction between temperature and other environmental factors such as wind velocity, humidity and precipitation, and factors such as altitude, habitat and species interactions may drive the use of thermal environments that appear suboptimal in our analysis. Moreover, the degree to which populations are locally adapted probably ranges considerably across our dataset, obscuring any real latitudinal relationship underlying the results.

Our work demonstrates that although increasing temperatures are potentially beneficial for many species, the interactive effects of mean and variance of daily temperatures generate a wide range of outcomes for invertebrate ectotherms under global change. This result arises because changing variance of the temporal distribution of temperatures exacerbates the effect of mean change, generating more climate extremes and buffering any performance advantages offered by a warmer mean temperature in temperate environments. These extremes have a relatively greater impact on population performance owing to the nonlinear relationship between temperature and performance. Ultimately, understanding how species will respond to climate change will involve a more complete match-up of their phenology and life history with temporal climate projections.

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