

Asymmetry of thermal sensitivity and the thermal risk of climate change

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Funding information

National Science Foundation, Grant/Award Number: DBI-1349865 and DEB-1951356

Abstract

Aim: Understanding and predicting the biological consequences of climate change requires considering the thermal sensitivity of organisms relative to environmental temperatures. One common approach involves 'thermal safety margins' (TSMs), which are generally estimated as the temperature differential between the highest temperature an organism can tolerate (critical thermal maximum, CT_{max}) and the mean or maximum environmental temperature it experiences. Yet, organisms face thermal stress and performance loss at body temperatures below their CT_{max} , and the steepness of that loss increases with the asymmetry of the thermal performance curve (TPC).

Location: Global.

Time period: 2015–2019.

Major taxa studied: Ants, fish, insects, lizards and phytoplankton.

Methods: We examine variability in TPC asymmetry and the implications for thermal stress for 384 populations from 289 species across taxa and for metrics including ant and lizard locomotion, fish growth, and insect and phytoplankton fitness.

Results: We find that the thermal optimum (T_{opt} , beyond which performance declines) is more labile than CT_{max} , inducing interspecific variation in asymmetry. Importantly, the degree of TPC asymmetry increases with T_{opt} . Thus, even though populations with higher T_{opt} s in a hot environment might experience above-optimal body temperatures less often than do populations with lower T_{opt} s, they nonetheless experience steeper declines in performance at high body temperatures. Estimates of the annual cumulative decline in performance for temperatures above T_{opt} suggest that TPC asymmetry alters the onset, rate and severity of performance decrement at high body temperatures.

Main conclusions: Species with the same TSMs can experience different thermal risk due to differences in TPC asymmetry. Metrics that incorporate additional aspects of TPC shape better capture the thermal risk of climate change than do TSMs.

KEYWORDS

critical thermal maximum, CT_{max} , optima, thermal performance curve, thermal safety margin, thermal tolerance, TPC

1 | INTRODUCTION

The impact of climate change on organisms depends not only on the magnitude of temperature change, but also on an organism's

sensitivity to the change (Buckley & Kingsolver, 2021; Deutsch et al., 2008). Organisms in the tropics may experience larger fitness impacts – despite a lesser magnitude of climate change – because relatively constant tropical climates select for thermal specialization

(Deutsch et al., 2008; Dillon et al., 2010; Janzen, 1967). Nevertheless, the greater and increasing magnitude of thermal variation in temperate areas may equalize fitness impacts across latitude (Kingsolver et al., 2013; Vasseur et al., 2014). These insights have led to the development of thermal risk indices that incorporate thermal sensitivity and environmental temperatures.

'Thermal safety margins' (TSMs) are commonly used to predict and index thermal risk (Clusella-Trullas et al., 2021; Deutsch et al., 2008). TSMs indicate the differential between temperatures an organism can tolerate and those it experiences. Deutsch et al. (2008) initially defined TSM as the difference between thermal optimum (T_{opt} , the temperature corresponding to peak performance) and annual mean habitat temperature, and they also defined 'warming tolerance' (WT) as the difference between the warmest temperature at which an organism can function – critical thermal maximum (CT_{max}) – and its 'habitat' temperature (Figure 1a). Subsequent analyses have often reversed these definitions, such that TSM is often the temperature difference between CT_{max} and maximum operative or habitat temperatures (Pinsky et al., 2019; Sunday et al., 2014). We employ the latter definition here. Large positive differences are usually interpreted as implying that an organism has relatively low risk of heat stress and of experiencing a performance decrement from high temperatures.

Analyses using TSMs suggest that tropical organisms are especially vulnerable to climate change (Deutsch et al., 2008; Diamond et al., 2012; Huey et al., 2009), that microclimate (Pincebourde & Casas, 2019) and temporal (Kingsolver et al., 2013; Vasseur et al., 2014) environmental variation are important, that thermoregulation is sometimes needed to buffer thermal stress (Kearney et al., 2009; Sunday et al., 2014), and that marine ectotherms are more vulnerable than terrestrial ones (Pinsky et al., 2019).

TSMs are conceptually useful because they relate an index of organismal heat tolerance (CT_{max} , an index of organismal failure) to an independent measure of environmental temperature. They are tractable because thousands of CT_{max} values have been measured (Bennett et al., 2018), and environmental temperatures are readily available. However, TSMs are challenging to interpret (Clusella-Trullas et al., 2021). A TSM of 1 °C likely implies more thermal risk than does a TSM of 10 °C, but is the magnitude of thermal risk a linear or curvilinear function of TSM? When TSMs are large, interspecific or intraspecific differences in TSMs will be of little biological significance as these organisms are unlikely to face thermal risk.

Another issue is deciding on the appropriate temporal scale of environmental data used to estimate TSMs (Clusella-Trullas et al., 2021; Clusella-Trullas & Chown, 2014). Studies of spatial (e.g., latitudinal) variation in TSMs have used various time-scales (e.g., hourly, annual) and different aggregation metrics (mean, maximum) (Clusella-Trullas et al., 2011). For example, Deutsch et al. (2008) used annual (also quarterly) average habitat temperatures, Kingsolver et al. (2013) used maximum monthly habitat temperature and Pinsky et al. (2019) used maximum hourly operative temperature. Risk of high-temperature exposure also depends on factors such as microclimate heterogeneity, habitat selection and behavioural thermoregulation (Garcia et al., 2019).

TSM analyses implicitly assume that risk is independent of duration of exposure to high temperature, when in fact CT_{max} declines with prolonged exposure to high body temperature (T_b ; Jørgensen et al., 2019; Kingsolver & Umbanhowar, 2018; Rezende et al., 2014, 2020). Many exposures to extreme temperatures are transient, at least for mobile organisms that can use behaviour to evade prolonged exposure (Kearney et al., 2009). Because TSMs use a single environmental temperature, they implicitly – and unrealistically – assume that the physiological impact of a single acute thermal extreme is the same as repeating such exposures (Sinclair et al., 2016) or that temperature means appropriately temporally integrate acute exposures (Buckley, 2021).

TSMs are in effect point estimates of thermal risk. An alternative and more comprehensive way to conceptualize cumulative thermal risk involves integrating environmental data with thermal performance curves (TPCs), which depict how performance changes with T_b (Huey & Stevenson, 1979; Vasseur et al., 2014; Figure 1a). TPCs are characterized by minimum and maximum temperatures at which performance is zero (critical thermal minima and maxima, CT_{min} and CT_{max} , respectively), T_{opt} , and the tolerance breadth over which an organism can perform (Figure 1a). Weighting environmental temperature data by TPCs aggregates risk over some specified interval, which may be more biologically meaningful and less sensitive to selected time-scales. Importantly, this approach accounts for the onset and relative rapidity of performance declines at high T_b and builds on previous studies of thermal risk (Gunderson & Leal, 2012; Huey et al., 2009; Vasseur et al., 2014).

TPCs are unimodal but asymmetric (Gilchrist, 1995; Huey & Kingsolver, 1989; Huey & Stevenson, 1979). Physiological and biochemical rates increase exponentially with temperature beyond CT_{min} until approaching T_{opt} (Asbury & Angilletta, 2010; Dell et al., 2013; Payne & Smith, 2017). Performance subsequently declines rapidly beyond T_{opt} as physical and physiological limits are approached (Knies & Kingsolver, 2010; Ratkowsky et al., 2005). This TPC asymmetry has ecological (Hurford et al., 2019) and evolutionary (Gilchrist, 1995) consequences: for example, by preferring body temperatures somewhat below their T_{opt} , organisms reduce performance declines at high body temperatures (Martin & Huey, 2008).

Unfortunately, TPCs have been measured far less often than has CT_{max} simply because TPCs require measuring performance at multiple temperatures as well as then selecting an appropriate functional curve (Angilletta, 2006; Izem & Kingsolver, 2005). In contrast, the endpoints of TPCs (CT_{min} and CT_{max}) can either be estimated directly using acute exposure to low and high, often ramping, temperatures or indirectly by extrapolation of the estimated TPC function (Deutsch et al., 2008). However, acute CT_{max} measures can be sensitive to the duration and rate of heating as well as acclimation state (Chown et al., 2009; Jørgensen et al., 2019; Kingsolver & Umbanhowar, 2018; Rezende et al., 2014, 2020; Terblanche et al., 2007), and may also vary with ontogenetic stage (Kingsolver & Buckley, 2020), sex, and condition (Chen et al., 2013).

TPCs also have methodological concerns. For example, TPCs can depend on the traits measured (Huey, 1982), levels of biological

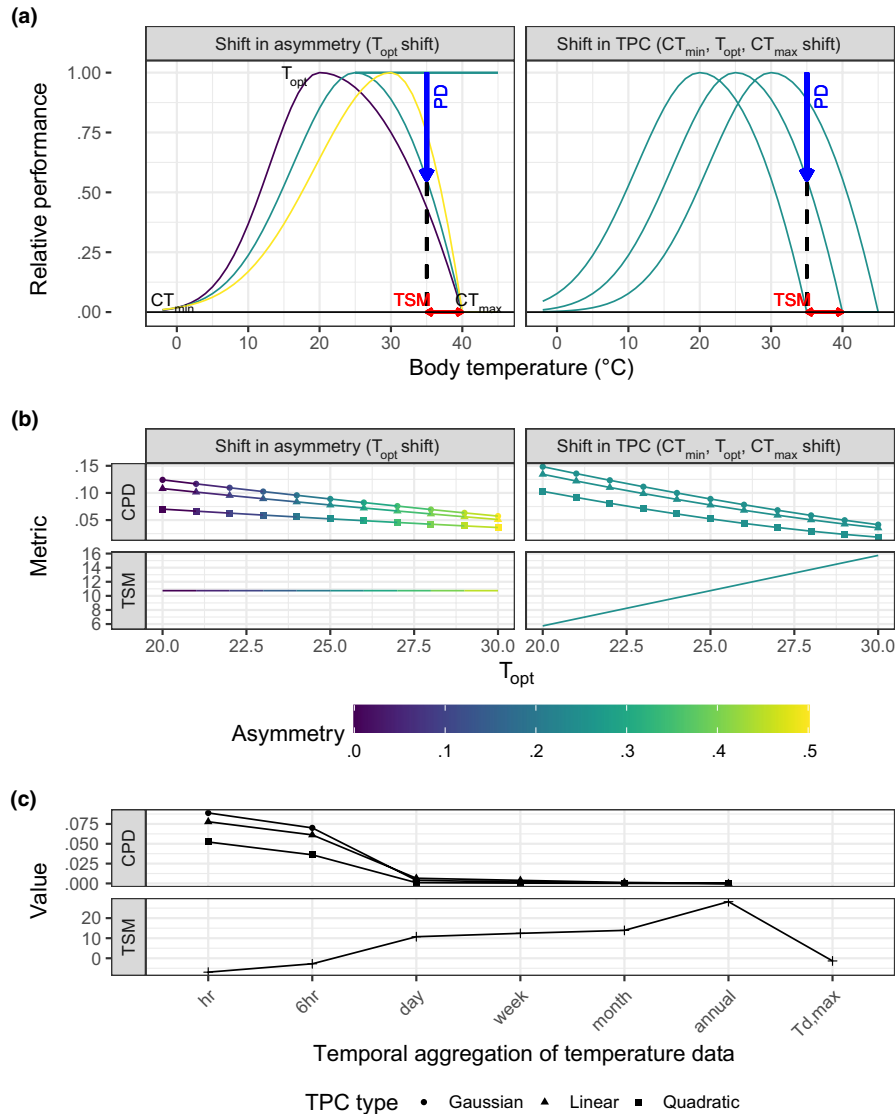


FIGURE 1 (a) Thermal performance curves (TPCs) are summarized by the lower and upper thermal limits for performance [critical thermal minimum (CT_{min}) and maximum (CT_{max}), respectively] and by the temperature of highest performance (thermal optimum, T_{opt}). We examine two extremes in the potential warm adaptation of TPCs: T_{opt} may shift without corresponding shifts in thermal tolerance, thereby shifting TPC asymmetry (left, depicted asymmetries = 0, .25, .5). Alternatively, T_{opt} and thermal tolerance shift in synchrony (right, asymmetry = .25). We quantify two metrics of thermal stress. We define thermal safety margin (TSM, red) as $CT_{max} - T_{day}$, where T_{day} is mean daily temperature. When maximal performance is normalized to 1, the performance detriment (PD) is defined as $1 - P(T_{hour})$ for $T_{hour} > T_{opt}$, where P is performance at hourly temperature T_{hour} . We depict each calculation for the middle curve in each panel. We aggregate the metrics to an annual scale by summing PD and dividing by the potential maximum performance (cumulative performance detriment, CPD) and as the minimum of TSM across days, respectively. We illustrate the metrics for Santa Fe, New Mexico, USA (35°37'3"N, -106°5'8"W, 2,132 m a.s.l.). (b) In both scenarios, CPD (top) declines as T_{opt} increases from 20 to 30 °C. However, TSM (bottom) increases with increasing T_{opt} only if TPC curves shift in synchrony (bottom right). We depict CPD under the assumption that $P(T_{hour})$ is a Gaussian, linear or quadratic decline between T_{opt} and CT_{max} . (c) CPD and TSM estimates vary with temporal resolution of temporally averaged data. We depict temporal averages from hourly to annual data plus $T_{d,max}$, which refers to the monthly average of daily maximum temperature data.

organization (Bozinovic et al., 2020; Rezende & Bozinovic, 2019), the time-scale of measurement and application (Kingsolver & Woods, 2016), and the selected TPC function (Angilletta, 2006; Knies & Kingsolver, 2010). Moreover, estimating T_{opt} is methodologically challenging, given that performance flattens at temperatures near T_{opt} (Huey & Stevenson, 1979); and individual variation is typically ignored (Adolph & Pickering, 2008). Sinclair et al. (2016) address these and related issues in the context of estimating responses to climate change.

We examine whether TPC shape (asymmetry) varies with T_{opt} for diverse taxa and environments and then consider the resulting implications for thermal risk. What are the implications of changes in TPC shape for the onset and rate of performance declines at high temperatures? How do these performance decrements correspond to TSM estimates and to their latitudinal trends? We will conclude that although TSMs have been useful, TPCs better account for how thermal sensitivity determines thermal risks posed by climate change.

2 | METHODS

2.1 | TPC data and comparisons

We used the terms 'thermal optima' and 'Topt' to search the literature for datasets that included all three thermal performance curve parameters (CT_{min} , T_{opt} and CT_{max}) or that permitted estimates of these parameters. Our final dataset includes a total of 384 TPCs (289 species) across multiple taxa. These TPCs vary in the type of performance measured and in the level of biological organization (see Supporting Information Table S1). We refer to five compiled datasets labelled by the taxonomic group and level of performance represented. The ant performance dataset describes foraging activity for 22 genera of ants, where T_{opt} is estimated based on the proportion of ants foraging as a function of ground surface temperature (Guo et al., 2020). CT_{min} and CT_{max} were replaced with minimum and maximum foraging temperatures, respectively, when they exceeded CT_{min} and CT_{max} estimates. The lizard performance dataset describes lizard sprint speed for 77 populations of 66 species, combining data from two studies (Huey et al., 2009; Muñoz et al., 2016). The fish growth dataset describes growth rates for 18 populations in three species of salmonid fish (Elliott & Hurley, 1995; Forseth et al., 2009; Jonsson et al., 2001; Larsson et al., 2005).

The final two datasets focus on the temperature dependence of fitness (r : intrinsic rate of population increase). The insect fitness dataset describes r for 67 populations (61 species) of insects, updating data (Frazier et al., 2006; Huey & Berrigan, 2001) that have been used in numerous analysis of climate change impacts (Deutsch et al., 2008 and subsequent papers) with additional recent observations (Rezende & Bozinovic, 2019). The plankton fitness dataset describes r for a total of 266 populations in 184 species of phytoplankton (Thomas et al., 2012, 2016).

It is important to appreciate the heterogeneity in biological levels and types of performance for interpreting the different patterns in TPCs (see Discussion). Note that performance is a rate for four of the five datasets but is a proportion for the ant performance data. T_{opt} values were estimated by fitting TPC curves to performance measured at multiple constant temperatures. For ants and lizards, CT_{min} and CT_{max} estimates were based on temperature ramping experiments. For the other taxa, CT_{min} and CT_{max} were estimated by extrapolating the fitted TPC curves (Deutsch et al., 2008). The TPC functions and fitting methods differed among the initial publications. The Rezende and Bozinovic (2019) insect dataset used a TPC function with a long left tail that was not designed for estimating CT_{min} . We thus re-estimated CT_{min} , T_{opt} and CT_{max} for this dataset using the fitting algorithm from the plankton dataset (Thomas et al., 2012). Quality control criteria for these TPC estimates are described in Supporting Information Table S1.

We quantified asymmetry using a TPC metric (Martin & Huey, 2008) that varies between -1 for a right-skewed right triangle to $+1$ for a left-skewed right triangle, with 0 indicating a symmetric TPC: $(2 \times T_{opt} - CT_{max} - CT_{min}) / (CT_{max} - CT_{min})$. Results were similar using an alternative TPC asymmetry metric $[(CT_{max} - T_{opt}) / (T_{opt} - CT_{min})]$, (Deutsch et al., 2008).

We used regressions (R Core Team, 2021) to assess how asymmetry, CT_{min} , CT_{max} , and tolerance range ($CT_{max} - CT_{min}$) vary with T_{opt} . We repeated these TPC shape analyses using phylogenetic generalized least squares maximum likelihood regressions to control for changes in shape associated with evolutionary history, independent of responses to thermal environments. We estimated Pagel's lambda using the `gls()` function in the `ape` R package (Paradis & Schliep, 2019). We used an Ant Wiki phylogeny (<https://www.antwiki.org>) for ants, the lizard phylogeny from Pyron et al. (2013), and taxonomic trees created based on the National Center for Biotechnology Information (NCBI) database in the `taxize` R package [functions `classification()` and `class2tree()`, (Chamberlain & Szöcs, 2013)] for insects and phytoplankton. We did not use a phylogenetic analysis for the fish, given that we have data for only three species.

We repeated analyses with a thermodynamic scaling of each TPC parameter to coarsely account for exponential increases in biological rates with increasing temperature [thermodynamic temperature: $\exp(-E/(k \times [T + 273.15]))$], where T is temperature ($^{\circ}\text{C}$), activation energy $E = 0.757$ and k is the Boltzmann constant]. This relationship, which makes the simplifying assumption of equal activation energies, provides an approximate assessment of whether shifts in TPC shape with higher T_{opt} reflect thermodynamics (Payne & Smith, 2017).

We used a principal component (PC) analysis to characterize variation in TPC shape to avoid the need to interpret simultaneous shifts in three parameters (Knies et al., 2009). We estimated PCs (R `princomp` function) using a covariance matrix (R `cor` function) based on the TPC parameters (T_{opt} , CT_{max} , tolerance range = $CT_{max} - CT_{min}$). We fixed the sign (`fix_sign = TRUE`) so that each PC corresponds to an increase in T_{opt} . We used the resultant loadings on the PCs and the scores to calculate new TPC parameters and produce TPCs reflecting variation along the first two PC axes (Knies et al., 2009).

2.2 | Performance detriment estimation

For taxa with location data, we analysed thermal risk metrics using hourly temperature data from the ERA5 reanalysis via the Copernicus Climate Change Service (<https://climate.copernicus.eu/climate-reanalysis>). ERA5 data are generated across a 0.25° latitude \times 0.25° longitude global grid by assimilating observational weather data into a forecast model. We estimated the thermal stress metrics over the year and then averaged across years (2015–2019). Our analyses used ERA5 earth skin surface temperatures (estimated surface temperatures at radiative equilibrium) rather than operative temperatures, and consequently they underestimate thermal stress for ectotherms in open habitats (see Sunday et al., 2014).

We employed several standard TPC shapes, enabling us to determine whether results are robust to selected curve shape. We plotted TPCs using a Gaussian rise in performance, $P(T)$, up to the optimal temperature, T_{opt} , and a quadratic decline to zero performance at CT_{max} .

$$P(T) = \begin{cases} \exp\left\{-\left(\frac{T-T_{\text{opt}}}{2\sigma_p}\right)^2\right\} & \text{for } T \leq T_{\text{opt}} \\ 1 - \left(\frac{T-T_{\text{opt}}}{T_{\text{opt}}-CT_{\text{max}}}\right)^2 & \text{for } T > T_{\text{opt}} \end{cases} \quad (1)$$

where T is hourly temperature and $1/\sigma_p$ represents the exponential increase in performance at lower temperatures [$\sigma_p = (T_{\text{opt}} - CT_{\text{min}})/4$] (Deutsch et al., 2008). We examined sensitivity to TPC shape by assuming this quadratic decline and well as linear [$1 - (T - T_{\text{opt}})/(CT_{\text{max}} - T_{\text{opt}})$] and Gaussian [as above except $\sigma_p = (T_{\text{opt}} - CT_{\text{min}})/3$] declines from T_{opt} to CT_{max} .

To explore TPC-based thermal risk metrics, we defined performance detriment as $PD = 1 - P(T)$ for hours when $T > T_{\text{opt}}$ (thus $PD = 0$ when $T = T_{\text{opt}}$ and $PD = 1$ when $T = CT_{\text{max}}$). We quantified the cumulative performance detriment (CPD) as the annual sum of PD divided by the annual number of time periods (Figure 1). We assumed zero performance for T above CT_{max} and omitted performance detriment corresponding to temperatures below T_{opt} , as our focus here is on high temperature that can result in physiological stress or damage (Somero, 2010). High CPD scores indicate reduced performance.

Next, we evaluated how well TSMs [computed as CT_{max} - annual maximum of mean daily temperature] correspond to CPD. We used hourly data for CPD estimation but average daily temperatures for TSM, which represents an intermediate time-scale used in previous TSM analyses. Comparisons were similar when we estimated TSM daily and examined quantiles (e.g., the 25th percentile of daily TSM), so we used the single warmest day for comparability with previous implementations of TSM.

We then isolated the two contrasting effects that TPC asymmetry has on performance detriments (see Figure 1a). TPCs that are more asymmetric have both (a) higher T_{opt} s (relative to CT_{max}) and (b) steeper performance declines above T_{opt} . We examined the influence of each by creating artificial TPCs that omit each effect by shifting T_{opt} and/or CT_{max} : (a) we assumed the T_{opt} of a completely symmetric TPC [where $T_{\text{opt}} = CT_{\text{min}} + (CT_{\text{max}} - CT_{\text{min}})/2$] but shifted CT_{max} to retain the steep warm side slope; (b) we retained the higher T_{opt} but shifted CT_{max} to correspond to the warm side slope of a symmetric TPC. Additionally, we constructed artificial TPCs using taxon-specific regression relationships between asymmetry and T_{opt} to estimate T_{opt} given observed CT_{min} and CT_{max} . This allowed us to assess the viability of assessing thermal stress using TPCs

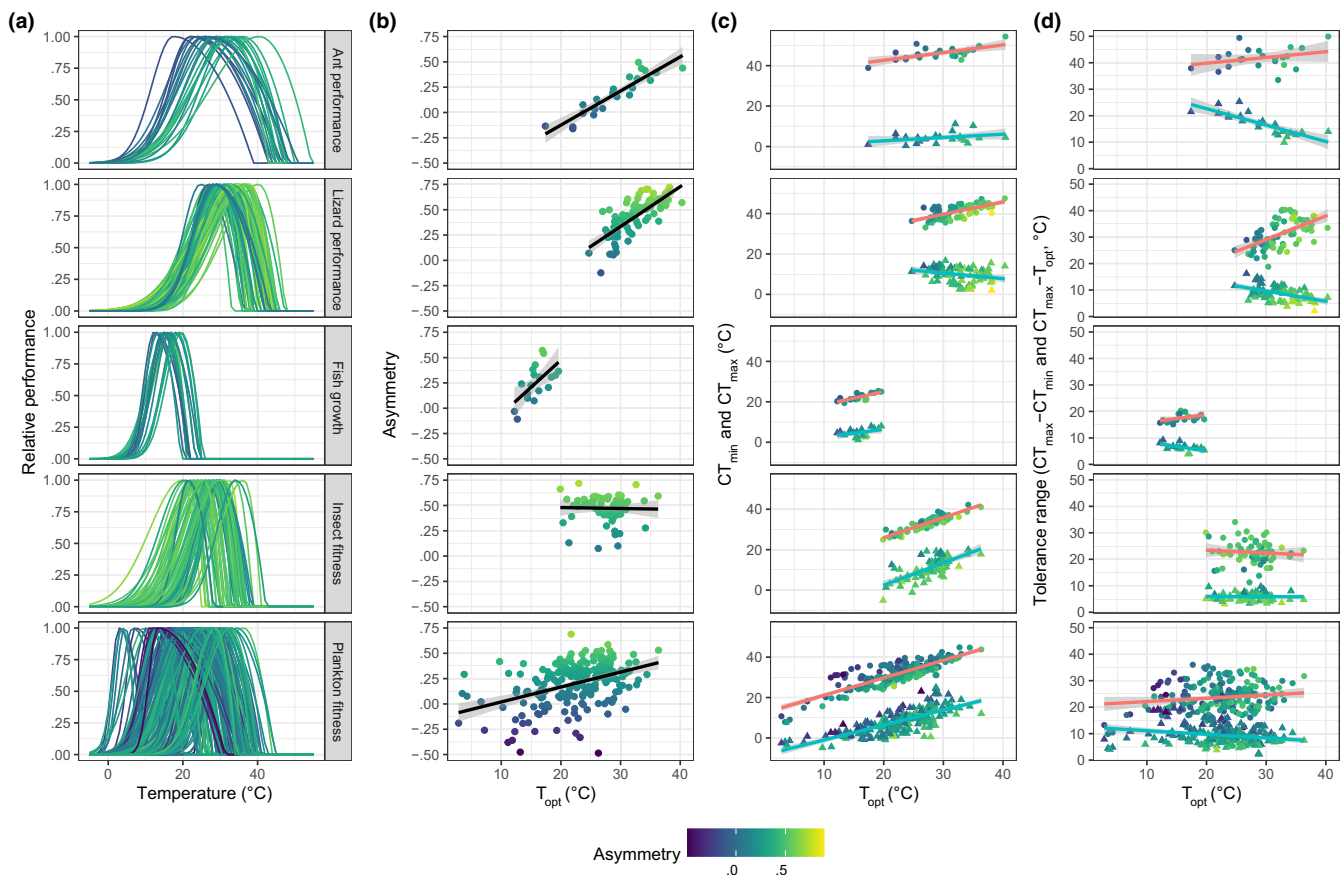


FIGURE 2 (a, b) Thermal performance curve (TPC) asymmetry (0: symmetric, 1: left-skewed right triangle) increases with higher thermal optima, T_{opt} , for most taxonomic groups. (c) As T_{opt} s increase, critical thermal maxima (CT_{max} ; red) increase and critical thermal minima (CT_{min} ; blue) exhibit a variable relationship across taxa. (d) With increasing T_{opt} s, the tolerance ranges ($CT_{\text{max}} - CT_{\text{min}}$, red) remain constant or increase, but the ranges of the warm side of the TPC ($CT_{\text{max}} - T_{\text{opt}}$, blue) decrease (excepting insects).

when only CT_{min} and CT_{max} – but not T_{opt} – had been measured for a particular species.

We used linear mixed effect models from the R package nlme (Pinheiro et al., 2013) to assess how well the thermal risk metrics correspond to CPD. Because changing TPC shape altered CPD qualitatively similarly across taxa (Figure 4b), we combined taxa in a single model for each response variable. We used the dataset name as a random effect to account for taxon and for level of biological organization differences. We used a second degree polynomial of CPD to regress against TSM to account for the observed shape of the relationship (Figure 4a).

2.3 | Implications of asymmetry for thermal risk

What are the implications of changes in TPC asymmetry for thermal risk? We contrast a scenario of a full TPC shifting (change in position, not shape) versus only TPC asymmetry changing (only T_{opt} shifts, not endpoints, Figure 1a). Both scenarios of TPC change are captured by CPD, whereas TSM does not capture the scenarios of altered thermal asymmetry because it only considers the position of CT_{max} (Figure 1b).

The predicted decline in performance detriment from T_{opt} to CT_{max} depends on whether the relationship is Gaussian, linear or quadratic, respectively (Figure 1b). We chose the intermediate scenario of linear decline for further analysis. We assessed the effect of temporal aggregation by examining time-scales ranging from hourly to annual averages along with the monthly average of daily maximum temperature (used by Sunday et al., 2014 to estimate TSM). CPD declines when temporal aggregation causes average temperatures to decline below T_{opt} (Figure 1c, i.e., a single hot hour is diluted when averaged over a day; Denny, 2017). Similarly, TSMs increase as temporal averaging reduces maximum temperatures (Figure 1c). The TSM corresponding to the monthly average of daily maximum temperature is similar to that with hourly temperatures. We selected a daily aggregation for TSM estimation because this intermediate time-scale is relevant to organismal thermal stress.

2.4 | Uncertainty in thermal risk metrics

Many published estimates of thermal limits and optima do not report errors, but we can gauge uncertainty using fish data. Nonlinear regressions of aerobic metabolic scope yielded roughly similar standard errors for TPC parameters across 10 populations (mean = 1.19 and 1.29°C; medians = 1.08 and 0.74°C, respectively, for T_{opt} and CT_{max} ; Payne et al., 2016). CT_{max} estimates from acute assays for nine sockeye salmon populations, including some of the same populations from the TPC data, had lower standard errors (means = 0.05 and 0.13°C; medians = 0.05 and 0.14°C for two different rearing temperatures; Chen et al., 2013). Rearing temperatures and standardization for development time or mass produced more variability in CT_{max} than between-individual variation or measurement issues (Chen et al., 2013).

Assuming a standard error of 1 °C (corresponding to the fish TPC parameters) and a sample size of 20, we explored how the resulting standard deviation (SD) of 4.5 °C for T_{opt} and CT_{max} influences TSM and CPD estimates. We generated 1000 parameter estimates using means of 25 and 40 °C for T_{opt} and CT_{max} , respectively, and a SD of 4.5 °C assuming a normal distribution (R function *rnorm*). We estimated errors using the environmental data in Figure 1. TSM errors were equivalent to CT_{max} errors (SD = 4.5 °C), so the proportional magnitude of the error depends on TSM values. CPD errors were SD = 0.02 and SD = 0.04 or 24 and 51% of CPD estimates when we varied only CT_{max} or T_{opt} plus CT_{max} , respectively.

3 | RESULTS

3.1 | TPC shape and asymmetry

Most species and taxa – except plankton – have left-skewed TPCs and thus positive asymmetry scores (Figure 2a,b). Asymmetry values increase with T_{opt} for most taxa (Table 1). In other words, T_{opt} generally

TABLE 1 Linear regression (top) and phylogenetic generalized least squares (bottom) results examining the slopes of the relationships of thermal traits with thermal optima (T_{opt}) in Figure 1

| | Asymmetry | | | | CT_{min} | | | |
|--------------------|-----------|--------|---------|------------------------|------------|-------|---------|------------------------|
| | Slope | SE | t value | p | Slope | SE | t value | p |
| Ant performance | 0.034 | 0.0033 | 10 | 2.10×10^{-9} | 0.16 | 0.1 | 1.6 | .13 |
| Lizard performance | 0.041 | 0.0041 | 9.9 | 2.90×10^{-15} | -0.28 | 0.12 | -2.4 | .019 |
| Fish growth | 0.054 | 0.017 | 3.2 | .0062 | 0.38 | 0.22 | 1.7 | .1 |
| Insect fitness | -0.00092 | 0.0048 | -0.19 | .85 | 1.1 | 0.14 | 7.9 | 4.40×10^{-11} |
| Plankton fitness | 0.015 | 0.0023 | 6.5 | 4.90×10^{-10} | 0.74 | 0.047 | 16 | 1.40×10^{-36} |
| Phylogenetic | | | | | | | | |
| Ant performance | 0.032 | 0.0032 | 10 | 1.50×10^{-8} | 0.12 | 0.11 | 1.2 | .25 |
| Lizard performance | 0.032 | 0.0042 | 7.6 | 1.50×10^{-9} | 0.36 | 0.14 | 2.5 | .014 |
| Insect fitness | 0.01 | 0.0086 | 1.2 | .24 | 0.7 | 0.23 | 3 | .0044 |
| Plankton fitness | 0.02 | 0.0031 | 6.4 | 7.60×10^{-9} | 0.56 | 0.064 | 8.7 | 1.00×10^{-13} |

Abbreviations: CT_{max} , critical temperature maximum; CT_{min} , critical temperature minimum.

increases more across species than either CT_{\min} or CT_{\max} (i.e., the slopes of CT_{\min} or CT_{\max} against T_{opt} are less than 1). Although CT_{\max} increases with T_{opt} across taxa (Table 1), CT_{\min} can either increase (most taxa), decrease (lizards), or be unrelated (ants) to increasing T_{opt} (Figure 2c). Consequently, the tolerance range (i.e., $CT_{\max} - CT_{\min}$) is unrelated to T_{opt} for most taxa but does increase with T_{opt} for lizards (Figure 2d, Table 1). The range of the warm side of the TPC ($CT_{\max} - T_{\text{opt}}$) generally decreases with increasing T_{opt} (except insects, Figure 2d, Table 1), indicating an increase in asymmetry. These relationships among TPC parameters largely hold when we control for phylogeny (Table 1).

T_{opt} increases more than CT_{\max} for TPCs positioned at warmer temperatures, such that performance starts to decline at relatively high T_b within the tolerance range. However, the higher T_{opt} and associated higher TPC asymmetry result in relatively rapid declines in performance when T_{opt} is exceeded. Steep declines in performance above T_{opt} are expected by thermodynamics (Payne & Smith, 2017) but the shifts in asymmetry persist even on a thermodynamic scale (Supporting Information Figure S1).

We used a PC analysis to characterize the primary axes of TPC changes with increasing T_{opt} (Figure 3). The first PC (accounting for 55–80% of shape variation) reflects increasing asymmetry for TPCs centred at warmer temperatures (Figure 3a). Increased T_{opt} is tightly correlated with increased asymmetry (but note the inverse relationship for lizards, Figure 3a). In the first PC, all three TPC parameters (T_{opt} , CT_{\max} , and tolerance range) increase, but the increase in tolerance range is of lesser magnitude for some taxa than for others (Supporting Information Figure S2). The second PC accounts for 14–43% of TPC variation and is dominated by decreasing tolerance range as T_{opt} increases.

3.2 | Estimates of thermal risk

How does TPC asymmetry alter estimates of thermal risk? Not surprisingly, TSMs are inversely related to CPD, but the relationship

between the metrics depends on TPC asymmetry (Figure 4a, see Supporting Information Figure S3 for relationship for Gaussian and quadratic performance declines). At a given TSM, more symmetric curves (blue points in Figure 4a) correspond to greater CPD, because T_{opt} is exceeded more frequently (ANOVA CPD: $F_{2,295} = 192.4$, $p < .0001$; asymmetry: $F_{1,295} = 22.9$, $p < .0001$; CPD \times asymmetry: $F_{1,295} = 0.9$, $p = .4$). Some high TSMs correspond to zero CPD in current environments, but others correspond to substantial performance detriment.

Next, we isolated the thermal risk implications of the two changes involved in increasing TPC asymmetry (i.e., increases in T_{opt} and a steeper slope of performance decline above T_{opt} , Figure 4b). If shifts in T_{opt} occur without shifts in TPC asymmetry (blue points in Figure 4b), CPD tends to be overestimated (slope +95% confidence interval = $1.23 + 0.33$) because more temperatures exceed the optimum and performance declines initiate earlier. Omitting the steepening of the slope of performance decline (purple points) leads to modest but statistically significant underestimates of CPD (slope +95% confidence interval = 0.73 ± 0.038). TPCs constructed with estimated T_{opt} s (yellow points) reasonably approximate CPD (slope \pm 95% confidence interval = 1.004 ± 0.044).

Increased TPC asymmetry with increased T_{opt} leads to different latitudinal patterns of thermal risk as indexed by TSM or CPD. We focused on latitudinal patterns of thermal risk for plankton, as this large dataset has location information (Figure 5). As in previous TSM analyses (Kingsolver et al., 2013; Pinsky et al., 2019), the lowest TSMs occur at mid-temperate latitudes (Figure 5a). This result differs somewhat from analyses based on temporally coarser and more aggregated environmental data (Deutsch et al., 2008) because daily data capture the greater short-term variability found at temperate latitudes. CPD peaks at a more tropical latitude than the latitude minimizing TSM, consistent with CPD but not TSM capturing how frequently temperatures exceed T_{opt} . Latitudinal patterns are similar whether or not asymmetry is accounted for in the estimate of CPDs (Figure 5b), but CPD divergences due to asymmetry are most pronounced at low latitudes.

| CT_{\max} | | | | Tolerance range ($CT_{\max} - CT_{\min}$) | | | | Warm range ($CT_{\max} - T_{\text{opt}}$) | | | |
|-------------|-------|---------|------------------------|---|-------|---------|-----------------------|---|-------|---------|-----------------------|
| Slope | SE | t value | p | Slope | SE | t value | P | Slope | SE | t value | p |
| 0.38 | 0.1 | 3.8 | .0011 | 0.22 | 0.15 | 1.4 | .18 | -0.62 | 0.1 | -6.2 | 4.90×10^{-6} |
| 0.62 | 0.077 | 8 | 1.30×10^{-11} | 0.89 | 0.14 | 6.5 | 9.70×10^{-9} | -0.38 | 0.077 | -5 | 3.80×10^{-6} |
| 0.66 | 0.14 | 4.7 | .00023 | 0.28 | 0.17 | 1.6 | .13 | -0.34 | 0.14 | -2.5 | .025 |
| 0.99 | 0.054 | 18 | 1.50×10^{-27} | -0.11 | 0.16 | -0.67 | .5 | -0.0059 | 0.054 | -0.11 | .91 |
| 0.86 | 0.039 | 22 | 9.90×10^{-56} | 0.12 | 0.066 | 1.9 | .062 | -0.14 | 0.039 | -3.5 | .00053 |
| 0.42 | 0.11 | 3.8 | .0015 | 0.28 | 0.16 | 1.7 | .11 | -0.58 | 0.11 | -5.3 | 5.80×10^{-5} |
| 0.71 | 0.073 | 9.6 | 2.10×10^{-12} | 0.19 | 0.21 | 0.94 | .35 | -0.29 | 0.073 | -4 | .00023 |
| 0.94 | 0.081 | 12 | 3.20×10^{-14} | 0.11 | 0.26 | 0.42 | .68 | -0.062 | 0.081 | -0.77 | .45 |
| 0.91 | 0.054 | 17 | 2.60×10^{-30} | 0.36 | 0.086 | 4.2 | 6.30×10^{-5} | -0.085 | 0.054 | -1.6 | .12 |

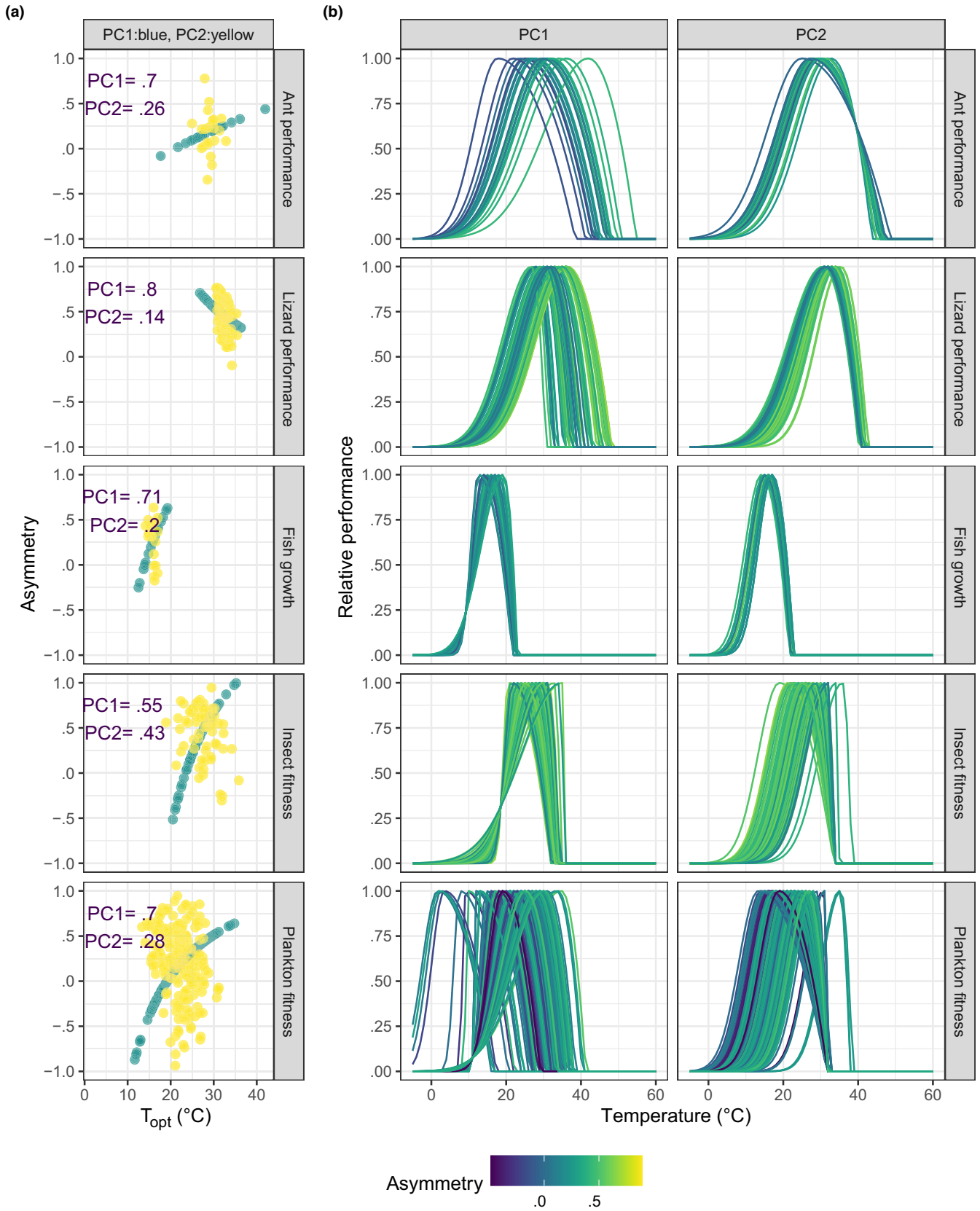


FIGURE 3 We use principal component transformations of the thermal performance curves (TPCs) to assess the primary forms of TPC variation across taxa. The inset numbers indicate the proportion of variance accounted for by the first two principal components. Asymmetry (0: symmetric, 1: left-skewed right triangle) increases (but decreases for lizards) with the thermal optima, T_{opt} , of the first principal component transformation (PC1, blue) but not the second (PC2, yellow). This indicates that asymmetry is the dominant variation (PC1) among TPCs differing in T_{opt} . PC2 relates primarily to breadth (see also Supporting Information Figure S2).

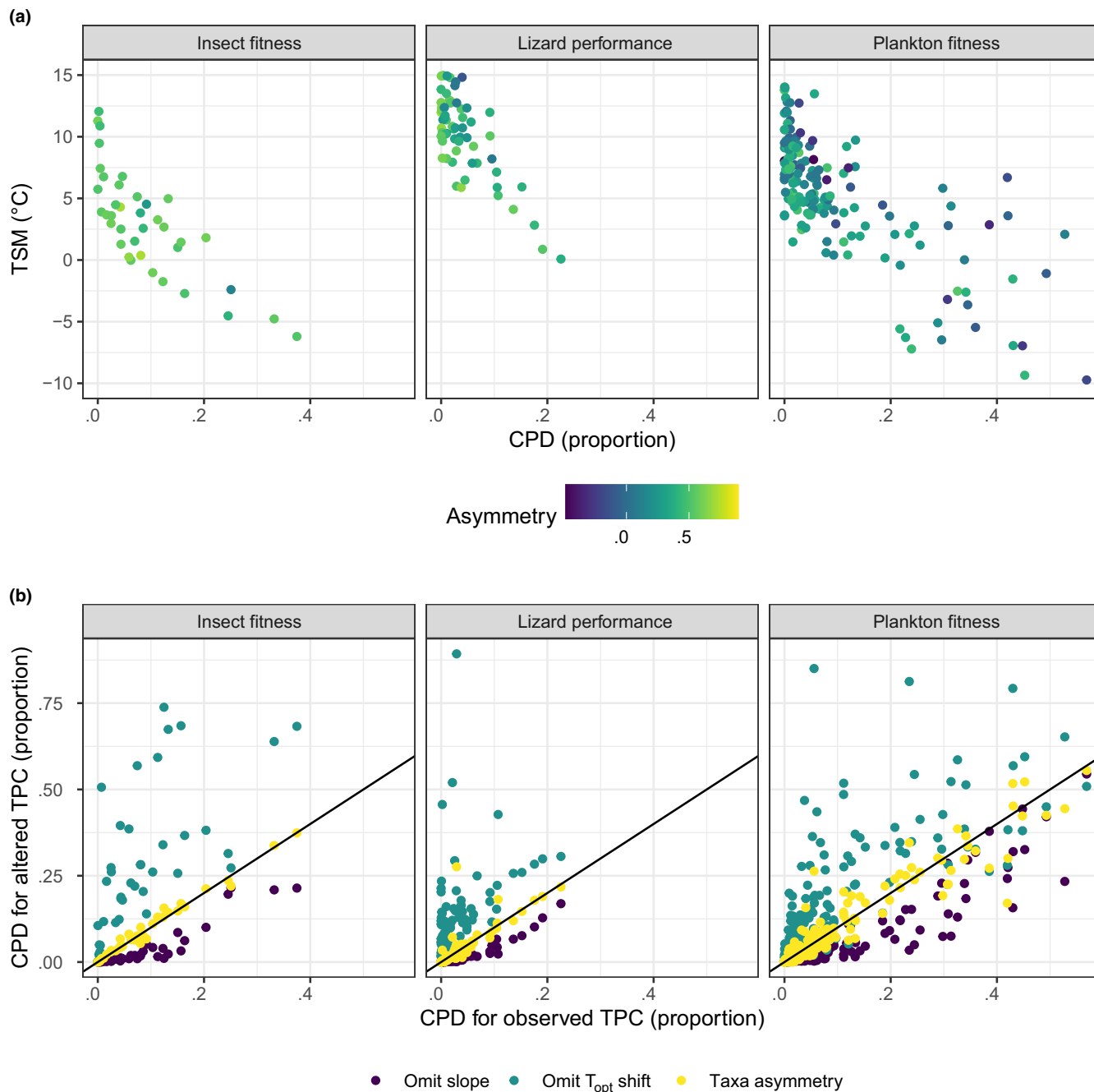


FIGURE 4 (a) Thermal safety margins (TSMs) can differ strikingly from a more comprehensive estimate of thermal risk – cumulative performance detriment (CPD). For a given level of performance detriment, more symmetric thermal performance curves (TPCs; 0: symmetric, 1: left-skewed right triangle) correspond to higher TSMs because the lower thermal optima, T_{opt} s, increase the incidence of thermally stressful temperatures. (b) The T_{opt} and slope shifts associated with asymmetric TPCs differentially impact thermal stress estimates (black line = 1:1). Estimating CPD while omitting the T_{opt} shift (blue points) leads to an overestimate whereas estimating CPD while omitting the steeper slope (purple points) leads to an underestimate. Estimating CPD using an estimate of T_{opt} (yellow points) based on mean asymmetry for the taxon reasonably approximates CPD.

4 | DISCUSSION

Both the temperature that maximizes performance (T_{opt}) and the rate of performance decline at temperatures above T_{opt} are important considerations in understanding organismal responses to climate change and variability. A key pattern uncovered here is that taxa with relatively high T_{opt} have relatively asymmetric TPCs. This

suggests that adaptation to warmer environments can increase sensitivity to changes in body temperatures above T_{opt} and thereby highlights limitations in thermal stress metrics based solely on CT_{max} . Specifically, a 3 °C TSM for a warm-adapted species (high T_{opt} , steep drop at higher temperatures) indicates more thermal risk than a 3 °C TSM for a cold-adapted (low T_{opt}) one. Steeper performance declines for organisms with higher T_{opt} s may augment climate change risks

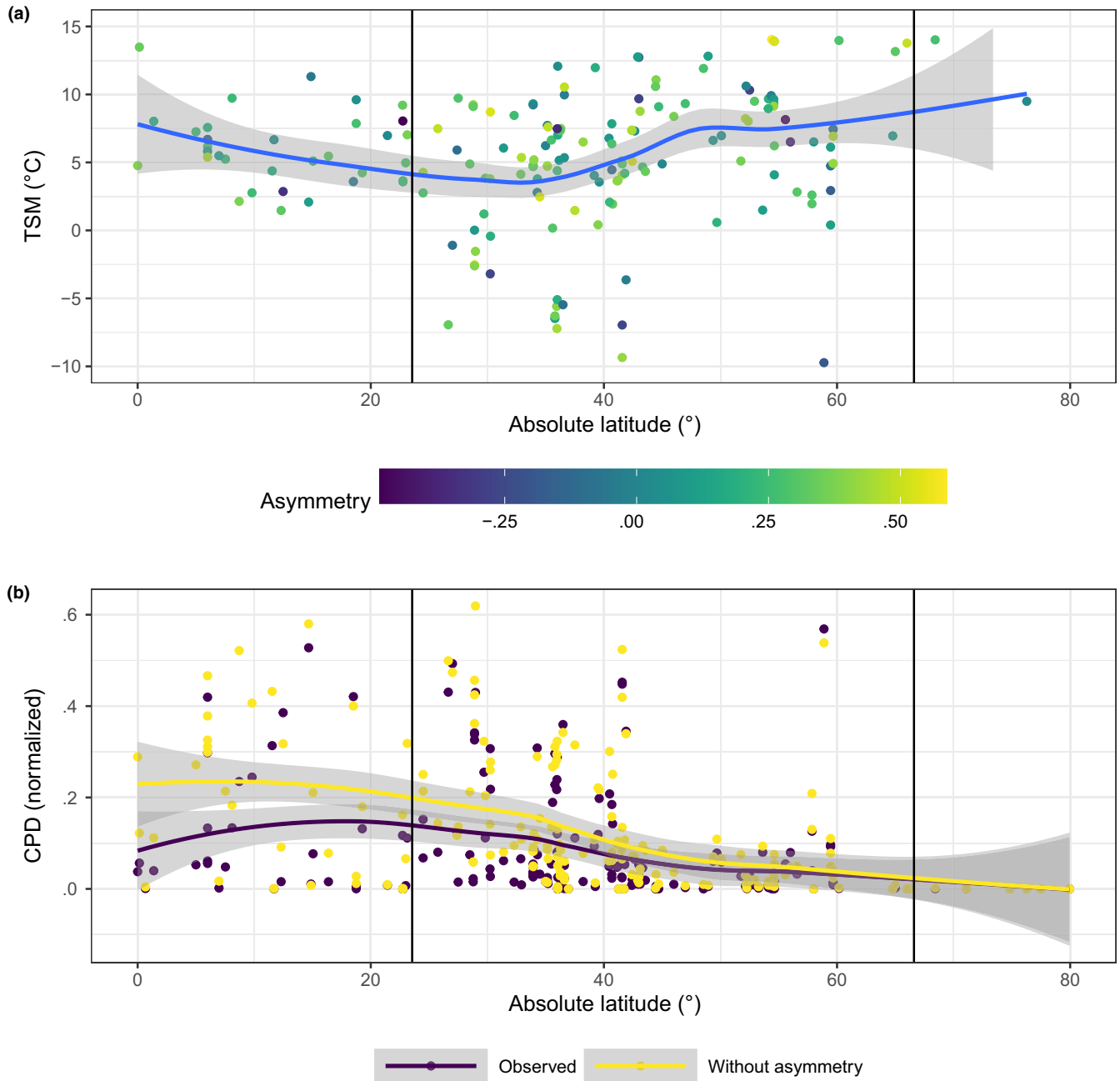


FIGURE 5 Metrics based on performance suggest divergent latitudinal gradients in plankton thermal stress from that for thermal safety margin (TSM), which we define as $CT_{max} - T_{max}$, where CT_{max} is the critical thermal maximum and T_{max} is the annual maximum of daily air temperature. (a) TSM declines at mid-temperate latitudes. Asymmetry (0: symmetric, 1: left-skewed right triangle) influences the latitudinal patterns of thermal stress. (b) Cumulative performance detriment (CPD) peaks at lower latitude than corresponds to the minimum TSM. We depict patterns for both the observed TPC and symmetric TPCs assuming $T_{opt} = CT_{min} + (CT_{max} - CT_{min})/2$ (omitting both the shift in T_{opt} and slope), where T_{opt} is the thermal optimum. The vertical lines delineate the tropical and temperate zones.

for species in warm environments, despite their high T_{opt} s (Huey et al., 2009). Also, TSM estimates differ substantially when temperature data are aggregated over time (Figure 1c) but the time-scale that best describes thermal exposure and sensitivity is rarely clear (Clusella-Trullas et al., 2021; Denny, 2017).

We quantified issues with TSMs and analysed an exemplar thermal risk metric that incorporates both the onset and the rapidity of performance declines at high temperature. A more comprehensive

metric would additionally account for thresholds and responses to thermal history (Marshall & Sinclair, 2015), including the duration of exposure (Jørgensen et al., 2019; Kingsolver & Woods, 2016; Rezende et al., 2014). Moreover, our analysis assumes TPCs are temporally invariant (thus, no acclimation or evolution – although both could be accommodated). Experiments quantifying integrated responses to realistic environmental variability and investigating thresholds will be crucial to refining thermal stress metrics that account for shifting

TPC shape as environments warm (Khelifa et al., 2019; Vázquez et al., 2017).

TPCs can differ substantially across performance traits and levels of organization (Huey, 1982; Kellermann et al., 2019; Rezende & Bozinovic, 2019). Care must be thus taken in choosing appropriate performance metrics, but our analysis suggests that shifts in TPC shape, and thus thermal risk, are rather consistent across performance metrics and taxa. CT_{max} measurement issues (Chown et al., 2009; Kingsolver & Umbanhowar, 2018; Terblanche et al., 2007) may account for some differences in patterns of TPC variation between our analyses and those from prior compilations. Many of the critical thermal limits in our compilation are measured as performance limits in constant conditions (excepting ants and lizards, see Methods) rather than via thermal ramping. Broad interspecific compilations for terrestrial species generally find that CT_{max} is rather independent of latitude, whereas CT_{min} decreases with an increase in latitude (Huey et al., 2009; Sunday et al., 2019). Within taxonomic groups we find that CT_{max} increases with T_{opt} but that the relationship with CT_{min} is variable.

Our compilation additionally detects that tolerance range ($CT_{max} - CT_{min}$) can remain constant or can increase with increasing T_{opt} (Figure 2d). Tolerance range tends to increase with latitude (Sunday et al., 2019), but tolerance range can have limited biological significance to warming scenarios if TPCs have long left tails. Tolerance range can also depend on habitat choice, as is the case for lizards, which have greater thermal tolerance ranges in more temperate areas that have cooler air temperatures but greater exposure to solar radiation in more open habitats (Huey et al., 2009). The observed shifts in thermal sensitivity are consistent with 'hotter is broader' observations for bacteriophages (Knies et al., 2009; see also related 'hotter is better', e.g., Angilletta et al., 2010). TPCs tend to narrow at higher levels of biological organization (e.g., photosynthesis to performance to fitness; Bozinovic et al., 2020; Rezende & Bozinovic, 2019).

Why do species and populations with higher T_{opt} s tend to have greater TPC asymmetry? Three factors are likely involved. First, in many taxa, lower limits vary more than do upper thermal limits (Sunday et al., 2010, 2019). For example, in most ectothermic Metazoa and plants, CT_{min} decreases with increasing latitude, whereas CT_{max} does not (Sunday et al., 2019). These shifts can lead to greater asymmetry and steeper performance declines above T_{opt} with latitude. Similar patterns are seen along latitudinal clines among populations within insect species (Chown et al., 2002). This can result from rare, hot extremes selecting for increased CT_{max} even in cool locations. Also, many organisms use behavioural thermoregulation to buffer hot temperatures (Kearney et al., 2009) more effectively than cold temperatures (Munoz et al., 2014). In contrast, the coldest temperatures tend to exhibit stronger latitudinal patterns (Sunday et al., 2019). Additionally, different physiological mechanisms underlie cold and warm stress (Angilletta, 2009), which likely contributes to CT_{min} and CT_{max} differentially shifting with T_{opt} .

Second, species with higher optimal temperatures can have higher maximal performances [the 'hotter is better' hypothesis (Frazier et al., 2006)]. This pattern has been reported in a number of studies

(Angilletta et al., 2010; Huey & Kingsolver, 1989; Kingsolver, 2009). Warmer environments, in which the frequency of high temperatures is elevated, will select for evolutionary increases in T_{opt} . But if CT_{max} is relatively evolutionarily constrained (Hoffmann et al., 2013), this will yield a positive association between T_{opt} and asymmetry. Third, asymmetry may also result from thermodynamics because physiological rates shift more rapidly at high temperatures, which can reduce the temperature range between T_{opt} and CT_{max} (Payne & Smith, 2017).

In conclusion, we appreciate that TSMs have proven useful to analyses of thermal risk. However, such CT_{max} -based analyses miss key components of thermal risk, and we argue that these can be better assessed using TPCs. Knowing that performance drops by 10% is more ecologically relevant than saying that TSM is only 4 °C, especially given that the rate of performance decline is not a constant but is steeper for populations with higher T_{opt} . Many populations are already experiencing performance declines associated with temperatures above T_{opt} . We argue that estimating ongoing or projected performance loss is more relevant to anticipating the thermal risk of climate change than is the coarse proxy of how close populations are to experiencing a single thermal extreme that exceeds CT_{max} (see also Parratt et al., 2021). The reliance of TSM on a single thermal extreme may overemphasize thermal risk at temperate latitudes, where temperature variability may result in pronounced extremes, relative to organisms more frequently experiencing performance loss at lower latitudes.

Unfortunately, TPCs or T_{opt} have been estimated much less often than has CT_{max} , potentially limiting the global feasibility of TPC thermal risk metrics. Our analysis suggests the importance of collecting additional T_{opt} data but also demonstrates that T_{opt} can be reasonably approximated using taxon-specific relationships between T_{opt} and asymmetry. We conclude that TPC asymmetry should be accounted for in assessing the onset and severity of thermal risk.

AUTHOR CONTRIBUTIONS

L.B.B. and R.B.H. conceptualized the study. L.B.B. gathered data, conducted the analyses, and wrote the first draft of the manuscript. L.B.B., R.B.H., J.G.K. designed and interpreted the work and revised the manuscript. All authors edited the manuscript.

ACKNOWLEDGMENTS

We thank A. Algar, A. Cannistra, C. Deutsch, and the referees for comments and discussions that improved the manuscript. This work was supported by the National Science Foundation [DBI-1349865 and DEB-1951356 to L.B.B.].

DATA AVAILABILITY STATEMENT

All biological data are available in Dryad: <https://doi.org/10.5061/dryad.vhhmqnqw>. The Methods indicate the source of the climate data. Code for analysis and figures along with data are available at <https://github.com/HuckleyLab/ThermalStress>.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Buckley, L. B., Huey, R. B., & Kingsolver, J. G. (2022). Asymmetry of thermal sensitivity and the thermal risk of climate change. *Global Ecology and Biogeography*, 00, 1–14. <https://doi.org/10.1111/geb.13570>