

RESEARCH REVIEW

Temperature extremes: geographic patterns, recent changes, and implications for organismal vulnerabilities

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*Department of Biology, University of Washington, Seattle, WA 98195-1800, USA***Abstract**

Extreme temperatures can injure or kill organisms and can drive evolutionary patterns. Many indices of extremes have been proposed, but few attempts have been made to establish geographic patterns of extremes and to evaluate whether they align with geographic patterns in biological vulnerability and diversity. To examine these issues, we adopt the CLIMDEX indices of thermal extremes. We compute scores for each index on a geographic grid during a baseline period (1961–1990) and separately for the recent period (1991–2010). Heat extremes (temperatures above the 90th percentile during the baseline period) have become substantially more common during the recent period, particularly in the tropics. Importantly, the various indices show weak geographic concordance, implying that organisms in different regions will face different forms of thermal stress. The magnitude of recent shifts in indices is largely uncorrelated with baseline scores in those indices, suggesting that organisms are likely to face novel thermal stresses. Organismal tolerances correlate roughly with absolute metrics (mainly for cold), but poorly with metrics defined relative to local conditions. Regions with high extreme scores do not correlate closely with regions with high species diversity, human population density, or agricultural production. Even though frequency and intensity of extreme temperature events have – and are likely to have – major impacts on organisms, the impacts are likely to be geographically and taxonomically idiosyncratic and difficult to predict.

Keywords: climate change, CLIMDEX, diversity, extreme events, heat, thermal stress, thermal tolerance

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Introduction

Monitoring and understanding the organismal impacts of recent and projected climate change have become a top priority for pure and applied ecology. Understanding of how biodiversity patterns arose (Fine, 2015) and how they may be altered by climate change (Thompson *et al.*, 2013; Lawson *et al.*, 2015) has relied primarily on mean temperatures (Garcia *et al.*, 2014). However, measures of climate variability or of acute thermal stress events may be equally or more relevant (Bumpus, 1899; Smith, 2011; Reyer *et al.*, 2013). From an ecological perspective, such events can trigger stress or physiological damage, reduce reproduction, or cause death (Hoffmann, 2010; Sinervo *et al.*, 2010; Somero, 2010; Reyer *et al.*, 2013; Ma *et al.*, 2015). In fact, population and biogeographic shifts are sometimes driven more by periodic, extreme events than by gradual shifts (Harley, 2011; Wetthey *et al.*, 2011). From an evolutionary perspective, extreme events may serve as major selective factors that influence the evolution of physiological capacities and resistances (Bumpus, 1899; Gutschick &

BassiriRad, 2003; Denny *et al.*, 2009; Somero, 2010; Hoffmann *et al.*, 2013). This highlights the need to filter climate changes through the lens of an organism's physiological sensitivities (Kingsolver & Watt, 1983).

Changes in the mean and variance of climatic drivers interactively affect biological dynamics (Benedetti-Cecchi *et al.*, 2006): Warming in a cool environment may increase fitness, but the associated increase in thermal variance – and thus in stressful heat events – may decrease fitness (Vasseur *et al.*, 2014). Therefore, selection on thermal tolerance can be complex, with short-term variability driving selection in directions differing from the long-term trend (Kingsolver & Buckley, 2015).

Our ability to evaluate the ecological and evolutionary consequences of climate shifts and extremes requires information on several factors. What are the performance and fitness consequences of acute and chronic thermal conditions (Angilletta, 2009)? To what extent are various organisms able to evade thermal stress through behavior (Kearney *et al.*, 2009; Sunday *et al.*, 2014) or acclimation (Somero, 2010; Gunderson & Stillman, 2015; Seebacher *et al.*, 2015)? Obtaining such insights can be challenging because extreme climate events are often rare (Denny *et al.*, 2009).

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The biological consequences of climate variability and extreme events are crucial to consider given that the incidence of climate extremes during climate change has and will likely shift more rapidly than mean temperatures (Easterling *et al.*, 2000; Hansen *et al.*, 2012; Diffenbaugh & Field, 2013; Field *et al.*, 2014). Even minor warming of temperature distributions can drive dramatic increases in the incidence of extreme events (Ma *et al.*, 2015). For example, the median daily average temperature at equatorial latitudes (0–10°N) shifted only 0.4 °C between 1961 and 1980 and 1991 and 2010, but this relatively small shift has increased the incidence of warm events by 76.3% (i.e., temperatures exceeding the 90th percentile of the baseline period) and decreased the incidence of cold events by 8.6% (Fig. 1a).

Recent increases in warm extremes have been especially dramatic in the tropics (Fig. 1b) due to the region's narrow temperature distributions. Recent decreases in the incidence of cold extremes are less substantial, but are pronounced in both the tropics and high northern latitudes. The shift toward warm extremes becoming more common and cold extremes becoming less common is also pronounced at high northern latitudes, despite broad temperature distributions there, due primarily to the relatively greater warming there (Fig. 1b). Even so, unprecedented climate extremes are projected to appear initially in the tropics due to its climate stability (Mora *et al.*, 2013). In

fact, normal growing season temperatures are projected to exceed baseline heat extremes in tropical areas and to match or exceed current records of extreme high temperature in temperate areas by the end of the 21st century (Battisti & Naylor, 2009).

Global maps exist for the incidence of various extremes over time (Hansen *et al.*, 2012; Diffenbaugh & Field, 2013; Sillmann *et al.*, 2013), but maps specifically of latitudinal gradients in extremes are sparse. Latitudinal gradients are a powerful tool for examining biodiversity patterns and organismal vulnerability to climate change because climatic gradients including mean temperatures and variability vary latitudinally with evolutionary consequences (Janzen, 1967; Ghalambor *et al.*, 2006; Tewksbury *et al.*, 2008). Consequently, we document global and latitudinal patterns in several indices of thermal extremes and examine the magnitude, direction, and correlations of their shifts during recent climate warming. The latitudinal gradients address the significance of extreme events in shaping the thermal sensitivity of organisms and enable evaluating geographic concordance – or lack thereof – between thermal extremes and the species diversity of several taxa, human population density, and agricultural production. We take advantage of the CLIMDEX (Datasets for Indices of Climate Extremes) indices developed by the Expert Team (ET) on Climate Change Detection and Indices (ETCCDI) (Zhang *et al.*, 2011).

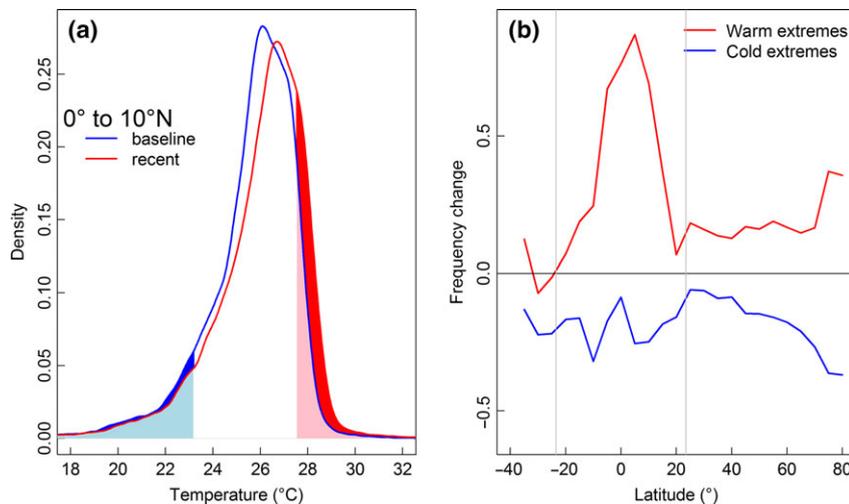


Fig. 1 (a) Average daily temperatures have increased in their mean and variance between the baseline (1961–1980) period and the recent (1991–2010) period at equatorial latitudes (0°–10°N). We abbreviate the baseline period here to maintain a constant duration for comparison. The proportion of days with temperatures in the lower 10% of the baseline temperatures has decreased (blue shading) whereas the proportion of days with temperatures in the upper 10% of the baseline temperatures has increased (red shading) substantially. (b) We next analyze shifts in the temperature distribution within 5° latitudinal bands. The frequency of days with temperatures in the upper (red) 10% of the baseline temperatures has increased dramatically in the tropics due to the narrow temperature distributions there. The frequency of days with cold extremes (blue) has decreased across latitudes.

Materials and methods

Climate data

We downloaded CLIMDEX indices for terrestrial temperatures (Table 1) from the Canadian Centre for Climate Modelling and Analysis (<http://www.cccma.ec.gc.ca/data/climdex/>). We used metrics defined by CLIMDEX, with the exception that we converted their warm and cold spell duration indices (WSDI and CSDI, respectively) from a count of the average number of days each year warmer than the 90th percentile or colder than the 10th percentile to the percentage of years with a warm or cold spell [warm spell incidence (WSI) and cold spell incidence (CSI), respectively]. CLIMDEX scores vary somewhat based on the reanalysis or observational product used (Sillmann *et al.*, 2013), but should be adequate for our application. We selected CLIMDEX indices based on daily data from the National Centers for Environmental Prediction (NCEP) global reanalysis 1 (Kalnay *et al.*, 1996) and estimated over a 192×94 Gaussian grid. That reanalysis performed data assimilation by combining observational data with a weather forecast model. We used the raw NCEP data in our analyses of daily mean temperatures (<http://www.esrl.noaa.gov/psd/data/gridded/data.xncep.reanalysis.derived.surface.html>).

Several indices (e.g., TXx – annual maximum temperature) are absolute measures of extreme temperatures. Others are defined relative to the distribution of temperatures within the grid cell over a baseline period (e.g., WSI – percentage of years with warm spells). [Thus, WSI for a given cell could be high, even though the TXx of that cell is low globally.] Absolute metrics are most biologically relevant if thermal sensitivities (temperature tolerance) of species are similar and independent of geography: In this case, a given high temperature (TXx) would be equally extreme to all organisms everywhere. Relative metrics are most biologically relevant if organisms are perfectly adapted to their local thermal environment. Of course, neither case is biologically valid, but we can investigate whether the two types of indices are geographically congruent.

The baseline period used in CLIMDEX indices is 1961–1990 (the recommended 30-year ‘normal’ baseline period, c.f. World Meteorological Organization). We averaged index scores across years within each grid cell for both the baseline period and the recent period of 1991–2010. For the baseline period, we illustrate geographic patterns across the globe (e.g., Fig. 2a). To depict latitudinal patterns in the baseline, we computed the average index value across all the grid cells at a given latitude (Fig. 2b). To depict temporal shifts in index scores (Δ), we computed the difference between the recent score and the baseline score for each grid cell and plotted the average for each latitude against latitude (Fig. 2c). We arbitrarily restricted the gradient to latitudes with land spanning at least 10 grid cells, thus excluding much of the Southern Hemisphere.

To explore patterns of correlations among indices, we computed correlation coefficients (R function ‘corrplot’) among scores for several sets of indices, but ignored spatial autocorrelations. First, we examined correlations among all pairs of

Table 1 The CLIMDEX (Datasets for Indices of Climate Extremes, <http://www.climdex.org/>) indices consist of absolute or relative metrics based on daily maximum (TX) and minimum (TN) temperatures. Absolute metrics are most biologically relevant absent geographic variation in thermal sensitivity. Relative metrics are most biologically relevant if organisms are perfectly adapted to their local thermal environment. Growing season length (GSL) is the number of days between spans of six consecutive days with daily average (\bar{T}) temperatures warmer than 5 °C (spring) and \bar{T} colder than 5 °C (autumn). Note that only the change from the baseline to recent period is informative for TX90p and TN10p

		Unit	Definition
Absolute metrics			
TXx	Annual maximum temperature	°C	Annual maximum of daily TX
TNn	Annual minimum temperature	°C	Annual minimum of daily TN
GSL	Growing season length	days	
DTR	Diurnal temperature range	°C	Mean of daily TX–TN
Relative metrics			
WSI	Warm spell incidence	%	% Years with ≥ 6 consecutive days when TX > TX90
CSI	Cold spell incidence	%	% Years with ≥ 6 consecutive nights when TN < TN10
TX90p	Warm days	%	% Days when TX > TX90
TN10p	Cold nights	%	% Nights when TN < TN10

indices within the baseline period (Fig. 5a, above diagonal): These indicate whether each pair of indices showed congruent geographic patterns during the baseline. Second, we computed correlations in the magnitude and direction of recent shifts of each pair of indices (Fig. 5a, below diagonal): These indicate whether each pair of indices shows congruent shifts from baseline to recent. Third, we computed correlations between baseline values of a given index with the shift in each index (within grid cells, Fig. 5b): These indicate whether the magnitude and direction of recent shifts are correlated with the value of that index during the baseline. Thus, are recent shifts relatively large in ‘hot’ spots?

The indices are calculated based on air temperature near the ground surface. Air temperature is often a poor proxy of body temperatures because the environmental heat load on an organism depends on radiation, convection, conduction, evaporation, and metabolism (Porter *et al.*, 1973; Bakken, 1992). Although solar radiation can be a major determinant of thermal stress (Kearney *et al.*, 2009; Sunday *et al.*, 2014), using air temperature-based indices provides a starting point for analyses of thermal extremes and avoids the need to make taxon-specific assumptions about exposure to solar radiation.

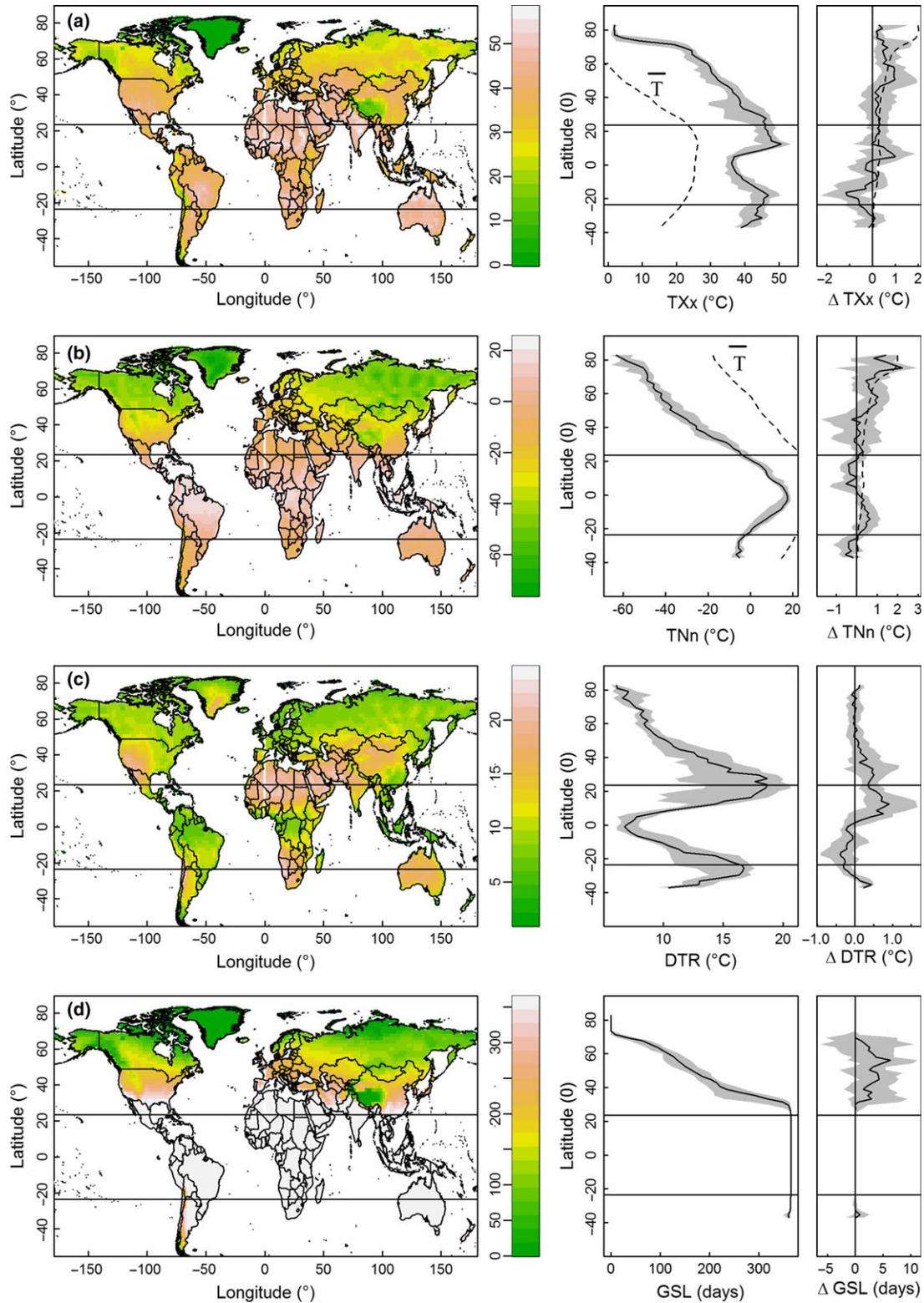


Fig. 2 Geographic patterns differ among the absolute metrics of (a) annual maximum temperature (TXx), (b) annual minimum temperature (TNn), (c) diurnal temperature range (DTR), and (d) growing season length (GSL). Latitudinal gradients show medians of the metrics (solid line) along with 25th and 75th percentiles (shading) during the baseline period (1961–1990). For TXx and TNn, we additionally show mean temperatures (\bar{T} , dashed lines). The right column depicts the shift in the latitudinal gradients between the baseline and recent (1991–2010) periods.

Additionally, air temperatures approximate the body temperatures of organisms seeking shade or retreats in hot conditions.

Thermal tolerance data

For ectotherms, thermal tolerance was estimated as either critical thermal limits or lethal limits. Critical thermal limits are usually defined as the lower (CT_{min}) or upper (CT_{max}) ramping temperature at which motor function is lost. Lethal temperatures reflect the fixed temperatures at which a given percentage (usually 50%) of individuals survive a predetermined duration of exposure (usually 24 h). We used two databases. One was for insects only and included 378 records of upper thermal limits and 358 records of lower thermal limits (Hoffmann *et al.*, 2013). The second was for squamate reptiles (lizards and snakes) plus amphibians (frogs and salamanders) and included 180 records of upper thermal limits and 150 records of lower thermal limits (Sunday *et al.*, 2014). For the second dataset, we restricted our analysis to species from below 2000 m in elevation to avoid confounding latitudinal and elevational clines. We did not correct for acclimation as this should not qualitatively alter the latitudinal pattern (Sunday *et al.*, 2014; Gunderson & Stillman, 2015). Similarly, we ignored methodology (e.g., exposure time), which can sometimes alter CT estimates (Terblanche *et al.*, 2007) and geographic patterns (Rezende *et al.*, 2014; Castañeda *et al.*, 2015).

For endotherms, we analyzed latitudinal patterns of the thermoneutral zone (TNZ), which is the range of ambient temperatures within which an endotherm is able to maintain its body temperature without increasing its metabolic rate above a basal rate (McNab, 2012). This zone is an endothermal parallel to the 'thermal performance breadth' of ectotherms (Huey *et al.*, 2012). However, endotherms, unlike ectotherms, can maintain body temperatures and performance at temperatures below the TNZ by increasing energy expenditure (Gavrilov, 2014). The database included the lower (T_{lc}) and upper (T_{uc}) critical temperatures bounding the TNZ for 161 bird species and for 297 mammal species (Khaliq *et al.*, 2014). We caution that this database contains some TNZ values based on small sample sizes and that some of the upper critical temperature values are minimum estimates (C. Hof, personal communication). TNZ and T_{lc} are affected by body mass (McNab, 2012; Khaliq *et al.*, 2014; Fristoe *et al.*, 2015), but we ignore these effects here.

Species diversity and agricultural data

To help elucidate whether many species exist in regions where climate extremes occur, we computed latitudinal patterns of terrestrial species richness of several animal taxa, of human population density, and of agricultural production. We estimated latitudinal patterns for amphibians, birds, and mammals by counting the range polygons intersecting grid cells. For amphibians, we used the Global Amphibian Assessment range maps (IUCN *et al.*, 2006) and calculated richness patterns using equal area (3091 km², approximately 0.5° × 0.5° at the equator) grid cells (Buckley & Jetz, 2007). For terrestrial reptiles exclusive of turtles, we used range maps compiled by

the IUCN Red List Spatial Data (<http://www.iucnredlist.org/>). Species richness was calculated over 1° × 1° grid cells in the WGS84 projection and is partial because range maps are only available for 3830 of approximately 9500 species. We ran a separate analysis for terrestrial turtles, for which a complete dataset from the Emy System is available. We used latitudinal data (maximum, minimum) of each turtle species and assumed each species occurred at all latitudes within those bounds (<http://emys.geo.orst.edu>).

For birds, we used range maps compiled by BirdLife International and NatureServe (BirdLife International and NatureServe, 2014). Species richness [R package 'letsR' (Vilela & Villalobos, 2015)] was calculated over 1° latitudinal bands in the WGS84 projection. For mammals, we used the database from Grenyer *et al.* (2006) and calculated richness patterns across equal area (110 km, approximately 1° at the equator) latitudinal bands. For ants, we used the compilation of the Global Ant Bioinformatics database by Diamond *et al.* (2012) and plotted the number of ant genera within 10° bins.

Estimates of total human population size were compiled over a 30-arc second (~1 km) grid for the year 2000 [Global Rural-Urban Mapping Project (GRUMP) v1, <http://sedac.ciesin.columbia.edu/data/collection/grump-v1>]. To estimate regions of agricultural productivity, we used gridded estimates of the percent of 5 min (~10 km) grid cells covered by crops in the year 2000 (Ramankutty *et al.*, 2008). We estimated agricultural yield (tons per hectare) in 2000 by summing yield estimates for major crops (maize, rice, soy, and wheat) over 5 min (~10 km) grid cells (Ramankutty *et al.*, 2008). Data were retrieved from EarthStat (<http://www.earthstat.org>).

Results and Discussion

We present and discuss geographic and latitudinal patterns for the various indices of temperature extremes. Some patterns (e.g., for minimum temperatures) are of course well known, but we include them here to provide a comprehensive assessment of the biological impacts of extremes. Also, we try to relate how and why each index might be stressful to organisms, but will argue that the organismal effects of these extremes are neither simple nor consistent.

Absolute indices (mean, maximum, and minimum temperatures)

Much of the literature of climate change biology concerns latitudinal patterns of mean annual temperatures (\bar{T}): \bar{T} is relatively flat in the tropics and then declines steadily toward the poles (dashed line in Fig. 2). \bar{T} has increased since the baseline period at most latitudes, but especially above ~60° latitude in the Northern Hemisphere (dashed line in Fig. 2) (Field *et al.*, 2014; Wang & Dillon, 2014).

High TXx and low TNn will stress organisms (at least those unable to use behavior to evade these extremes)

when those temperatures approach or exceed the organism's thermal tolerances or reduce its energy balance (Sinervo *et al.*, 2010). Although increases in TNn can reduce acute cold stress, warmer winter temperatures can paradoxically increase chronic stress by increasing metabolism and depleting energy reserves for ectotherms (Zani, 2008; Williams *et al.*, 2014). Thus, consequences of shifts in TXx or TNn are unlikely to be universal.

Latitudinal gradients in TXx, \bar{T} , and TNn are generally similar in direction but not in magnitude (Fig. 2). Mean temperatures decline on average ($\pm 95\%$ CI) 0.69 ± 0.2 °C with a 1.0° movement northward within the temperate zone. However, maximum temperatures decline somewhat less steeply (0.50 ± 0.03 °C), whereas minimum temperatures decline much more steeply (1.05 ± 0.08 °C, Fig. 2). Consequently, the range of temperatures between TXx and TNn (thus the maximum annual temperature range) is narrowest by far at the equator and then broadens progressively with latitude (not shown). A pronounced dip in TXx near the equator – but not mean temperature – accentuates this relationship (Fig. 2a).

The change in TXx from the baseline to the recent period is slightly positive north of the equator (Fig. 2a), does not mirror the large shift in mean temperature at high northern latitudes, and is slightly negative near the Tropic of Capricorn. TNn has become decidedly warmer since the baseline period, but only above about 45°N (Fig. 2b).

Large diurnal temperature range (DTR) is potentially stressful, because an exposed ectotherm would need to deal daily with large shifts in body temperature (Wang & Dillon, 2014). On the other hand, organisms exposed to high DTR may evolve compensating resistance (Navas, 1997). The daily temperature range (DTR) is narrowest at the equator, maximal near the Tropics of Cancer and of Capricorn and then declines toward the poles (Fig. 2c) (Wang & Dillon, 2014; their Figs 1f and S7). DTR has increased from the baseline to the recent from the equator to about 45°N in our dataset (Fig. 2c), but relatively little elsewhere. In contrast, Wang & Dillon (2014, Fig. 2) found the increase (baseline 1975–1990, to the recent decade) was greatest in northern polar region, less in the temperate zone, and least in the tropics. These differences may reflect use of station data (Wang & Dillon, 2014) vs. gridded data (herein).

Growing season length (GSL, defined in Table 1) provides a general index of biological opportunity and closely reflects latitudinal trends in thermal seasonality. Short GSL is potentially stressful because primary productivity is related to GSL and because short GSL requires organisms to compress activities (foraging, growth, reproduction) into short periods, as well as to

accumulate resources to survive a long winter. On the other hand, a long GSL can expose organisms at low latitudes to predators for longer periods, such that over-winter mortality there can be elevated relative to that at high latitudes (Wilson & Cooke, 2004). GSL is thermally limited only outside the tropics and shortens rapidly by 7.4 ± 0.6 days per ° latitude north of the Tropic of Cancer (Fig. 2d). GSL remains long throughout the Southern Hemisphere, probably reflecting ocean buffering there. Thus, at mid-to-high latitudes, GSL – and thus opportunities for growth and reproduction – are most constrained in the Northern Hemisphere. GSL has lengthened modestly at midlatitudes in the Northern Hemisphere since the baseline time period, reflecting recent warming in spring and autumn (Linderholm, 2006).

Relative indices

Warm spell incidence and CSI index the percentage of years during the recent period that have at least six consecutive days with maximum (minimum) temperatures that exceed the 90th percentile (or are below the 10th percentile) of the baseline period for that grid cell. Superficially, a WSI (or CSI) of 50% might seem more stressful than one of 5%, but that might not be the case: If frequent heat (cold) waves select for high heat (cold) tolerance, then organisms living in sites where heat (cold) waves are rare might actually experience more stress from a single heat (cold) wave than would organisms routinely subjected to heat waves (Navas, 1997; Hoffmann, 2010). Similarly, a high WSI might not be stressful to an organism that has a high thermal tolerance.

Warm spell incidence is relatively high (42%) in the northern temperate and arctic regions, low in most tropical regions (10% at the equator), and low in the Southern Hemisphere (Fig. 3a). WSI has increased substantially in recent decades at all latitudes, especially north of the equator (Fig. 3), reflecting the warming driven increase in the number of days above the baseline threshold (Fig. 1, Ma *et al.*, 2015). CSI is lowest near the equator (~10%) and fairly constant at latitudes north of 10°N (Fig. 3b). CSI has changed less in the recent period than has WSI (with most shifts $\pm 10\%$).

We looked at temporal shifts in two other relative indices. TX90p is the average percentage of days during a year in which temperatures exceed the 90th percentile for the baseline period, and TN10p is the average percentage of days during which temperatures were below the 10th percentile. The recent increase in TX90p and the recent decrease in TN10p reflect in part the warmer global temperatures since the baseline period (Fig. 1). TX90p has increased recently at most latitudes, but

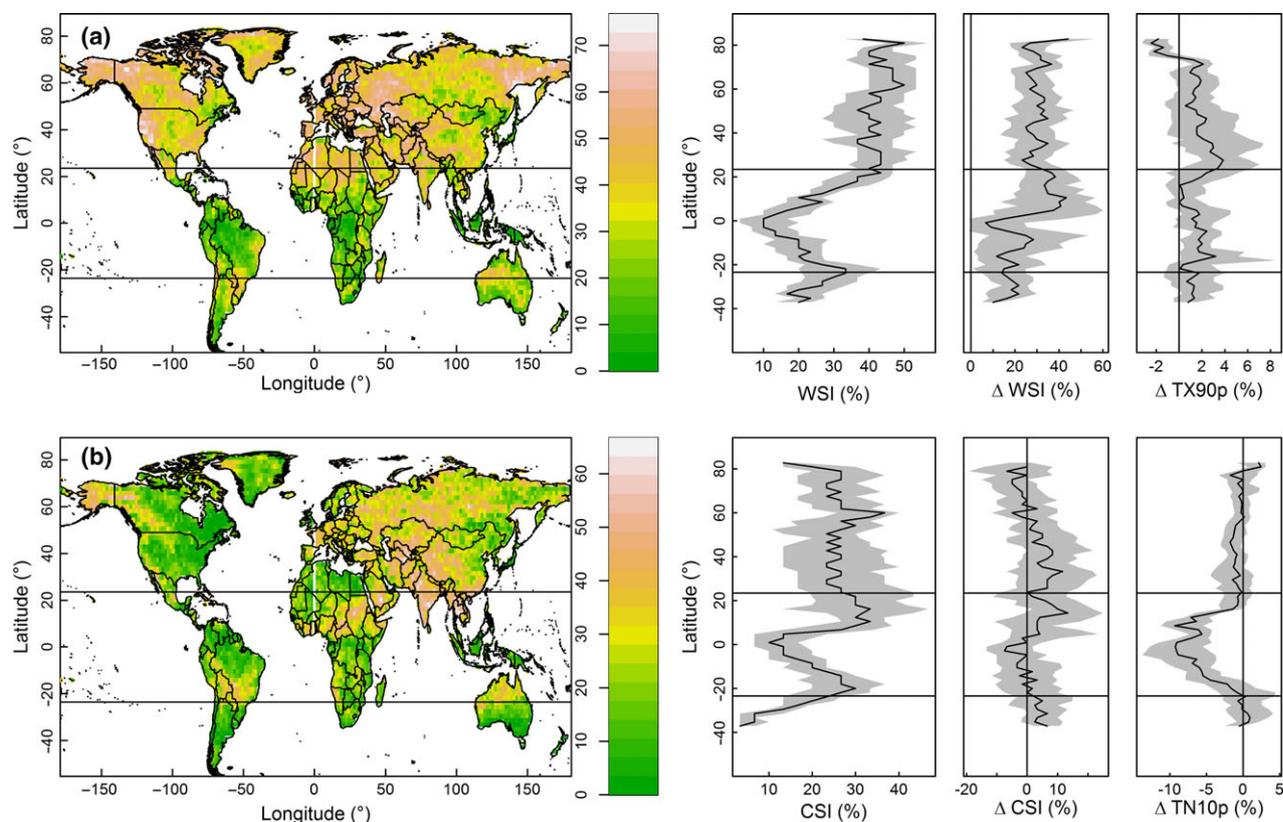


Fig. 3 Geographic patterns differ among relative metrics of warmth and of cold. We depict the geographic and latitudinal patterns during the baseline period along with the shift in the latitudinal gradient between the baseline and recent periods for warm spell incidence (WSI, (a)) and cold spell incidence (CSI, (b)). In the right-hand panels, we depict the shift (across latitudes) between the baseline and recent periods for the percent of warm days (top) and cold nights (bottom) that exceed the 90th (or 10th) percentile during the baseline period. Latitudinal gradients are medians (line) along with 25th and 75th percentiles (shading).

mainly north of the Tropic of Cancer (up to 4%, Fig. 3a). Conversely, TN10P has decreased modestly at most latitudes, but especially in the tropics (Fig. 3b). This latter pattern contrasts with increases in TNn at high northern latitudes (Fig. 2b), demonstrating that shifts in absolute extremes do not always correspond to shifts in the area in the tail of the distribution. The narrow temperature distributions in the tropics accentuate these differences (Fig. 1).

Organismal data

Whether extremes in temperature are stressful to organisms depends on tolerances to those extremes. Consequently, we examine whether latitudinal patterns of thermal tolerances of various taxa correspond to those of minimum (TNn) and maximum (TXx) ambient temperatures (Fig. 4). If tolerances exceed thermal extremes by small margins (thermal safety, Deutsch *et al.*, 2008; Sunday *et al.*, 2014), then thermal tolerances probably reflect past selection to survive thermal extremes (Hoffmann, 2010). Even so,

the resultant narrow safety margins imply that such species will be subject to selection from future thermal extremes.

At low and midlatitudes, latitudinal patterns in upper thermal tolerance of insects, reptiles, and amphibians loosely parallel those in TXx (Fig. 4a and b), but closer to the poles, upper thermal tolerances decline less rapidly with latitude than does TXx. Indeed, the rate of decline in upper thermal limits of ectotherms from the equator to the poles (0.07 ± 0.05 °C per ° latitude for insects and no significant decline for reptiles and amphibians) is much less than the decline in TXx (0.50 °C per ° latitude). Both ecological and evolutionary processes may account for the shallow slope in heat tolerance. Occasional heat waves may maintain high upper thermal limits even at high latitudes (Hoffmann, 2010). High limits may reflect historical factors (post-Pleistocene colonization of high latitudes) plus evolutionary inertia (Hertz *et al.* 1983), or selection favoring 'hotter is better' even at high latitudes (Huey, 2010). Alternatively, exposure to solar radiation will raise body temperatures above

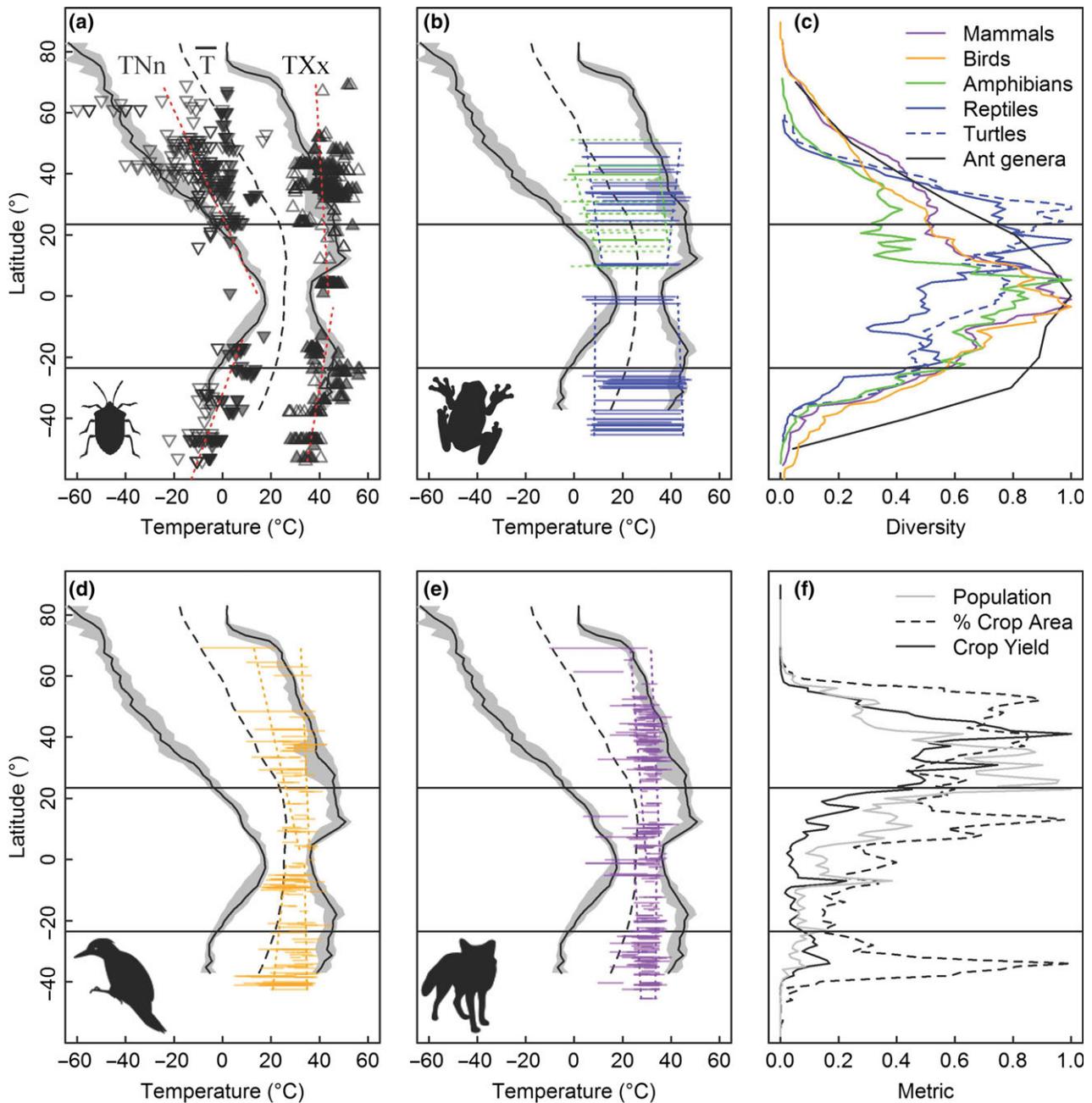


Fig. 4 Latitudinal gradients in thermal limits and their relationship to thermal extremes vary among taxa. Data are critical thermal limits or lethal limits for ectotherms and thermal neutral zones for endotherms. We present the lower upper and lower thermal limits of (a) insects (lower: down pointing triangle, upper: up pointing triangle; critical thermal limits: filled, lethal thermal limits: open), (b) reptiles (squamates, blue) and amphibians (green) (critical thermal limits: solid lines, lethal thermal limits: dashed lines) (d) birds, and (e) mammals. We depict the annual maximum temperature (TXx), annual minimum temperature (TNn), and average temperature (\bar{T} , dashed lines in Fig. 2). Linear regressions of thermal limits in the northern and Southern Hemispheres are shown (dotted lines). The (c) species diversity (number in each latitude) of various taxa generally peaks in the tropics, whereas (f) human population and agricultural intensity tends to peak in temperate regions. Species diversity, human population, and crop metrics are scaled to the latitudinal maximum for each.

ambient temperatures, potentially maintaining selection for high upper limits at most latitudes (Sunday *et al.*, 2014).

Lower thermal limits of insects decline steeply with latitude (0.57 ± 0.13 °C per ° latitude, Fig. 3a) (Addo-Bediako *et al.*, 2000). Lower thermal limits of reptiles

(Huey *et al.*, 2009) and of amphibians (Snyder & Weathers, 1975) also decline with latitude, but the shift (0.18 ± 0.07 °C per ° latitude) is substantially less than that for insects. Because TNn outside the tropics are much lower than are the lower thermal limits of amphibians and of reptiles, these taxa must rely on overwintering in retreats that are thermally buffered (e.g., underground) (Sunday *et al.*, 2014).

$T_{uc,s}$ (upper critical temperatures) of both birds and mammals are relatively invariant with latitude, except at high latitudes (>45 °C), where $T_{uc,s}$ drop somewhat in both groups (McNab, 2012; Khaliq *et al.*, 2014). Mammals have slightly lower $T_{uc,s}$ than do birds (Fig. 4d and e), consistent with the lower body temperatures of mammals (Clarke & Rothery, 2008). $T_{uc,s}$ of birds and mammals are similar to maximum ambient temperatures (Fig. 4d and e) except in the tropics, where $T_{uc,s}$ are noticeably lower than are TXx and are undoubtedly lower than are operative temperatures by day. Of course, most tropical mammals are nocturnal and thus can behaviorally evade the warmest daytime temperatures. In contrast, most birds are diurnal and may need to rely on evaporative cooling to reduce mortality during heat waves (McKechnie & Wolf, 2009): more frequent heat waves may increase water requirements of birds.

The $T_{lc,s}$ of birds and mammals are well above both mean annual temperatures and TNn (Fig. 4d and e). Thus, warming during cool seasons may be energetically beneficial to endotherms (Porter & Kearney, 2009). The $T_{lc,s}$ of birds and mammals do drop somewhat with latitude, although some tropical mammals also have very low $T_{lc,s}$. $T_{lc,s}$ of birds decline more rapidly with latitude (0.29 ± 0.11 °C per ° latitude) than do those of mammals (0.09 ± 0.05 °C per ° latitude). Birds have broader thermal neutral zones (TNZs) than do mammals, and their TNZs broaden more (0.23 ± 0.08 °C per ° latitude) with increases in latitude (Khaliq *et al.*, 2014).

The biological impacts of extreme events depend on not only the magnitude and frequency of those events, and on organismal tolerances, but also on the numbers of species exposed. As is well known (Pianka, 1966), species diversity peaks near the equator for ant genera, amphibians, birds, and mammals and just north of the tropics for squamate reptiles and turtles (Fig. 4c). Consequently, relatively few species will experience increases in extreme events at high latitudes (Fig. 4c). Furthermore, the species living there have broad thermal tolerances and thus may be well suited to deal with temperature fluctuations, even extreme ones (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Khaliq *et al.*, 2014).

The tropics may present a different story. Many species live there (Fig. 4f), and they are already facing a

pronounced increase in the incidence of extreme warm events (Fig. 1b) and are likely to encounter entirely novel thermal regimes later this century (Battisti & Naylor, 2009). Thermally specialized tropical species may be ill equipped to deal with the extreme events and shift in mean conditions (Tewksbury *et al.*, 2008; Huey *et al.*, 2009), although their thermoregulatory capacities may help (Kearney *et al.*, 2009; Logan *et al.*, 2013; Sunday *et al.*, 2014). Although high species diversity multiplies the potential impacts of extremes, diversity may sometimes confer resilience. Across experiments manipulating grassland plant diversity, plant diversity was observed to buffer the impact of extreme events on productivity (Isbell *et al.*, 2015).

Unlike most other organisms (Fig. 4c), humans and their food resources are concentrated outside the tropics. Human population numbers, the yield of four major crops, and the proportion of land area devoted to agriculture are concentrated in north temperate areas (Fig. 3f). Thus, for humans, the biggest impacts of extreme events may lay outside the tropics. However, the impact of extreme events on humans is complicated by behavioral adjustments (Patz *et al.*, 2005; Bobb *et al.*, 2014). We do not attempt to summarize all the complexities of human sensitivity to extremes as these are covered extensively elsewhere (Field *et al.*, 2012), but we highlight that regions of human vulnerability to extremes may differ from other species.

Correlations among indices

Given that different indices of temperature extremes are available (Table 1), we consider whether the various temperature indices show concordant geographic patterns and also show concordant shifts from baseline to the recent. A lack of concordance would suggest that organismal responses to extreme temperatures will likely be difficult to predict, as various taxa are likely to be differentially sensitive to the various types of extremes.

As a group the absolute extreme indices (TXx, TNn, GSL, but not DTR) generally show strong correlations across locations during the baseline period (Fig. 5a, cells with dark gray backgrounds above the diagonal). Specifically, cells that have high maximum (day) temperatures tend to have high minimum (night) temperatures, and long growing seasons, but are uncorrelated with daily temperature range. However, the recent shift in each absolute index is largely uncorrelated with the recent shift in other absolute indices (Fig. 5a, dark gray cells, below the diagonal); thus, recent shifts in these indices are not congruent.

Absolute indices are weakly correlated with relative indices. Thus, sites with a mild TXx might still have a

high WSI. The two relative indices (WSI, CSI; Fig. 5a, tan cell background) are strongly and positively correlated during the baseline; thus, grid cells that have a high probability of a heat wave are also likely to have a cold spell. This may reflect a continental effect: Sites that are distant from oceans are likely to experience both extreme warm and extreme cold events, whereas more coastal sites are likely to be buffered. Even so, recent shifts in each index are negatively correlated because areas that have warmed are likely to experience more warm spells and fewer cold spells (Fig. 5a, below the diagonal). Locations with the biggest decreases in the incidence of cold events (ΔTN_{10p}) tend to be cold areas but also those (tropical) areas with low incidence of cold and warm spells.

These correlation matrices indicate that different indices of extreme temperatures and their shifts show limited geographic concordance. Thus, baseline and shifting patterns of environmental stress are complex: some regions have high scores for some indices, but low scores for others.

The shifts in all indices between the baseline and recent period are only weakly related across locations (Fig. 5a lower triangle). Consequently, inconsistent thermal shifts are subjecting organisms to diverse new stresses. Examining shifts in climate variability associated with climate change rather than extremes could help clarify these stresses (Reyer *et al.*, 2013). There is also little association between the baseline values of the

indices and recent shifts (Fig. 5b). This indicates that the areas that faced frequent extremes in the past are not necessarily those experiencing the greatest increase in extreme events. These overall weak associations among indices indicate that increases in extreme events are likely to pose substantial challenges for organisms: Organisms inhabiting even relatively constant environments will experience large shifts in multiple axes of extreme events.

Caveats

At the risk of appearing nihilistic, we need to mention issues that inevitably complicate attempts to map thermal extremes onto biological impacts. Behavioral and physiological adjustments can of course buffer the impact of environmental extremes (Kearney *et al.*, 2009; Somero, 2010; Gunderson & Stillman, 2015), but opportunities to use such adjustments will differ among taxa and among environments (Huey *et al.*, 2009; Kaspari *et al.*, 2015). Analyses such as ours suffer from a mismatch between the fine spatial scales at which organisms interact with their environment and the coarse scale of climate data (Potter *et al.*, 2013). The climate data underlying our indices has coarse spatial resolution (2.5°), but temporal resolution (6 h) that should more appropriately capture extremes (Kearney *et al.*, 2012). Even so, the spatial resolution here should be adequate to capture latitudinal trends.

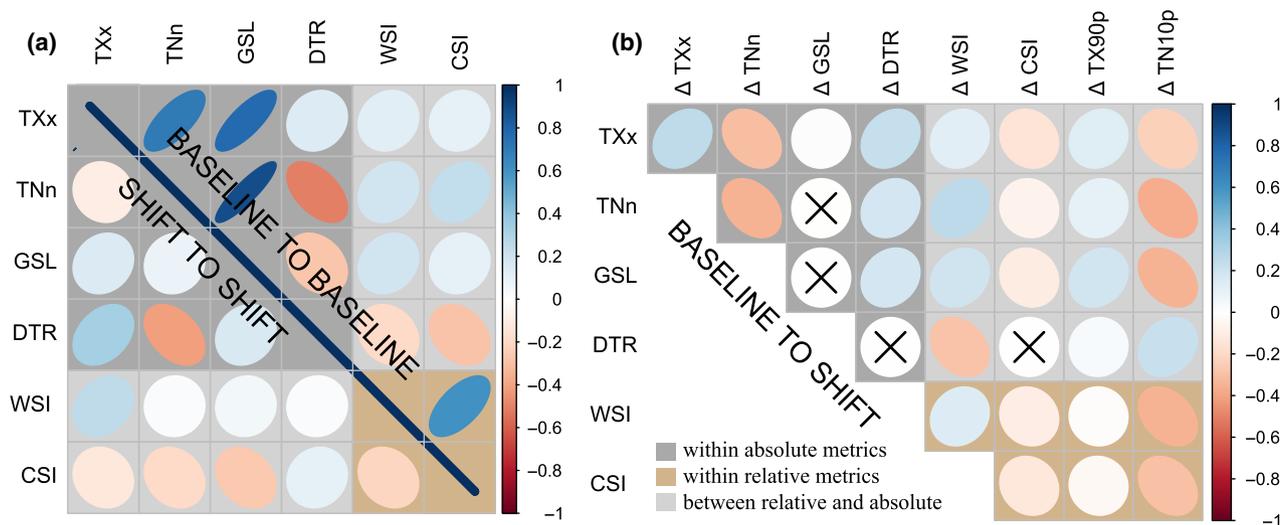


Fig. 5 The (a) correlations among the metrics listed in Table 1 during the baseline period (upper triangle) and among shifts in the metrics during the recent period (lower triangle) are generally weak. The orientation of the ellipse depicts the direction and the length of the minor axis, and the color depicts the strength of the correlation (scale bar at the right of each plot). Baseline correlations are strongest among absolute metrics of warmth and coldness (dark gray background) and among relative metrics (tan background), but weak between the absolute and relative metrics (light gray background). Recent shifts in the metrics (lower triangle) show little correlation. The (b) the baseline values of the metrics show little relationship to the extent of change during the recent period. Correlations marked with an \times are not significant at $P < 0.05$. Others are significant despite weak correlations due to the large number (~ 1800) of grid cells.

Moreover, current indices of extremes are based on air temperatures and thus strictly apply only to organisms in shade. Organisms in the sun can, however, be exposed to dramatically elevated – thus dramatically stressful – operative temperatures (Kearney *et al.*, 2009; Sunday *et al.*, 2014; Kaspari *et al.*, 2015); thus, future studies of extreme temperatures must develop and incorporate indices that are based on operative temperatures in both sun and shade, and how these relate to organismal tolerances (Kearney *et al.*, 2009; Sunday *et al.*, 2014). This will be especially important if warming and extreme events cause vegetation dieback (Reyer *et al.*, 2013), which will open canopies and elevate operative temperatures and stress. Moreover, the spatial distribution of operative temperatures can influence whether a habitat constrains thermoregulatory opportunities (Sears & Angilletta, 2015). Further, for wet-skinned ectotherms (e.g., salamanders, slugs), evaporative cooling can result in operative temperatures much lower than of dry-skinned ectotherms (Tracy, 1976; Sunday *et al.*, 2014); but access to water for rehydrating may be more critical to wet-skinned ectotherms than a thermal event itself. Access to water for evaporative cooling is also crucial for endotherms (McKechnie & Wolf, 2009).

Another way in which current indices of thermal extremes do not fully predict biological impacts is that air (or even operative) temperatures are measured and analyzed on a linear scale, whereas as physiological responses are nonlinear with temperature (Dillon *et al.*, 2010; Dell *et al.*, 2011) (Fig. S1). Thus, a 1 °C shift at high temperature will generally induce greater physiological shifts than will a similar shift at low temperature. If warming or extreme events not only elevate metabolic rates but also reduce food resources, net energy gain will decline substantially (Brett, 1971). Further, biotic interactions may be modified by thermal extremes, especially if interacting species have different thermal optima (Dell *et al.*, 2014).

Conclusions

Biological responses to changing climates can be mediated by both mean and extreme conditions (Garcia *et al.*, 2014). However, geographic and latitudinal patterns in means and of extreme indices are not always parallel (Fig. 2), thus complicating attempts to predict biological impacts of climate change. Doing so is made daunting by our finding that different extreme indices show little geographic concordance during the baseline period or the recent period, or between baseline and recent values, either within or between indices (Fig. 5).

Poleward organisms have generally been considered more vulnerable to climate change because they are

experiencing absolutely greater changes (Root *et al.*, 2003). However, limited seasonality and constant temperatures in the tropics have led many tropical organisms to evolve specialized thermal physiologies (Janzen, 1967; Ghalambor *et al.*, 2006). Thus, even a small temperature change may exceed the thermal tolerances of tropical organisms, leading to greater biological vulnerability in tropical areas (Deutsch *et al.*, 2008; Tewksbury *et al.*, 2008; Huey *et al.*, 2009; Khaliq *et al.*, 2014). Moreover, recent increases in the frequency of extreme high temperatures has been especially pronounced in the tropics (Fig. 1b), and what is extreme for the tropics now is projected to become average by the end of the century (Battisti & Naylor, 2009). On the other hand, the highly variable climates in the temperate zone may challenge temperate zone organisms, despite their relative broad tolerance ranges (Kingsolver *et al.*, 2013; Vasseur *et al.*, 2014).

Given the limited concordance among indices of extremes, it will be important to understand how the biology of particular taxa affects their sensitivity to the various extreme indices. Such assessments will be challenging but should address whether organisms are more affected by rare but acute extreme events or by chronic exposure to less extreme conditions. Here we make a first attempt at identifying the factors governing the vulnerability of different taxa.

Arthropods are ecologically important organisms that drive pollination and are a food resource for many taxa. They live in all terrestrial environments and thus as a group are exposed to diverse environmental challenges, but have exceptional physiological tolerances (Addo-Bediako *et al.*, 2000). Their small size makes them vulnerable to acute shifts in temperature, but also gives them ready access to sheltered retreats. Small size and high mass-specific metabolic rates makes them sensitive to energy and water balance during chronic exposure to extremes (Williams *et al.*, 2014).

Reptiles might seem relatively insensitive to climate extremes. As a group they tolerate high temperatures, have limited water loss, and are good behavioral thermoregulators (Huey *et al.*, 2010). And as ectotherms, their metabolic rates are relatively low, providing some buffer against chronic exposures to thermal extremes. Even so, chronic constraints on activity times during the breeding season may compromise reproductive output and lead to local extinctions (Sinervo *et al.*, 2010). Eggs and juvenile stages may be especially vulnerable to acute and chronic events, because they often have smaller tolerance ranges than do adults, have less thermal inertia, and may have lesser abilities to use behavior to evade extreme conditions. Unfortunately, the vulnerability of eggs and of juveniles has been understudied (Muth, 1980; Levy *et al.*, 2015).

Amphibians have some capacity to use evaporative cooling to buffer thermal stress (Tracy, 1976; Sunday *et al.*, 2014). On the other hand, their need to replenish water supplies makes them vulnerable to chronic exposures to high temperatures or to desiccating environments. Environmental stress for amphibians (and for other animals, too) can be exacerbated by direct and interactive effects of pathogens (Rohr, 1997).

Because of their very high metabolic heat production and their insulation, birds and mammals are exceptionally tolerant of climate extremes and thus have large 'climate spaces' (Porter & Gates, 1969). Both groups have high stamina and mobility and thus can often evade extreme conditions. However, their high rates of metabolism and of water loss can make them vulnerable when food and water become limited (McKechnie & Wolf, 2009). Despite their large climate spaces, birds and mammals sometimes do suffer from thermal extremes (McKechnie & Wolf, 2009; Fey *et al.*, 2015).

For those organisms likely to be most impacted by acute thermal stress events, absolute indices of extremes may be most relevant. The rough correspondence between TXx and TNn and thermal tolerance and the weak latitudinal gradient in thermal tolerance suggest that the stress imposed by rare, extreme warm temperatures may be fairly independent of local conditions (Hoffmann, 2010). The widespread observation that upper thermal limits vary less across latitude than do lower thermal limits may reflect evolutionary constraints (Addo-Bediako *et al.*, 2000; Huey *et al.*, 2009; Kellermann *et al.*, 2012; Araújo *et al.*, 2013; Hoffmann *et al.*, 2013; Khaliq *et al.*, 2014; Sunday *et al.*, 2014). Another reason that absolute metrics may be appropriate for thermal stress events is that the acclimation capacity of thermal tolerance varies little with latitude, seasonality, or warm or cool adaptation (Gunderson & Stillman, 2015).

Although our analyses highlights serious challenges in evaluating the biological impacts of thermal extremes, we choose to end on a positive note. The increasingly widespread availability of high spatial and temporal resolution climate data will certainly facilitate analyses of extreme events, for both contemporary and future climates. In addition, biophysical tools are now available so that meteorological data – not just air temperature – can be mapped onto microclimates and the operative temperatures of organisms (Kearney *et al.*, 2014). On the physiological side, climate change experiments are increasingly moving away from fixed-temperature studies and instead starting to incorporate experimental regimes with natural daily and seasonal variation in temperatures (Williams *et al.*, 2014) or with exposure to extreme events (Jentsch *et al.*, 2007; Thompson *et al.*,

2013; Ma *et al.*, 2015). Further incorporation of ontogenetic variation in physiological sensitivity is increasingly studied (Coyne *et al.*, 1983; Kingsolver *et al.*, 2011; Levy *et al.*, 2015). We will not assert that a study of the biological impacts of extreme thermal events will ever be easy, but we feel confident that such studies will be critical to attempts to predict the biological consequences of climate and of climate change.

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Supporting Information

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

Figure S1. Geographic patterns on a thermodynamic scale.