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Global metabolic impacts of recent climate warming

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Documented shifts in geographical ranges[1,2], seasonal phenology[3,4], community interactions[5], genetics[3,6] and extinctions[7] have been attributed to recent global warming[8–10]. Many such biotic shifts have been detected at mid- to high latitudes in the Northern Hemisphere[4,9,10]—a latitudinal pattern that is expected[4,8,10,11] because warming is fastest in these regions[8]. In contrast, shifts in tropical regions are expected to be less marked[4,8,10,11] because warming is less pronounced there[8]. However, biotic impacts of warming are mediated through physiology, and metabolic rate, which is a fundamental measure of physiological activity and ecological impact, increases exponentially rather than linearly with temperature in ectotherms[12]. Therefore, tropical ectotherms (with warm baseline temperatures) should experience larger absolute shifts in metabolic rate than the magnitude of tropical temperature change itself would suggest, but the impact of climate warming on metabolic rate has never been quantified on a global scale. Here we show that estimated changes in terrestrial metabolic rates in the tropics are large, are equivalent in magnitude to those in the north temperate-zone regions, and are in fact far greater than those in the Arctic, even though tropical temperature change has been relatively small. Because of temperature's nonlinear effects on metabolism, tropical organisms, which constitute much of Earth's biodiversity, should be profoundly affected by recent and projected climate warming[2,13,14].

Global warming is probably having profound and diverse effects on organisms[1–11]. Organisms living at mid- to high latitudes in the Northern Hemisphere are predicted to be the most affected by climate warming[4,8,10,11], because temperatures have risen most rapidly there[8]. Indeed, the vast majority of biotic impacts of warming have been documented in this region, but few studies have yet searched for impacts in other areas, especially the tropics[2,4,8,10,13,14]. One way to circumvent this geographical sampling bias is to use temperature data with broad geographical coverage to predict global patterns of physiological responses to observed temperature change[13]. Metabolic rate is a heuristic metric here because it is a fundamental physiological index of an organism's energetic and material needs, its processing capacity and its ecological impact[12].

Metabolic rates of ectotherms depend principally on body mass (m) and body temperature (T), as described by a fundamental equation[12]:

$$B(m,T) = b_0 m^{3/4} e^{-E/kT} \quad (1)$$

where B is metabolic rate, b_0 is an empirically derived and taxon-specific normalization constant, m is body mass, E is the average activation energy for biochemical reactions of metabolism, T is body temperature (in Kelvin), and k is the Boltzmann constant. When standardized for mass, this equation enables metabolic comparisons among different sized organisms[12]. These mass-normalized metabolic rates are proportional to the 'Boltzmann factor' ($e^{-E/kT}$; the familiar 'Q_{10}' effect in physiology is an approximation of the Boltzmann factor)[15].

Although the thermodynamic and statistical validity of equation (1) is debated[16–18], it provides a useful approximation of metabolic rates[12,15] for exploratory macrophysiological investigations[16,19]. In the context of climate warming, it predicts that metabolism will shift more in response to a unit change in temperature at high temperature than at low temperature[15], at least over biologically common and non-stressful temperatures (~0 °C to ~40 °C; see Methods)[12].

To estimate geographical patterns of warming-induced changes in metabolic rates of terrestrial ectotherms, we compiled high-frequency temperature data for the period of 1961 to 2009 for 3,186 weather stations across the world (~500 million temperature measurements; Methods and Supplementary Fig. 1)[20]. We derived average values of E (0.69) and of b_0 (23.66) from empirical estimates for diverse ectotherms (Supplementary Table 1)[12]. We substituted these 'average ectotherm' values into equation (1) to estimate mass-normalized metabolic rates ($Bm^{-3/4}$) from global temperature data. Because metabolic rate varies nonlinearly with temperature, calculating mean metabolic rates from mean temperatures is inappropriate (the 'fallacy of the averages'; see Methods and Supplementary Fig. 2)[15]. Therefore we estimated metabolic rate for each temperature measurement and subsequently determined average temperature and average metabolic rate for each station during the Intergovernmental Panel on Climate Change (IPCC) standard reference period (1961–1990) and for all five-year intervals from 1980 to 2009. To account for non-uniform distribution of stations and to enable comparisons among latitudinal regions, we determined averages for all stations within 5° latitude by 5° longitude grid cells and then area-corrected grid-cell means and standard errors of temperature measurements and metabolic rate estimates for each region (Methods).

Temperature changes since 1980 in this data set are consistent with recent findings[8]: temperatures rose fastest in the Arctic, somewhat less quickly in the north temperate zones, and more slowly in the tropics, but remained essentially unchanged in the south temperate zone (Fig. 1a).

Predicted absolute changes in metabolic rates show a markedly different pattern: metabolic rates increased most quickly in the tropics and north temperate zones, and less so in the Arctic (Fig. 1b). In fact, the latitudinal ordering of changes in temperature since 1980 fails to predict the latitudinal ordering of changes in metabolic rate ($P = 0.68$), even when a powerful ordered-heterogeneity test is used[21]. The predicted increase in metabolism in the tropics was large, despite the small rise in temperature there (Fig. 1a), because tropical warming took place in an environment that was initially warm.

Absolute changes in metabolic rates determine an organism's total energy use and thus the impacts of climate change on ecosystem-level processes, but per cent changes in metabolic rates are nonetheless relevant to the impacts of climate change on individual organisms[22]. Such relative changes in metabolic rates (expressed as per cent of the standard reference period on a per-station basis) closely match temperature changes (Fig. 1c), indicating that impacts on individual ectotherms have probably been relatively large in the Arctic and north temperate zones.

To evaluate whether the patterns described earlier (Fig. 1b) are robust to our use of average values of E and b_0, we re-ran analyses using estimates of E and b_0 specific to diverse ectotherm taxa (Supplementary Table 1)[12]. Large effects of recent climate warming on metabolic rates are predicted for invertebrates, amphibians and reptiles in equatorial

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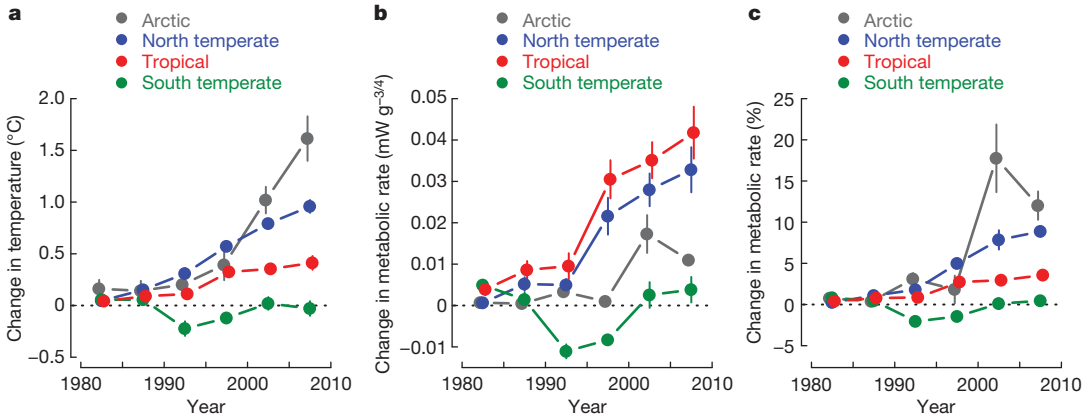

Figure 1 | Global changes in temperature and in metabolic rates since 1980. **a**, Changes in mean temperature (5-year averages) for Arctic ($n = 100$ grid cells), north temperate ($n = 356$), south temperate ($n = 51$) and tropical ($n = 169$) regions. **b**, Predicted absolute changes in mass-normalized metabolic rates by geographical region. **c**, Predicted relative changes in mass-normalized metabolic rates. Both temperature and metabolic rate are expressed as differences from the standard reference period (1961–1990), calculated on a per-station basis, on the basis of E and b_0 for an average ectotherm (Supplementary Table 1). Data points are means ± s.e.m. of area-corrected, gridded weather-station data (Methods).

West Africa, the Caribbean and Central America, Ecuador, eastern equatorial Brazil, and the Persian Gulf region (Fig. 2c–e). However, we emphasize that weather station coverage in some of these regions is sparse and each taxonomic group is not found in all geographical regions. Overall, general patterns in Fig. 1b are robust for different taxa (Fig. 2b–e): the largest predicted absolute shifts in metabolic rate for all taxa are in the tropics. Nevertheless, small differences in the relationship between metabolism and temperature (that is, E and b_0) can alter the magnitude of the effects of climate warming on organism physiology (Fig. 2).

The patterns under discussion are for mass-normalized metabolic rates, but the magnitude of metabolic shift will necessarily differ for small versus large ectotherms. Of course, absolute shifts will be greater for larger ectotherms, but equation (1) indicates that mass-specific metabolic rates of small ectotherms will show larger increases (Supplementary Fig. 3).

Several assumptions underlie the patterns shown in Fig. 1b, c. The exponent (3/4) for metabolic rate as a function of mass is debated[16–18], but reasonable shifts of this exponent for given taxa will only alter the heights of all latitudinal lines, not their relative ordering. We assume that surface air temperatures approximate ectotherm body temperatures; therefore, our metabolic estimates apply to thermoconforming and exposed ectotherms. This is reasonable for small ectotherms living in shaded environments[23], but less so for large ectotherms that live in thermally heterogeneous environments, where behavioural thermoregulation is possible, or for organisms that spend extensive periods in retreats[24]. Also, we assume that the coefficients (E, b_0) of equation (1) are independent of latitude. However, some high-latitude ectotherms have relatively elevated metabolic rates; and this is thought to represent an evolutionary metabolic compensation for the physiologically depressing effects of low body temperature[16,25,26]. With reference to equation (1), metabolic compensation would be indicated[26] by latitudinal increases in b_0 and/or in E. In fact, the patterns of metabolic responses shown in Fig. 1b hold even when we shift these parameters over a large

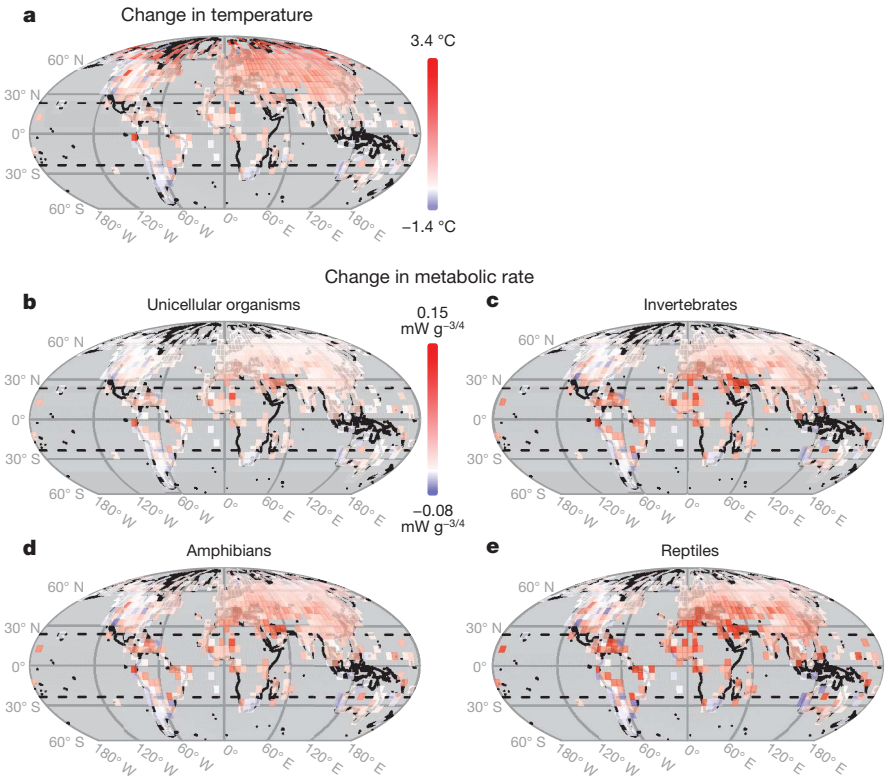

Figure 2 | Predicted changes in metabolic rates of diverse terrestrial ectotherms. **a**, Difference in temperature between 1961–1990 and 2005–2009, with scale bar shown on right. **b–e**, Difference in mass-normalized metabolic rates (predicted) for the same period for four terrestrial ectothermic animal taxa for which empirical estimates of E and b_0 are available (Supplementary Table 1)[12]. Colour bar to right of **b** indicates scale for **b–e**. Grey shading indicates grid cells with no temperature data.

range of biologically reasonable values[26] to simulate extreme metabolic compensation at high latitude (Methods and Supplementary Fig. 4).

Our analyses indicate that warming during the past three decades has had its biggest absolute impacts on metabolic rates in tropical and north temperate zones (Fig. 1b). The outlook for future warming is less clear. Without predictions of future daily and seasonal temperature cycles (not merely of mean annual temperatures), we cannot directly estimate future metabolic changes without violating the fallacy of averages[15]. Nevertheless, our analyses of recent temperature data indicate that even when the temperature shifts in the north temperate region are more than double those in the tropics (Fig. 1a), absolute shifts in metabolic rates are similar in the two regions (Fig. 1b). If this pattern holds, projected increases in median surface air temperature by the end of the twenty-first century for the two regions (3.5–4.0 °C in the tropics, and 4.0–5.5 °C in the north temperate zone)[8] should cause roughly similar absolute increases in metabolic rates of tropical and north temperate organisms.

Recent studies using diverse physiological and biophysical approaches indicate that tropical ectotherms may be particularly vulnerable to climate warming[2,7,13,14,24,27], even though observed and predicted tropical warming is relatively small[8]. Our estimates suggest that tropical ectotherms are also experiencing large increases in metabolic rate (Fig. 1b). Such increases will have physiological and ecological impacts: warmed tropical ectotherms will have an increased need for food and increased vulnerability to starvation unless food resources increase, possible reduced discretionary energy for reproduction[22], increased rates of evaporative water loss in dry environments and altered demographies[13]. Larger increases in metabolic rates of tropical soil biota may explain larger absolute changes in tropical soil respiration[28]. Furthermore, metabolic increases should alter food web dynamics, leading to elevated rates of herbivory and predation, as well as changes in the spread of insect-borne tropical diseases[29]. Because the tropics are the centre of Earth's biodiversity and its chief engine of primary productivity, the relatively large effects of temperature change on the metabolism of tropical ectotherms may have profound local and global consequences.

METHODS SUMMARY

We obtained hourly temperature records from 22,486 weather stations spread across the world[20], but then included only stations that sampled throughout the IPCC standard reference period (1961–1990)[8] as well as 1991–2009, in all seasons and on average at least every six hours. We also excluded five Antarctic stations, such that 3,186 stations remained. Geographical coverage is uneven (Supplementary Fig. 1), but all regions are well represented in this restricted data set (Supplementary Table 2). Furthermore, including data from 5,561 stations with data from 1961 to 2009 (but with no other limitations; Supplementary Table 2), does not alter our conclusions (Supplementary Fig. 5). To correct for the uneven spatial distribution of stations (Supplementary Figs 1 and 5A), we computed mean temperatures and metabolic rates for all stations within 5° latitude by 5° longitude cells. We calculated means and standard errors for latitudinal regions by weighting grid-cell means by the interpolated rectangular mid-cell areas[30]. To estimate whether metabolic compensation at high latitude might alter patterns, we recalculated metabolic rates after substituting extreme values of E and of b_0. Specifically, we used very high values of E (0.76) and b_0 (26.85) for the north temperate and Arctic areas, but very low values of E (0.50) and b_0 (15.68) for tropical areas (see Supplementary Table 1). Such extreme metabolic compensation (these values span most of the known range of E)[26] does not alter our conclusions (Supplementary Fig. 4).

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions M.E.D., G.W. and R.B.H. conceived the project, designed the analyses and wrote the paper; M.E.D. and G.W. collated weather station data and did temperature and metabolic rate calculations.

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METHODS

Weather station data. We downloaded all available 'isd-lite' weather-station data (http://www.ncdc.noaa.gov/oa/climate/isd/index.php)[20]. From the initial 22,486 weather stations, we extracted a 'restricted' data set (3,186 stations) that sampled throughout the entire IPCC standard reference period (1961–1990)[8] as well as up to 31 December 2009, in all seasons, and at least every six hours. (We did not include Antarctic stations.) This data set had a total of 493,256,415 temperature measurements with an average of 8.8 temperature measurements per station per day; it was used for Figs 1 and 2 and Supplementary Figs 1–4. For the 'unrestricted' data set, we included all stations (other than Antarctic) that had data for the above time period, independent of the seasonality or frequency of sampling. This data set had 5,561 stations (used for Supplementary Fig. 5).

Metabolic rate estimates. To estimate metabolic rates from temperature data, we used empirically derived estimates of the coefficients (E and b_0) of the equation relating metabolic rate to temperature and body mass for unicellular organisms, multicellular invertebrates, amphibians and reptiles[12]. We excluded fish because our data are air (not water) temperatures. We excluded birds and mammals because their body temperatures will not match air temperatures. We excluded plants because the temperature dependence of their metabolic rates differs fundamentally from that of animal ectotherms[31].

Mean temperatures are expedient for analyses of the impacts of climate warming. However, because the relationship between temperature and metabolic rates is inherently nonlinear, the use of mean rather than individual temperatures to predict metabolic rates will induce spurious results[32]—an effect known as the 'fallacy of the averages'[15]. To illustrate this fallacy, we recomputed metabolic rates for geographical regions using mean annual temperatures (Supplementary Fig. 2) for comparison with rates predicted from 'instantaneous' temperatures (Fig. 1b). Note that the use of mean temperatures underestimates the predicted increases in metabolic rates[15], and also de-emphasizes the impact of warming in the north temperate zones relative to the tropics. Consequently, it is imperative to use high-frequency temperature data and to compute metabolic rate separately for each temperature measurement.

Our analysis includes temperatures that fall outside the normal tolerance range of most organisms (that is, below ~0 °C and above ~40 °C). We include these values for analytical transparency, and because their inclusion is conservative for our analyses. Eliminating negative temperatures (for example, substituting metabolic rates at 0 °C for all temperatures below 0 °C) will have little effect because metabolic rates are negligible at these extremely cold temperatures. Substituting metabolic rates at 40 °C for temperatures above 40 °C will tend to reduce metabolic rates at mid-latitudes where these hot temperatures occur in summer; this would induce a downward bias in our predicted metabolic rates for the north temperate zone. In other words, by not truncating metabolic rates to the normal tolerance range (0–40 °C), we avoid a bias that would favour increased metabolic rates in the tropics.

Geographical coverage. Weather stations are not equally spaced across the world (summarized in Supplementary Table 2, Supplementary Figs 1 and 5a). To adjust for the uneven spatial distribution (and non-independence) of stations, we computed mean temperatures and metabolic rates for all stations within 5° latitude by 5° longitude grid cells (see Fig. 2). We then calculated means and standard errors for latitudinal regions (see Fig. 1) by weighting grid-cell means by interpolated rectangular mid-cell areas[30]. We further tested the effects of weather station spatial coverage on our conclusions by comparing analyses using restricted (3,186 stations) and unrestricted (5,561 stations) data sets. Our conclusions are robust and independent of the data set used (Supplementary Fig. 5).

Assumptions. We assume that station temperatures match the temperature of a dry-skinned ectotherm positioned in shade at 2-m height. Of course, mobile ectotherms can often use behaviour (for example, microhabitat selection) to buffer body temperatures against changes in air temperatures[23,24]. Thus our metabolic estimates should be viewed as an estimate for a non-regulating, inert and exposed ectotherm.

We assume that a single metabolic curve (equation (1)) applies to all ectotherms, independent of latitude. However, some high-latitude ectotherms have relatively raised metabolic rates, which may reflect metabolic compensation for temperature[26]. To estimate whether metabolic compensation at high latitude might alter latitudinal patterns (Fig. 1), we recalculated metabolic rates after substituting extreme values of E and b_0. Specifically, we used very high values of E (0.76) and b_0 (26.85) for the north temperate and Arctic areas, but very low E (0.50) and b_0 (15.68) for tropical areas (see Supplementary Table 1). Such extreme metabolic compensation (these values span most of the known range of E)[26] does not alter our conclusions (Supplementary Fig. 4).

Statistics. We used an ordered-heterogeneity test[21] to evaluate whether latitudinal ordering of changes in temperature since 1980 predicts the latitudinal ordering of changes in metabolic rate.

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