Physiological plasticity increases resilience of ectothermic animals to climate change

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Understanding how climate change affects natural populations remains one of the greatest challenges for ecology and management of natural resources. Animals can remodel their physiology to compensate for the effects of temperature variation, and this physiological plasticity, or acclimation, can confer resilience to climate change[1,2]. The current lack of a comprehensive analysis of the capacity for physiological plasticity across taxonomic groups and geographic regions, however, constrains predictions of the impacts of climate change. Here, we assembled the largest database to date to establish the current state of knowledge of physiological plasticity in ectothermic animals. We show that acclimation decreases the sensitivity to temperature and climate change of freshwater and marine animals, but less so in terrestrial animals. Animals from more stable environments have greater capacity for acclimation, and there is a significant trend showing that the capacity for thermal acclimation increases with decreasing latitude. Despite the capacity for acclimation, climate change over the past 20 years has already resulted in increased physiological rates of up to 20%, and we predict further future increases under climate change. The generality of these predictions is limited, however, because much of the world is drastically undersampled in the literature, and these undersampled regions are the areas of greatest need for future research efforts.

In theory, environmental variability represents a selection pressure that results either in thermal adaptation or in the evolution of phenotypic plasticity[1,2]. The efficacy of genetic adaptation depends on the relationship between generation time and rate of climate change. Under rapid human-induced climate change, short-lived animals may adapt successfully if the change in climate is relatively slow and the direction of change is constant to permit directional selection[3,4]. In most cases, however, climate change is rapid and can occur across few generations or even within generations[5]. Furthermore, fluctuating climates do not provide a clear signal to drive directional selection, and selection in one generation may be maladaptive in subsequent generations[4]. Temperature fluctuations are predicted to increase under climate change, and plastic phenotypes should therefore be favoured[4].

Many individual ectotherms can remodel their physiology to reduce the extent to which physiological rates change in response to a chronic, recurring, or extemporaneous change in temperature (that is, thermal compensation via the process of thermal acclimation (in response to a single environmental variable) or acclimatization (in response to multiple environmental variables under field conditions)[6]). If thermal compensation were perfect, physiological rates would remain constant across environmental conditions, so that animals could maintain fitness across a broader

temperature range compared to animals that show little or no plasticity[7].

We collated data from the literature (1968–2012) for ectothermic animals ($n = 637$ measurements of 202 species) that were chronically exposed (acclimated or acclimatized) to at least two temperatures and in which physiological rates (metabolic rates, heart rates, enzyme activities and locomotor performance) were measured acutely at these two acclimation temperatures (see Supplementary Methods and Data). These data allowed us, first, to determine by how much physiological rates changed in response to an acute change in temperature (Fig. 1). 'Acute thermal sensitivity' was defined as the change in a physiological rate function in response to a rapid change in environmental temperature in the absence of thermal acclimation—that is, within the acclimation set temperatures (see Fig. 1 for details). Second, we calculated by how much a physiological rate changes when an animal was allowed to acclimate to different thermal conditions—that is, across chronic acclimation conditions (Fig. 1; see ref. 8). This 'post-acclimation thermal sensitivity' thus provides the most physiologically realistic estimate of how sensitive ectothermic animals are to a temperature change that lasts longer than several days to weeks.

We used a derivation of the Arrhenius equation[9] to express both acute thermal sensitivity and post-acclimation thermal sensitivity as the fractional change in rate relative to a $10\,^\circ C$ change in temperature (Q_{10}; see Fig. 1 for equations). $Q_{10} = 1$ indicates that rates do not change with a change in temperature, $Q_{10} < 1$ indicates that rates decrease with an increase in temperature, and $Q_{10} > 1$ shows that rates increase with an increase in temperature. The closer Q_{10} is to 1, the less affected animal physiology will be to a change in environmental temperature, meaning that animals will be more resilient to climate change (Fig. 1).

The geographical distribution of data in the literature is heavily biased towards North America and Europe, with very few data points outside these continents (Fig. 2a). For both marine and freshwater animals, Q_{10} values for acclimation thermal sensitivities were lower than for acute thermal sensitivities (marine: paired $t_{65} = -2.19$, $p = 0.03$; freshwater: $t_{162} = -4.68$, $p < 0.001$; Fig. 2b), meaning animals from these habitats responded less strongly to a change in temperature when given the opportunity to acclimate. There was no difference between post-acclimation and acute sensitivities for terrestrial species (paired $t_{62} = 1.09$, $p = 0.28$). Calculating the response to climate change on the basis of acute thermal sensitivities (for example, ref. 10) will therefore overestimate the effect of temperature change for freshwater and marine animals. A decrease in physiological rates with increasing temperature ($Q_{10} < 1$) could indicate either that animals overcompensate for the effects of increasing temperature, or that physiological systems become damaged as a result of chronic

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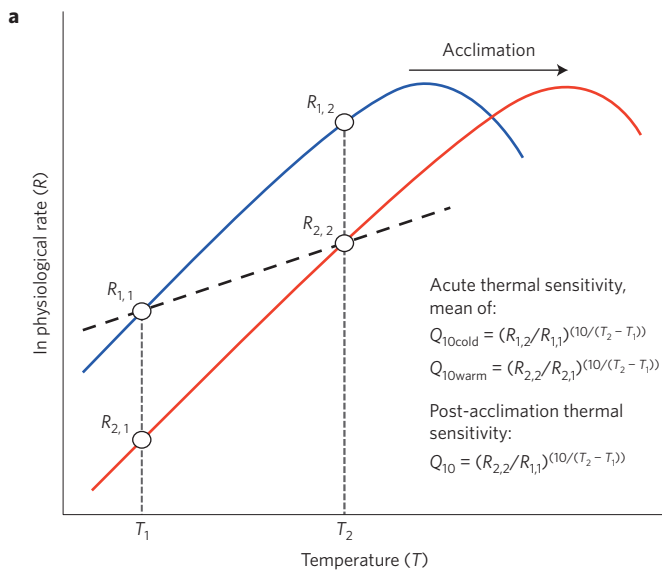
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Figure 1 | Generalized thermal responses of physiological rates to a temperature change. The schematic shows that acclimation to chronic warm conditions (red line) causes a shift to the right in reaction norm from cold conditions (blue line). The change in physiological rates with an increase in temperature is described by the Q_{10} effect, which is derived from van't Hoff's equation. Q_{10} values of 1 indicate no change in rate following a temperature change, $Q_{10} < 1$ indicates a decrease in rates with an increase in temperature, and $Q_{10} > 1$ shows an increase in rates with increasing temperature. We calculated Q_{10} values for acute thermal sensitivities from data for animals kept at single constant long-term (acclimation) conditions in which responses were measured at two different acute temperatures. Q_{10} values for post-acclimation thermal sensitivities were calculated across acclimation conditions; that is, as the change in rate of a physiological process between a cold acclimated animal measured at the same cold test temperature as acclimation temperature, and a warm acclimated animal measured at the same warm test temperature (broken line).

exposure to high temperatures. The experimental temperature ranges in the literature are generally below damaging levels (see Supplementary Data, ref. 10), making the former explanation more likely.

There was a weak, but significant (linear regression $R^2 = 0.01$, $F_{1,578} = 4.59$, $p < 0.04$), increase in post-acclimation Q_{10} values with increasing latitude (Fig. 2c). This trend in the literature as a whole contradicts the relatively common assumption that animals living in stable environments in the tropics have limited capacity for thermal acclimation[11]. Metabolic rates and the activities of metabolic enzymes, particularly of the glycolytic enzyme lactate dehydrogenase and the mitochondrial enzymes citrate synthase and cytochrome c oxidase, were the most commonly measured physiological responses in the literature, followed by locomotor performance (Fig. 2e). In all measured traits, post-acclimation Q_{10} values were lower than acute values (Fig. 2d). Acclimation responses to temperature change differed at different taxonomic levels from phylum to species (see Supplementary Tables 1–12 and Fig. 3). As an overall trend, post-acclimation thermal sensitivities were significantly lower than acute thermal sensitivities in molluscs and fish (Fig. 3b,c; paired t-test, $p < 0.005$ for both groups), but responses were too variable within arthropods, amphibians and reptiles (Fig. 3a,d,e; paired t-test, $p > 0.2$ for all groups) to draw any conclusions at this broad taxonomic level.

We resolved these data geographically, and we determined associations between post-acclimation thermal sensitivities and climate by determining climate variables from 1900 to 2010 at the geographical origin of the study species in each publication.

Furthermore, we predicted climate change at each geographic location from which species were sourced, and constructed candidate sets of possible models describing the relationship between thermal sensitivities and climate variables. We compared among these models on the basis of Akaike's Information Criterion to determine how acute and post-acclimation thermal sensitivities were related to aspects of climate variability and predictability (Supplementary Tables 1–12 and Figs 1–4). We restricted predictive analyses to those traits for which sufficient data to determine post-acclimation thermal sensitivity were available (Fig. 2e and Supplementary Methods). Hence, the traits we considered were whole-animal metabolic rate, which represents an integrated measure of aerobic energy turnover[10], and the activities of three key metabolic enzymes for predictions: lactate dehydrogenase, citrate synthase and cytochrome c oxidase, which quantify the capacities of glycolytic ATP production, the mitochondrial Krebs cycle and the mitochondrial electron transport chain, respectively.

In freshwater ectotherms, the post-acclimation Q_{10} of enzyme activities is positively related to both mean annual temperature and to the variability of temperature; hence, following acclimation, species from cool and thermally stable environments are less sensitive to temperature variation than species from warm and variable environments (Supplementary Tables 1–3 and Fig. 1). However, the post-acclimation thermal sensitivity of metabolic rate in freshwater animals was unrelated to climate (Supplementary Tables 4–6 and Fig. 1). The difference in thermal sensitivities of metabolic rates and enzyme activities indicates that maximal capacities (enzyme activities) respond differently to environmental change than the actual energy turnover (metabolic rate). The implication is that metabolic rates are not constrained by mitochondrial capacities, but other physiological systems, such as the cardiovascular system, could limit metabolic rates.

In marine animals, the post-acclimation Q_{10} of metabolic rate was also influenced by the variability of temperature, and species from thermally stable environments are less sensitive to temperature variation than species from more variable environments (Supplementary Tables 10–12 and Fig. 3). The post-acclimation Q_{10} of metabolic rate in terrestrial animals was negatively associated with mean annual temperature (Supplementary Tables 7–9 and Fig. 2). Thus, in contrast to freshwater animals, terrestrial animals from warm environments are less sensitive to temperature variation than animals from cool environments. There were insufficient data to test for effects of climate on enzyme activities for terrestrial and marine animals.

We used the mean values of thermal sensitivity to estimate changes in physiological rates over the past 20 years (1990–2010). Although the overall spatial coverage of the available data is poor, it is nonetheless clear that metabolic rates of terrestrial and freshwater species are likely to have increased relative to the 1900–1990 average. However, acclimation has reduced the extent of the increase that would otherwise have been observed (Supplementary Fig. 4). Marine species are less affected than terrestrial and freshwater species, because the magnitude of temperature change in the ocean is smaller than on land. Our predictions of acute responses are generally in good agreement with other predicted increases in metabolic rates of ectotherms[10].

The expected future responses of ectothermic animals to climate change (using climate predictions for 2080 under the A1B SRES emission scenario; Supplementary Methods) are that metabolic rates will increase substantially in terrestrial and freshwater species (Fig. 4), even though many species possess the capacity for thermal acclimation. Acclimation reduces the effect of temperature change, but in most instances the magnitude of the change outstrips the compensatory capacity of animals (Fig. 4). Again, marine species are predicted to be less affected than freshwater or terrestrial species, because the magnitude of temperature change is relatively smaller
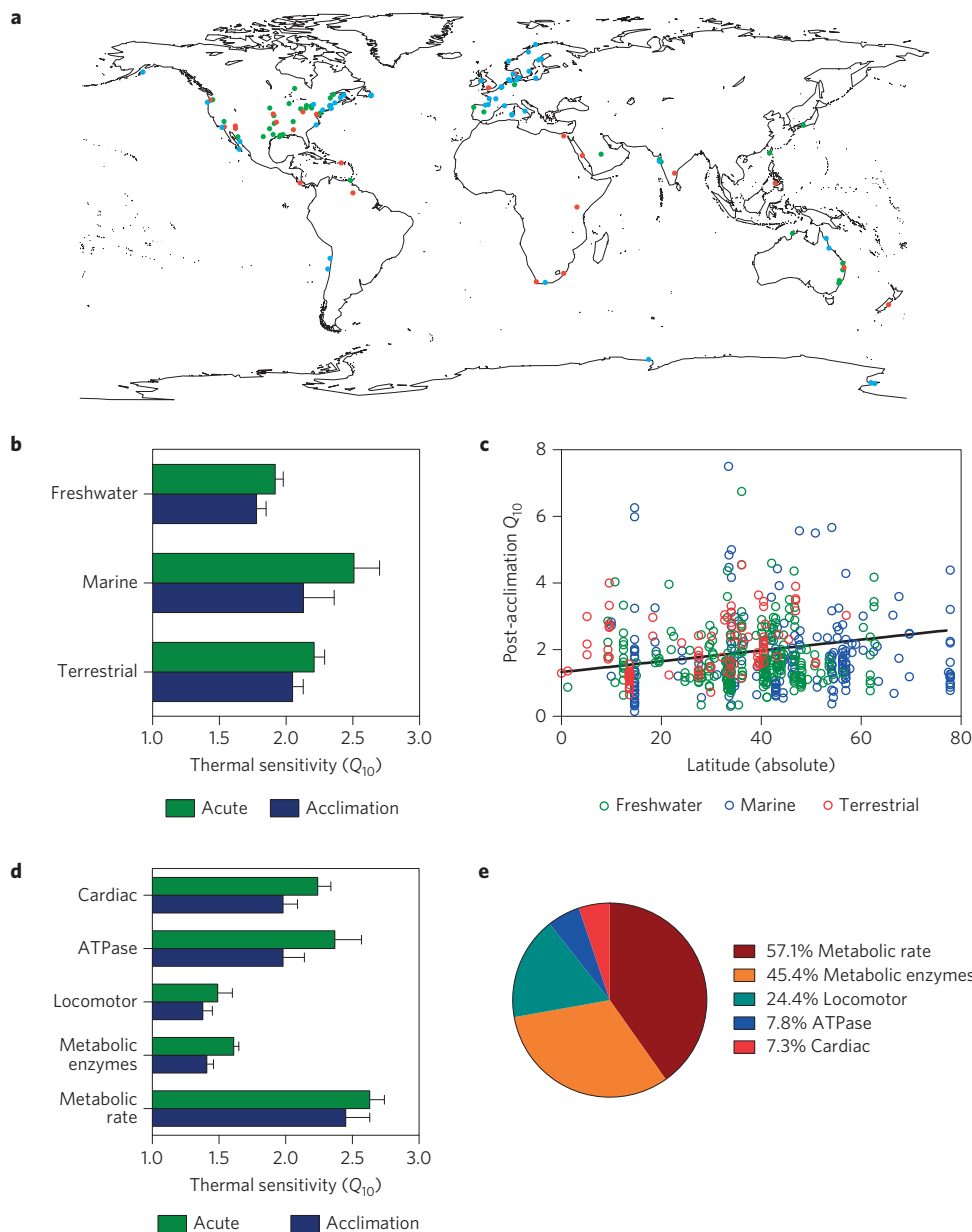
Figure 2 | The state of knowledge of the effect of thermal acclimation on physiological rates. a, Geographical distribution of organisms used in studies on thermal acclimation from 1968 to 2012; red circles represent data from terrestrial animals, green circles from freshwater animals, and blue circles from marine organisms. **b**, Acute and post-acclimation thermal sensitivities, expressed as Q_{10} values (means $\pm$ s.e.m.; note again, $Q_{10} = 1$, there is no change with changing temperature; $Q_{10} < 1$, rates decrease with increasing temperature, and $Q_{10} > 1$, rates increase with increasing temperature), in freshwater, marine and terrestrial habitats. In freshwater and marine animals, the increase in physiological rates with an increase in environmental temperature was less pronounced when animals had the opportunity to acclimate to the environment (mean acclimation period = 39.4 $\pm$ 1.9 (s.e.m.) days); these differences are indicated by the greater acute Q_{10} values (acute; green bars) compared to the post-acclimation (acclimation; blue bars) values. **c**, When given the opportunity to acclimate, physiological rates of animals from lower latitudes responded less positively to an increase in environmental temperature than animals from higher latitudes—that is, there was a significant increase in post-acclimation Q_{10} values with increasing latitude; data for different habitat types (freshwater—green circles; marine—blue circles; terrestrial—red circles) are shown separately, and the regression line is shown. **d**,**e**, The most commonly measured physiological responses in the literature were, in decreasing order, whole-animal metabolic rates, activities of metabolic enzymes, locomotor performance, cardiac responses and ATPase activities (**e**, the percentage of studies in which these traits were measured are shown in the legend; note that many studies measured several traits; therefore, the percentages do not add to 100). Post-acclimation Q_{10} values (blue bars) were lower than acute responses (blue bars) in all traits (**d**).

in the ocean. However, we would like to emphasize that the data available at present represents very biased coverage of the globe, and little is known about physiological responses of ectothermic fauna on most continents (Fig. 4 and Supplementary Fig. 4).

Climate envelope modelling which predicts that anthropogenic climate change may cause the extinction of up to 37% of all species[12]

is based on models of environmental equilibria with the underlying assumption that the present distribution of species (that is, the realized niche) also represents their potential distribution (that is, the fundamental niche). However, climate change does not simply change equilibrium conditions, but also causes environmental disequilibria, with rapidly changing conditions. Hence, the focus
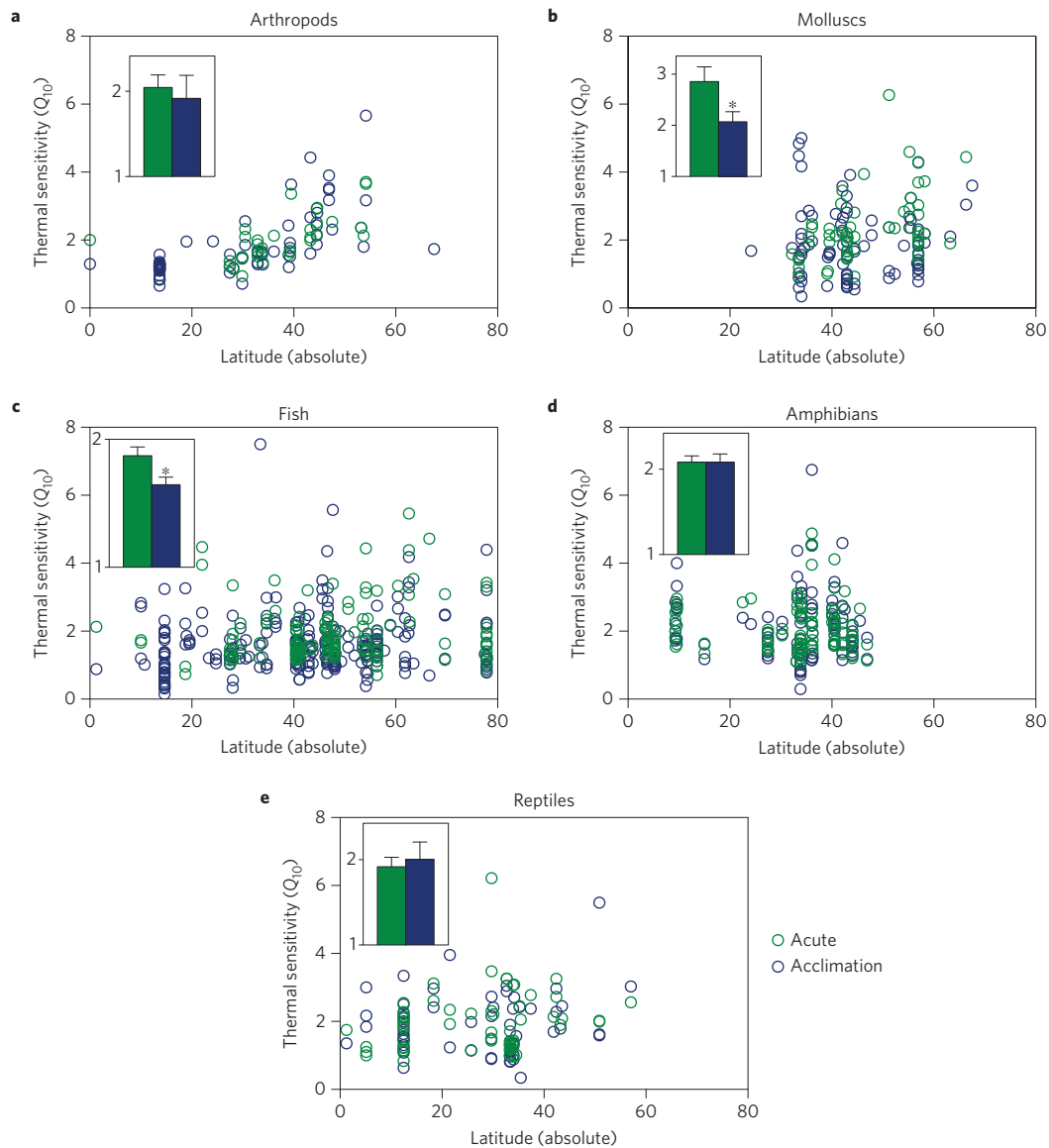
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Figure 3 | Thermal sensitivity of different taxa reported in the literature. a–e, Acute (green circles) and post-acclimation (blue circles) Q_{10} values for the ectothermic animal taxa that are most represented in the literature: arthropods (**a**), molluscs (**b**), fish (**c**), amphibians (**d**) and reptiles (**e**). Mean ($\pm$ s.e.m.) acute (green bars) and post-acclimation (blue bars) Q_{10} values for each taxonomic group are shown in the graphs inset within each panel; asterisks represent significant differences.

needs to shift to the capacity of animals to respond to change[13]. Current equilibrium conditions and distributions are of little interest, because the biological processes that buffer animal performance and fitness from change will determine distributional limits and extinctions. Most fundamentally, such buffering occurs physiologically, which in turn enables animals to function and interact ecologically.

Our analysis indicates that, regionally, physiological rates have increased already, and will continue to increase according to climate modelling. Increases in physiological rates are not necessarily detrimental per se. Increased temperatures may even be beneficial for ectotherms that are at present cold-limited by shifting performance closer to its optimum[14]. Hence, the effect of changes in temperature on fitness depends on where on the thermal performance curve environmental conditions are at present[15]. Plastic responses, such as acclimation, can shift performance towards its optimum regardless of environmental conditions, such that acclimation is beneficial by stabilizing reaction rates across temperature gradients[16,17]. The concern about environmentally

induced changes in physiological rates is that it disrupts the stoichiometry or homoeostasis of animal physiology as a whole. Physiological rates are not necessarily regulated to maximize flux, but to match flux between interconnected biochemical pathways, and disruption of these relationships will affect higher physiological systems[18]. Our analysis shows, however, that the efficacy of thermal acclimation is limited in its capacity to buffer animals from changes in the thermal environment. Costs associated with plasticity may limit its benefits in variable environments, leading to the evolution of fixed phenotypes[19]. Furthermore, there are limits to physiological compensation that are at least partly set by biochemical constraints to respond to temperature change. Hence, fitness costs and biochemical constraints can explain differences in acclimation between species, which in some cases may leave genetic adaptation as the principal response to climate variation[2]. The future direction in ecophysiological research should be to determine whether the predicted increases in physiological rates will compromise the function of the physiological system as a whole, and to what extent this can affect population persistence[20]. A second
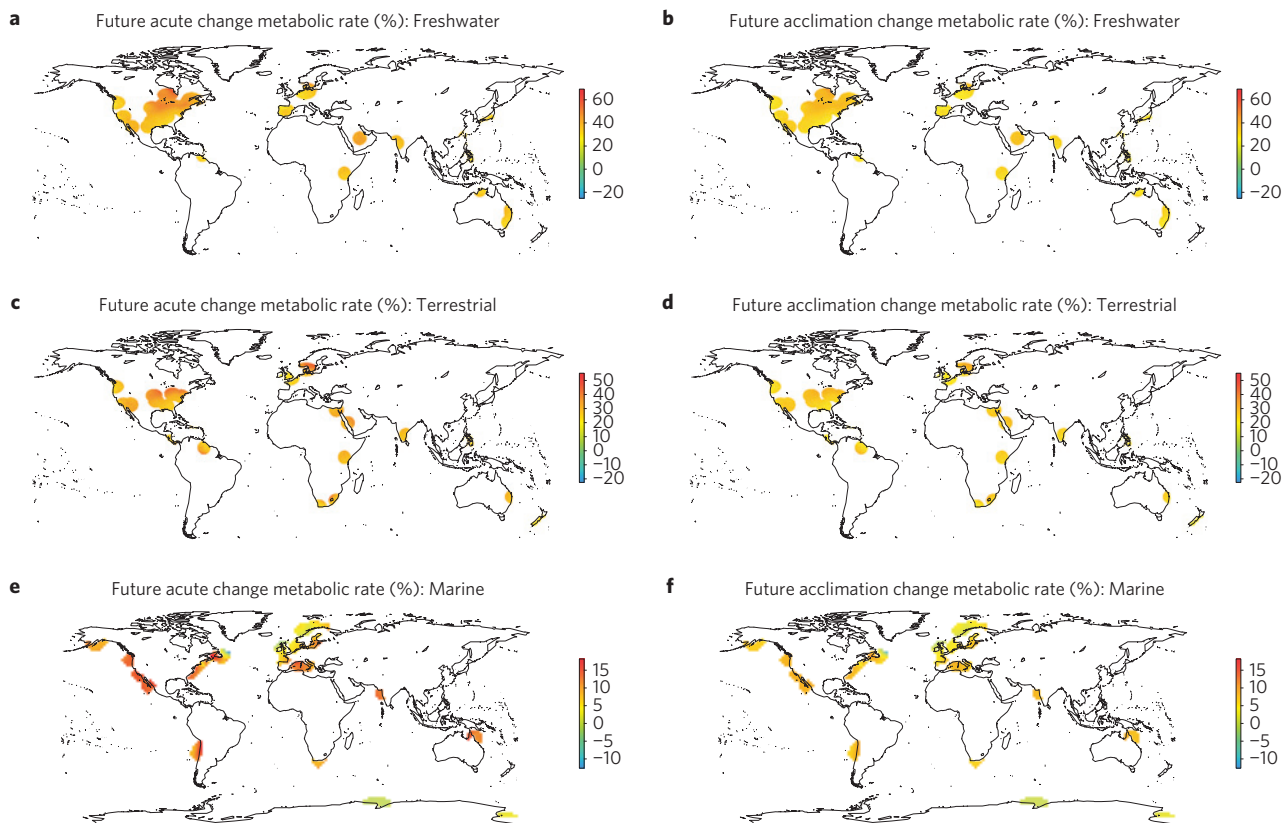
Figure 4 | Spatially explicit prediction of the effect of projected future climate change on metabolic rates. a–f, Predictions are made separately for freshwater animals (**a,b**), terrestrial animals (**c,d**) and marine animals (**e,f**). Changes in metabolic rates are expressed as the percentage change between the 1960–1990 climatology and the predicted conditions in 2080 for the CSIRO Mk3 projections under the A1B SRES emission scenario. Predictions are for an animal in the same location, calculated using either the acute thermal sensitivity of metabolic rates (**a,c,e**) or the acclimation sensitivity of metabolic rates (**b,d,f**), and are based on the change in climate at each location and the mean thermal sensitivity of the species from each habitat. Predictions are constrained to within 500 km of source localities, except for predictions for high latitudes (>70° S) in the Antarctic, which are constrained to within 300 km of source localities. Source localities used for plotting are those for post-acclimation thermal sensitivity, and represent source locations for 40 freshwater species (38 locations), 26 terrestrial species (24 locations) and 47 marine species (43 locations).

important gap in our understanding of how resilient animals are to environmental variability lies in sampling bias. Our meta analysis clearly shows a geographical bias in sample collection. Hence, the current state of knowledge of acclimation lacks generality, and there is an urgent need for experimental verification of our predictions in areas that are as yet not covered by the literature.

Methods

We performed a Web of Science (Thompson Reuters) search in January 2013 and from the resulting 4,000+ papers we analysed those that actually performed thermal acclimation treatments, or investigated acclimatization in ectotherms. We extracted data from those studies where ectothermic animals were exposed to at least two temperatures for at least one week. We included only those studies that, following acclimation, measured physiological rates at acute test temperatures that at least matched the acclimation temperatures. Hence, we extracted data from 205 publications (1968–2012), which yielded 637 measurements from 202 species. The physiological rates measured were burst and sustained locomotion, metabolic rates (standard, resting, routine and maximal), heart rates and enzyme activities. We recorded rates from each acclimation group at each test temperature, as well as taxonomic information, the geographical origin of the study species, and whether the animals were terrestrial or inhabited freshwater or marine environments (see Supplementary Methods for more detail).

Data analyses were conducted in R (ref. 21) using lme4 v0.999999-0 (ref. 22), with linear mixed models fit using maximum likelihood. The non-independence of data for related species was incorporated by including nested random effects for the taxonomic levels of phylum, class, family and genus. The non-independence of data representing multiple measurements of the same species was accounted for by including species as a random effect (nested within the taxonomic levels). Outliers were excluded before analysis, and were defined as

chronic slopes greater than 0.2 ($Q_{10}=7.4$) and acute slopes less than -0.05 ($Q_{10}=0.007$); this resulted in the exclusion of six and seven data points, respectively. Note also that in >90% of studies in our data set (Supplementary Data) physiological rates of animals from each acclimation treatment were measured either at a single acute test temperature which coincided with acclimation temperature, or at two acute test temperatures per treatment which coincided with the two acclimation conditions. In the former cases, it was not possible to calculate acute responses within acclimation treatments.

We further subdivided the data by trait for post-acclimation responses. Of the 32 different traits in the full data set (Supplementary Data) only 12 traits were represented by six or more measurements across all species; of these 12, only 10 traits were represented by six or more measurements for either freshwater, terrestrial or marine species. Four of these (metabolic rate, lactate dehydrogenase activity, citrate synthase activity, cytochrome c oxidase activity) are represented across species for at least two habitat types. Examination of the post-acclimation thermal sensitivity of these traits revealed that the enzyme activities all have broadly similar thermal sensitivities, which are lower than that of metabolic rate, so we have pooled their data. To estimate the relationship between climate variables and the post-acclimation thermal sensitivities of metabolic rate and enzyme activities, we constructed candidate model sets to explain variation in the post-acclimation thermal sensitivities (see Supplementary Method and Results).

Climate data for species from terrestrial and freshwater habitats were extracted in R (ref. 22) from WorldClim climatologies[23] and long-term monthly climate grids[24] using raster v2.1-16 (ref. 25) and rgdal v0.8-6 (ref. 26). Note that we used air temperature variation for predictions of freshwater environments as well because mean water temperatures track mean air temperatures, and variations in temperatures are proportional in air and water[27]. For marine environments, data were extracted from long-term monthly sea surface temperature grids[28]. To avoid the problems associated with data dredging and model overfitting (see, for example, ref. 29), we selected, a priori, a set of three predictor variables that captured spatial and temporal variation in biologically

important abiotic variables at the scales relevant to acclimation (weeks to years). From the long-term records, we calculated the following three climate variables: mean trend in ambient temperature at monthly resolution from 1960 to 1990; temperature standard deviation of monthly mean temperature from 1900 to 1990; 12-month autocorrelation of temperature from 1900 to 1990; higher values mean that variation in temperature is predictable from year to year—that is, climate is predictable—and lower values indicate a less predictable climate. We verified whether temporal resolution of the data and acclimation duration influenced our conclusions, which was not the case (see Supplementary Methods and Results for details).

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Author contributions

F.S. and C.E.F. conceived the idea and extracted the data from the literature, C.R.W. conducted the analysis, wrote the manuscript and prepared figures, F.S. wrote the manuscript and prepared figures, and C.E.F. edited the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to F.S.

Competing financial interests

The authors declare no competing financial interests.