

Impacts of climate warming on terrestrial ectotherms across latitude

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The impact of anthropogenic climate change on terrestrial organisms is often predicted to increase with latitude, in parallel with the rate of warming. Yet the biological impact of rising temperatures also depends on the physiological sensitivity of organisms to temperature change. We integrate empirical fitness curves describing the thermal tolerance of terrestrial insects from around the world with the projected geographic distribution of climate change for the next century to estimate the direct impact of warming on insect fitness across latitude. The results show that warming in the tropics, although relatively small in magnitude, is likely to have the most deleterious consequences because tropical insects are relatively sensitive to temperature change and are currently living very close to their optimal temperature. In contrast, species at higher latitudes have broader thermal tolerance and are living in climates that are currently cooler than their physiological optima, so that warming may even enhance their fitness. Available thermal tolerance data for several vertebrate taxa exhibit similar patterns, suggesting that these results are general for terrestrial ectotherms. Our analyses imply that, in the absence of ameliorating factors such as migration and adaptation, the greatest extinction risks from global warming may be in the tropics, where biological diversity is also greatest.

biodiversity | fitness | global warming | physiology | tropical

Global warming in this century may be the largest anthropogenic disturbance ever placed on natural systems (1, 2). Its impact on species is likely to vary geographically (2–4), but a mechanistic framework to predict its magnitude and global distribution has not yet been developed (5). One important determinant of biological responses to climate change will be the degree of warming itself, which will continue to be greater at high latitudes (6). Also relevant, however, is the physiological sensitivity of organisms to changes in the temperature of their environment (7, 8). The thermal tolerance of many organisms has been shown to be proportional to the magnitude of temperature variation they experience (9–11), a characteristic of climate that also increases with latitude. Evaluating the impacts of rapidly changing climates on population fitness and survival thus requires linking geographic patterns of the magnitude of temperature change with the physiological sensitivity of organisms to that change (12).

Ectotherms constitute the vast majority of terrestrial biodiversity (13) and are especially likely to be vulnerable to climate warming because their basic physiological functions such as locomotion, growth, and reproduction are strongly influenced by environmental temperature. The ability of ectotherms to perform such functions at different temperatures is described by a thermal performance curve (14), which rises gradually with temperature from a minimum critical temperature, CT_{min} , to an optimum temperature, T_{opt} , and then drops rapidly to a critical thermal maximum, CT_{max} (Fig. 1). Critical temperatures CT_{min} and CT_{max} , operationally defined by the limits of organism performance, have been measured for diverse ectotherms (15–18) and usually covary with latitude, reflecting at least partial

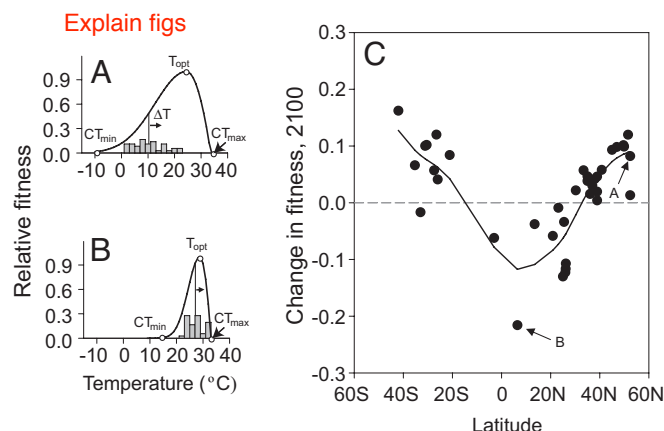


Fig. 1. Fitness curves for representative insect taxa from temperate (A) and tropical (B) locations, and (C) the change in fitness because of climate warming for all insect species studied, as a function of latitude. (A and B) Fitness curves are derived from measured intrinsic population growth rates versus temperature for 38 species, including *Acyrthosiphon pisum* (Hemiptera), from 52°N (England) (A), and the same for *Clavigralla shadabi* (Hemiptera) from 6°N (Benin) (B). CT_{min} , T_{hab} , T_{opt} , and CT_{max} are indicated on each curve. Climatological mean annual temperature from 1950–1990 (T_{hab} , drop lines from each curve), its seasonal and diurnal variation (gray histogram), and its projected increase because of warming in the next century (ΔT , arrows) are shown for the collection location of each species. For each of 38 species, fitness is integrated over both seasonal and diurnal temperature cycles for both the observed climate of the late 20th century (1950–1990) and for a model-simulated climate of the late 21st century (2070–2100) (23). (C) Predicted change in fitness of insects versus latitude is a measure of the impact of 21st century climate warming on population growth rates. Negative values indicate decreased rates of population growth in 2100 AD and are found mainly in the tropics. Positive values are found in mid- and high-latitudes. Line is a spline-fit with a span of 0.9.

adaptation of ectotherms to their climate (9–11). Thermal performance curves index the direct effect of temperature on organism fitness (14–15), and thus provide a physiological framework for elucidating a fundamental component of the

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impact of global climate change in a spatially explicit and empirically constrained way.

Results

Estimating Impact on Insects. Insects are the largest group of terrestrial organisms. The impact of temperature on intrinsic rates of population growth (r), a direct measure of Darwinian fitness, has been quantified experimentally for numerous insect species from around the globe (15). We use these data to construct fitness curves for each species to calculate the fractional change in population growth rate from the observed climate of the late 20th century (1950–1990) (19) to a model-simulated climate (20) of the late 21st century (2070–2100), where climate data were taken at the source site of each species (see [supporting information \(SI\) Methods](#) and [Figs. S1 and S2](#)). In both time periods, insect body temperature is assumed to track ambient air temperature, and fitness is averaged through diurnal and monthly temperature variations, implicitly accounting for potential shifts in organisms' preferred activity times (see [SI Methods](#)). The difference between population growth rates under current versus projected climates quantifies the direct thermal impact (positive or negative) of future warming on the fitness of organisms.

After a century of warming, population growth rates of insects change dramatically and exhibit a conspicuous latitudinal trend (Fig. 1). At mid- to high-latitudes, population growth rates are predicted to increase, indicating enhanced population fitness because of warming. In the tropics, however, intrinsic rates of population growth are expected to decrease by up to 20%, implying that warming will substantially reduce fitness. This latitudinal trend is robust: it is insensitive to how fitness is averaged through time, or to potential differences between environmental and body temperatures (see [SI Methods](#) and [Figs. S3 and S4](#)). Instead, the pattern of global warming's impact on insect fitness derives from fundamental geographic relationships between climate and physiological performance that can be distilled into two simple heuristic indicators, and that are observed among several other taxa.

Warming Tolerance and Thermal Safety Margin. The impact of warming on insect fitness at each location depends on several factors, including the breadth of each performance curve, its position relative to the mean climate, and the spectrum of local temperature variability. However, the basic latitudinal trend in impact can be qualitatively elucidated by using two simple metrics that characterize the geographic covariations of fitness curves and climate. In addition to providing a heuristic explanation for the impact of warming across latitude, these two metrics allow impacts diagnosed for insects at point locations to be extrapolated globally and generalized to other ectotherm taxa.

In the context of long-term climate warming, a key characteristic of an ectotherm's performance curve is the difference between its critical thermal maximum and the current climatological temperature of the organism's habitat, T_{hab} , here taken to be mean annual surface air temperature. This quantity approximates the average amount of environmental warming an ectotherm can tolerate before performance drops to fatal levels, and we refer to this difference as an organism's "warming tolerance," ($WT = CT_{max} - T_{hab}$). Although annual mean temperature provides a single robust climate statistic for referencing the position of performance curves, its use does not imply that mean temperature determines an organism's fitness, which will vary throughout the year.

For insect species, CT_{max} decreases slightly with latitude (11), but not as rapidly as does surface air temperature, either on an annual basis or during the hottest months ([Fig. S1](#)). The warming tolerance of tropical insects is, on average, only one-fifth that of

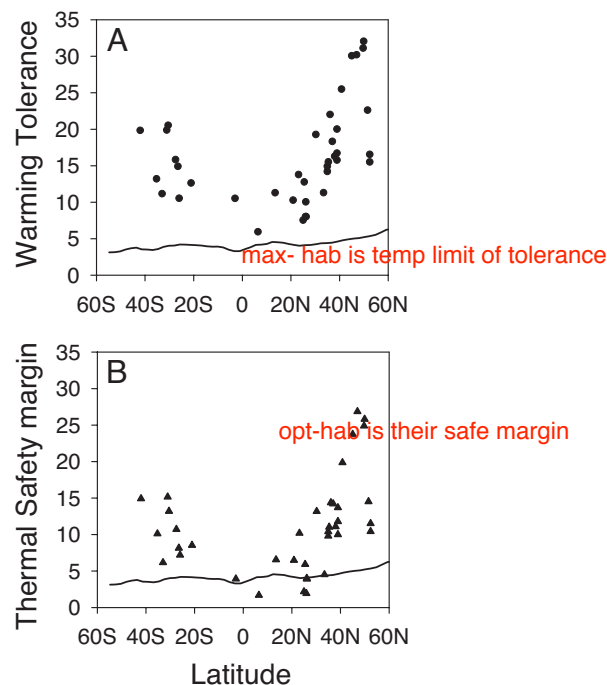


Fig. 2. Latitudinal trends in warming tolerance ($CT_{max} - T_{hab}$; A) and thermal safety margin ($T_{opt} - T_{hab}$; B), the primary heuristic indicators of the impact of warming on the thermal performance of insects. The projected magnitude of warming by 2100 (ΔT ; black line) erodes $\approx 50\%$ of the warming tolerance of tropical insects and raises the temperature of their habitats above their thermal optima for much of the year, resulting in decreased thermal performance, whereas temperatures will remain below the thermal optimum for many high latitude species. Although these heuristic indicators are defined by using annual mean temperature (T_{hab}), the calculated impact of warming on performance takes into account both seasonal and diurnal temperature variations.

mid-latitude insects (Fig. 2A). Tropical insects will thus approach near-lethal temperatures much faster than will insects from temperate climates, even though the rate of warming in the tropics is predicted to be half that of high latitudes (6). The latitudinal trend in warming tolerance alone will tend to increase the impact of tropical warming relative to that at higher latitudes.

A second important characteristic of performance curves is the difference between an organism's thermal optimum (T_{opt}) and its current climate temperature, T_{hab} . We call this difference the "thermal safety margin" ($TSM = T_{opt} - T_{hab}$). Species living in environments that are already close to their physiological optimum have small thermal safety margins, and thus even small amounts of warming will likely decrease performance. In contrast, species with large thermal safety margins are living in environments that are on average cooler than optimal, and should experience initial increases in population growth rates and performance as temperatures rise.

For insect species, thermal safety margins increase sharply with latitude (Fig. 2B). Tropical insects are already living at environmental temperatures very close to their physiological optimum ($TSM \approx 0$; see *Acyrtosiphon pisum* in Fig. 2), whereas higher-latitude insects are experiencing environmental temperatures significantly below T_{opt} , even during summer ($TSM > 0$, see *Clavigralla shadabi* in Fig. 2). The latitudinal trend in the impact of climate change inferred from warming tolerance alone is thus accentuated by the poleward increase in thermal safety margins, because it allows insect performance to increase in colder climates, at least initially. Taken together, warming tolerance and thermal safety margin thus provide simple but

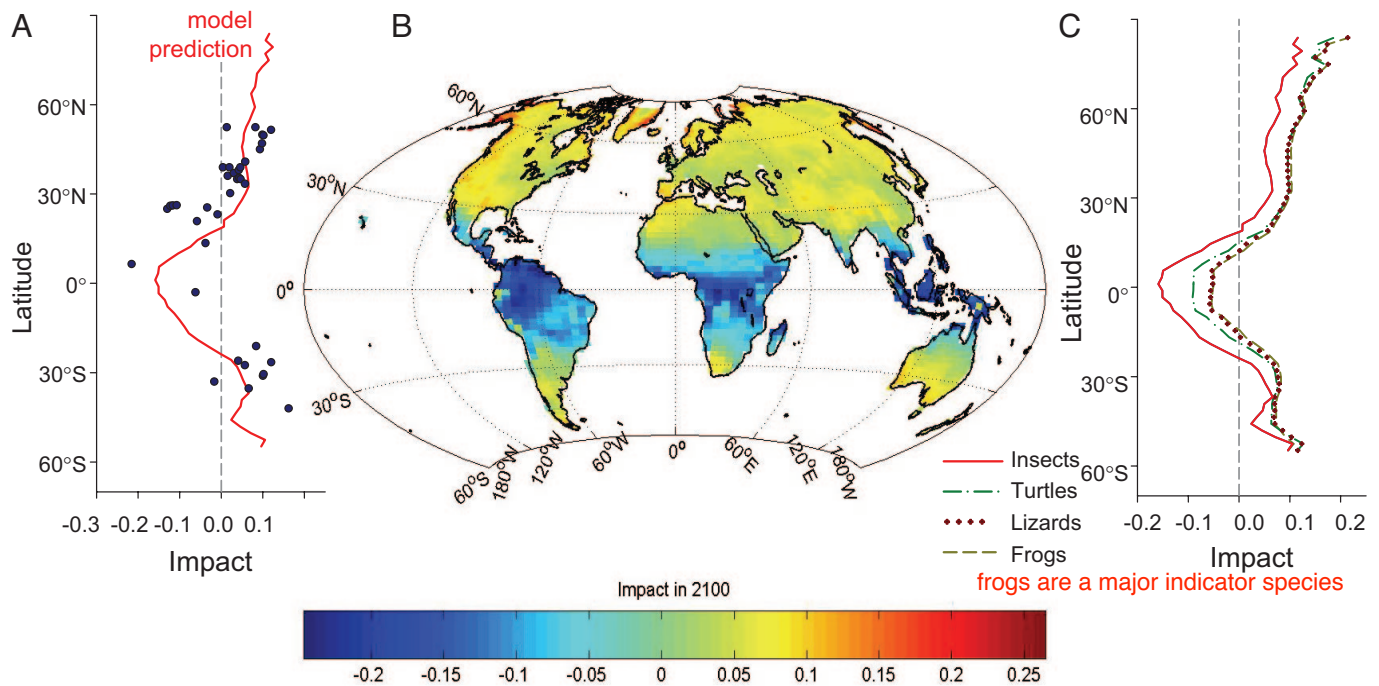


Fig. 3. Predicted impact of warming on the thermal performance of ectotherms in 2100. (A) Impact versus latitude for insects using thermal performance curves fit to intrinsic population growth rates measured for each species (black circles, from Fig. 1) and for a global model (red line) in which performance curves at each location are interpolated from empirical linear relationships between seasonality and both warming tolerance and thermal safety margin. (B and C) Results from the simplified conceptual model are shown globally for insects (B) for which performance data are most complete, and versus latitude for three additional taxa of terrestrial ectotherms: frogs and toads, lizards, and turtles (C), for which only warming tolerance was available. On the basis of patterns in warming tolerance, climate change is predicted to be most deleterious for tropical representatives of all four taxonomic groups. Performance is predicted to increase in mid- and high-latitudes because of the thermal safety margins observed there for insects, and provisionally attributed to other taxa.

useful indicators for understanding the latitudinal trend in the impact of warming calculated from detailed climate data and individual insect performance curves (Fig. 1).

Global and Taxonomic Extrapolation. We now combine these metrics into a simple conceptual model that we use first to extrapolate results for insects to the global scale, and next to estimate impacts of warming on other taxonomic groups for which only limited performance data are available. In this model, warming tolerance and thermal safety margins are assumed to capture the most salient geographic variations in the performance curves of ectotherms. Patterns of warming tolerance and thermal safety margins are estimated from their empirical relationships to the magnitude of the seasonal temperature cycle. Climate variability has long been considered a mechanistic driver of differences in thermal performance across latitude (10); high latitudes have greater climatic variability, which should favor organisms with a broad thermal tolerance. Indeed, seasonality is a strong predictor of both warming tolerance and thermal safety margin of insects (Fig. S5 and Table S1). We use these relationships to interpolate insect fitness curves from specific locations to the global scale. We then compute the impact of warming on fitness worldwide, accounting for both seasonal and diurnal temperature cycles (see SI Methods).

The global impact of 21st century warming on insects in this simplified model reproduces the qualitative pattern diagnosed above using actual fitness curves of individual insect species (Fig. 3A). This concordance confirms that the most important geographic variations in fitness curves are indeed captured by the heuristic indicators, warming tolerance, and thermal safety margin. The most deleterious impacts of warming on population growth rates are again predicted to occur in the tropics (Fig. 3B).

This result depends only on the latitudinal increase in warming tolerance and is independent of the latitudinal increase in thermal safety margins (see SI Methods and Fig. S6). In contrast, the predicted increase in population growth rates at higher latitudes is due entirely to the relatively large thermal safety margins observed in cold climates and thus depends strongly on the poleward trend in thermal safety margins (see SI Methods and Fig. S6).

To examine the generality of these results beyond insects, we investigated three groups of terrestrial vertebrates (frogs, lizards, and turtles), using published studies in which critical thermal limits were experimentally determined for at least 12 populations of closely related taxa across large climate gradients [(16–18), Table S1]. In each taxonomic group, warming tolerance of an organism increases strongly with the seasonal temperature variability of its habitat (Fig. S5). This consistent pattern indicates that warming will cause tropical vertebrate ectotherms to approach their critical maximum temperatures proportionately faster than similar high-latitude species, despite lower absolute rates of tropical warming. Consequently, tropical representatives of all four taxonomic groups will likely experience the most deleterious changes in thermal performance during warming (Fig. 3C).

In contrast, many mid- to high-latitude vertebrates should experience enhanced thermal performance because of warming, because they tend to inhabit climates that are currently cooler than optimal. Some high-latitude ectotherms may have narrower thermal safety margins than do insects, and such species would show more modest increases in performance than we have predicted (Fig. 3C). In addition, if global temperatures continue to rise beyond the 21st century, as projected under most climate scenarios (6), even high-latitude species will begin to experience

The global model developed for insects can now be extended to three other taxonomic groups: frogs, lizards, and turtles. For these vertebrate taxa, measured critical thermal limits have been published for multiple related species at locations spanning large climate gradients (see Fig. S5 and Table S1), but empirical thermal performance curves are generally unavailable. Using the same procedure as for insects, we compute warming tolerance and its linear correlation to seasonality at the site where each species was collected. We find strong positive relationships between seasonality and warming tolerance that are highly consistent across all taxa (Fig. S5).

Because estimates of T_{opt} were not available for these taxa, we have provisionally ascribed the relationship between thermal safety margin and

seasonality for insects to these taxa as well. Although this assumption introduces some uncertainty into our prediction of increasing high-latitude performance, it does not affect our conclusion that the most deleterious impacts will be in the tropics. The strong latitudinal gradient in warming tolerance permits no realistic pattern of thermal safety margins that could reverse the overall latitudinal trend in impact (see SI Methods and Fig. S6).

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