ECOLOGY

Insect thermal baggage

Strong positive selection on cold hardiness and relaxed selection on heat hardiness experienced by range-expanding populations may help to explain why ectothermic animals generally have broader thermal tolerance towards the poles, and shed new light on their climate vulnerabilities.

Caroline Williams

The global climate is changing rapidly, challenging the ability of organisms to persist. In response, species can move to new habitats, adapt *in situ,* or go extinct[1]. One of the major goals of contemporary biology is to find ways to predict future responses based on historical patterns of responses to climate. This requires that we understand the causes underlying existing patterns. One of the most robustly supported macrophysiological patterns for ectothermic animals is that of the increasing thermal tolerance breadth towards the poles. Now, a study by Lesley Lancaster[2] suggests a hypothesis to explain this pattern — one that takes into account the large-scale poleward movement of organisms that has been occurring since the last glacial maximum, and which has been accelerating due to contemporary climate change[3]. The thermal tolerance breadth describes the range of temperatures over which a species, population or individual can persist, survive or sustain activity. It is bounded by upper and lower critical temperatures beyond which these activities are not possible. In marine and terrestrial ectotherms, the thermal tolerance breadth increases with latitude[4,5]. This occurs because lower critical temperatures decrease strongly toward the poles, whereas upper critical temperatures remain relatively invariant across latitude. Two primary (non-exclusive) hypotheses have been put forth to account for this pattern: (1) upper critical temperatures are conserved due to strong thermodynamic constraints on heat tolerance, leading to weak responses to selection; or (2) selection on upper critical temperatures is relatively invariant because maximum body temperatures remain similar across latitude, whereas selection on lower critical temperatures is stronger because minimum body temperatures decrease strongly towards the poles[6–8]. Wide thermal tolerance breadth in high-latitude species may buffer them from the negative effects of future warming. However, these hypotheses both assume that animals are in evolutionary equilibrium with their environments — an assumption that may not hold because the changing climate has long been driving large-scale poleward movements.

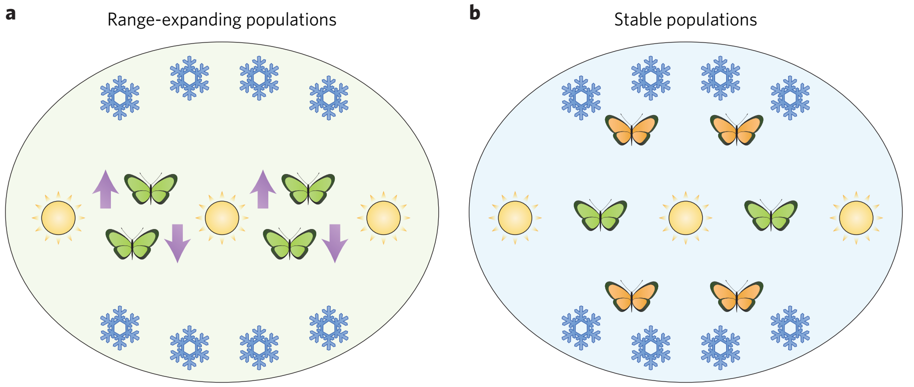

Figure 1 | A comparison of the thermal tolerances of range-expanding and stable populations. **a**, Strong selection in range-expanding populations causes a rapid decrease in lower thermal limits; relaxed selection causes a slow decay in upper thermal limits. The thermal breadth increases with latitude. **b**, Stable populations are locally adapted to the environment, and thermal breadth remains constant across a latitude.

In her study, Lancaster suggests an alternate, third hypothesis to explain the increasing thermal tolerance breadth with latitude. As animals move poleward, they encounter strong positive selection on cold hardiness, whereas selection on heat hardiness is relaxed (Fig. 1). If having heat hardiness in excess of requirements is not unduly costly, it could take many generations for heat hardiness to decay from historical levels, whereas strong selection on cold hardiness could produce a rapid evolutionary response. This asymmetric selection would produce the observed pattern of increasing thermal tolerance breadth towards the poles. By contrast, stationary (non-range-expanding) populations would have had time to adapt to their local conditions, and thermal breadth would remain more constant across latitude as both maximum and minimum critical temperatures followed environmental gradients.

Lancaster tested this hypothesis by augmenting and analysing a previously compiled dataset on insect thermal tolerance[4]. She classified species either as range expanding or non-range expanding, and fit models describing upper and lower thermal limits as a function of latitude. The best models separated the range-expanding and non-range-expanding species, and showed that range-expanding species showed the traditional pattern of increasing thermal breadth towards the poles (due to invariant upper thermal limits across latitude, whereas lower thermal limits declined); but non-expanding species had constant thermal breadth across latitude, with concordant decreases in both upper and lower thermal limits towards the poles. This is consistent with her hypothesis that increases in thermal tolerance breadth with latitude are caused by ongoing poleward range expansions.

As with any study relying on a meta-analysis of previously collected data, the available dataset had limitations. In particular, latitudinal coverage is patchy, with few measurements in low latitudes, and most of the non-range-expanding species are island endemics, which could reduce the generality of the findings. To address this concern, Lancaster performed a second analysis using only species with measurements on two populations, allowing her to test the prediction that a latitudinal increase in thermal tolerance breadth would be more likely near the poleward range boundary, where range expansions are most recent. In concordance with this prediction, tolerance breadths increased with latitude most often when both populations were in the poleward portion of their species range, consistent with the hypothesis that older equatorial populations are more likely to be locally adapted to their thermal environment. Fruitful avenues for future research would include improving sample sizes, latitudinal coverage, and information on range dynamics in this dataset, which would increase confidence in the findings and perhaps modify the precise shapes of the response of upper and lower thermal limits across latitudes.

These two independent analyses are consistent with the hypothesis that the increasing thermal breadth towards the poles is influenced by ongoing poleward range expansions. Lancaster's study highlights the role of biogeography and migration patterns in shaping global patterns of thermal physiology, and suggests that knowing the biogeographic history of populations could help predict their responses to climate change. The research does not refute the hypotheses that upper critical limits are constrained to some degree, nor that the selection on upper limits is relatively invariant across latitude, compared to selection on lower thermal limits. Laboratory selection experiments confirm that lower limits are less evolvable than upper limits[9], and it is undeniable that maximum temperatures change less than minimum temperature across latitude. However, this work suggests that these explanations, which are based around natural selection, may not be necessary to explain apparent invariance of upper thermal limits across latitude. An important implication is that stable, insular or endemic species, with narrower thermal breadths and less gene flow to provide heat adapted southern alleles, may be at greater risk than previously thought. Finer-scale and experimental approaches examining evolution of thermal tolerances during range expansion are required, and are already providing some support for the range-expansion hypothesis[10].

This work[2] has added a plausible and well-supported third hypothesis to the table regarding the causal mechanisms underlying increases in thermal tolerance breadth with latitude, and promises to stimulate research that may ultimately improve our ability to predict organismal responses to climate change.

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Acknowledgements

The author thanks Mary Power for helpful comments.

AGRICULTURAL IMPACTS

Mapping future crop geographies

Modelled patterns of climate change impacts on sub-Saharan agriculture provide a detailed picture of the space- and timescales of change. They reveal hotspots where crop cultivation may disappear entirely, but also large areas where current or substitute crops will remain viable through this century.

William R. Travis

Climate change is sometimes illustrated as shifting geography. A future, warmer Vermont, for example, can be mapped as climatologically shuffling south-westwards across Ohio, down to present-day Alabama (http://go.nature.com/ePEBnn). Such animations can be quite effective at communicating climate trends. Geographical analogues and other spatiotemporal approaches, when applied technically with due attention to eco-climatological dynamics and spatial arrangements, can also yield insights into potential resource patterns of the Earth's climatic future. Rippke and colleagues[1], reporting in *Nature Climate Change*, apply spatiotemporal analysis to agricultural impact and adaptation assessment to provide a glimpse of how climatic changes might change crop production patterns in sub-Saharan Africa. The results are both encouraging and concerning. Some crops are geographically robust, shifting little over this century, so that they are able to maintain their role in regional food production even on a markedly warming planet. Others are squeezed from much of their current territory, signalling the need for proactive adaption planning to avoid serious production losses.

Geographical analogues were among the earliest approaches to assessing what climate change might mean for natural resource systems. Rough maps of shifting climate futures became iconic symbols of the climate change threat in the 1970s and 1980s. If the climate conditions at the time placed the American Corn Belt in the Upper Midwest, where might it shift in a climate affected by increasing concentrations of atmospheric carbon dioxide? With just 1 °C of warming, it would move about 100 miles north with an edge slipping into Canada, according to a frequently reproduced map from the 1980s[2]. Agro-ecological zonation was also applied as a tool for projecting changes in data-poor areas such as Africa[3], and for historical reconstructions of climate impacts[4]. The geographical approach has since been eclipsed by the more reliable statistical and process-based crop models, which have become available for most major crops in most regions. Meta-analysis on large suites of crop model runs has become the standard in agricultural impact