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The role of tolerance variation in vulnerability forecasting of insects

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Quantifying the amount of climatic change organisms can withstand before exceeding their physiological tolerance is a cornerstone of vulnerability forecasting. Yet most work in this area treats tolerance as a fixed trait. We review recent work that quantifies variation in high temperature tolerance across bioclimatic gradients, and we explore the implications for vulnerability to climate change. For some sources of variation, including differences in the evolutionary potential of heat tolerance across latitude, the typical biogeographic pattern of high vulnerability in the tropics is exacerbated. For other sources of variation, including certain types of plastic variation in heat tolerance, the biogeographic pattern of high tropical vulnerability is diminished. As a consequence, thermal tolerance variation should not be ignored in vulnerability forecasting.

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Forecasting vulnerabilities to climate change with tolerance traits

Insects provide critical ecosystem services that support biodiversity and human well-being [1]. However, several recent studies point to an alarming rate of decline in insect populations over the last several decades [2]. In some cases, these declines have occurred even within protected areas and are not a direct consequence of habitat loss [3], but rather point to the effects of recent climate change. As humans continue to modify the environment, insect declines are likely to increase in the future [4]. The ability to forecast insect declines, with respect to species identity and geographic location, is therefore of paramount importance, as this information that can be used by conservation planners to help mitigate insect declines [5,6]. How best to forecast insect responses to global change remains an area of active research and debate [7].

Trait-based approaches have met with considerable success, especially those which examine the relationship between temperature change — a hallmark of global change — and thermal physiological traits [8]. However, a major shortcoming of these approaches is that they treat the tolerance traits as fixed, when in reality, trait values can shift as individuals remodel their physiology under different environmental conditions within a generation (phenotypic plasticity) or as populations exhibit changes in their mean tolerance across generations (evolutionary change) [9•]. Here we review current biogeographic patterns of thermal tolerance in insects, and explore the implications of these patterns with respect to insect vulnerability to global climate change. We further consider how plastic and evolved variation in thermal tolerance might influence forecasts of vulnerability to global change.

Thermal physiology-based measures of vulnerability: metrics and patterns

Ectothermic species tend to exhibit stereotypical performance responses to temperature, where performance rises from some lower threshold temperature up to a thermal optimum, at which performance is greatest, before declining sharply until the upper threshold is reached [10]. The difference between measures of heat tolerance (such as the lethal thermal limit or the critical thermal maximum, CT_{max}, which defines the loss of coordinated movement) and environmental temperature are broadly termed 'warming tolerance' and have been used extensively to assess the vulnerability of insects (and closely related arthropods) to global climate change. Relatedly, the difference between environmental temperature and the thermal optimum is called the 'thermal safety margin' and has been used in a similar manner to estimate how much of a thermal buffer an organism has before becoming vulnerable to climate change [11,12,13,14,15••,16] (Figure 1, Box 1, Table 1).

The emerging biogeographic picture from the current research is one of increased vulnerability of tropical insects [16]. This pattern appears to be driven by species at low latitudes exhibiting narrow thermal tolerance breadths (the range between cold and heat tolerance), which places them very close to their thermal optimum and heat tolerance relative to the environmental

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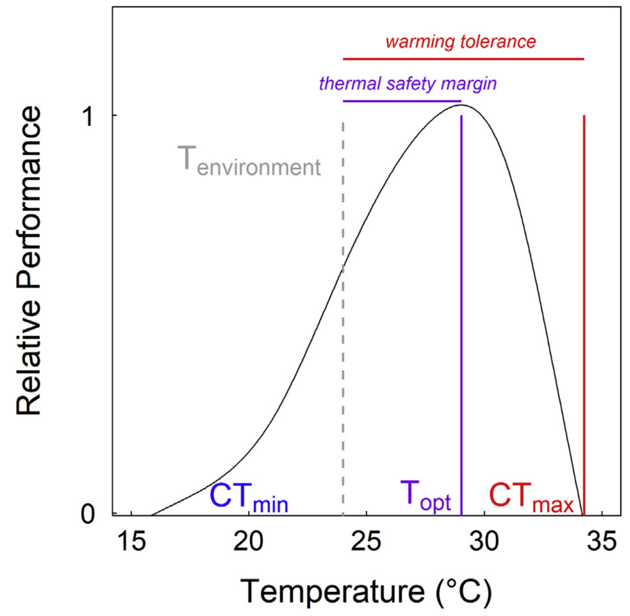
Figure 1



Thermal performance curve, indicating cold tolerance (as assessed by the minimum critical temperature for performance, CT_{min}); heat tolerance (as assessed by the maximum critical temperature for performance, CT_{max}); thermal optimum (T_{opt}, the temperature at which performance is greatest). Environmental temperature is shown in the dashed line, and vulnerability indices are presented relative to $T_{environment}$: thermal safety margin is the difference between T_{opt} and $T_{environment}$, and warming tolerance is the difference between CT_{max} and $T_{environment}$.

Box 1 Glossary of terms.

Descriptors of thermal performance and vulnerability

Thermal tolerance – the upper or lower endpoint of performance across a range of environmental temperatures, and a key trait in vulnerability forecasting with organismal physiology

CT_{max} — the critical thermal maximum, often defined by the (upper) temperature at which coordinated activity is lost; a commonly used measure of heat tolerance, and which forms the basis for many assessments of warming tolerance

CT_{min} — the critical thermal minimum, often defined by the (lower) temperature at which coordinated activity is lost

T_{opt} — the optimal temperature at which performance is maximized for a given response, and which forms the basis for assessment of the thermal safety margin

Thermal safety margin — the difference between the thermal optimum and environmental temperature

Warming tolerance — the difference between a measure of heat tolerance and environmental temperature

Microclimate — the climatic conditions nearer to those that organisms inhabit rather than air temperature at a height of 2 m in the shade as is the basis for most warming tolerance assessments, for example, from climatic databases such as WorldClim

Mechanisms underlying variation in thermal tolerance

Plasticity — remodeling of an organism's thermal tolerance within a generation; for example, exposure to a warmer temperature environment which increases the expressed heat tolerance trait value

Evolutionary change — shifts in tolerance trait values across generations; here, we are specifically interested in allele frequency changes over generations, as contrasted with, for example, maternal effects which also manifest across generations

Evolutionary potential — a general term that describes the potential for a trait to evolve based on the amount of additive genetic variation; for example, narrow-sense heritability (the amount of additive genetic variation divided by the total phenotypic variation) is a common measure of evolutionary potential

Genetic accommodation — a process by which unexpressed genetic variation is revealed under novel environments and selection then acting on this variation; an example of the potential interaction between plastic and evolutionary mechanisms that generate variation in tolerance traits under climate change

temperatures that they currently experience and will experience in the future [13]. Despite the smaller anticipated magnitude of climate warming at lower compared with higher latitudes, the negative consequences of narrow thermal tolerance breadths at lower latitudes is sufficient to overwhelm the effects of diminished warming [11]. Higher latitude species are generally less vulnerable to climate change because they have broader ranges of thermal tolerance and are much farther from their thermal optimum and upper thermal tolerance. Yet while these forecasts of vulnerability allow environmental temperature to shift (e.g. by comparing warming tolerance under current and future climates), the tolerance traits are treated as fixed. Below we consider the sources of variation in insect thermal tolerance and how this variation might alter vulnerability assessments. Specifically, we consider intraspecific sources of variation in tolerance including plastic and evolved differences in tolerance across space and time, and then summarize the patterns across different insect species and biogeographic regions, as these are the levels at which warming tolerance analyses are typically performed. Of particular interest is whether the consideration of tolerance variation quantitatively, or perhaps even qualitatively, alters assessments of vulnerability to climate change as compared with assessments derived from mean trait values. In the case of such alterations, global to local-scale patterns of vulnerability based on trait means could be inaccurate, with downstream consequences for conservation planning and management.

Ecological and evolutionary sources of variation in tolerance traits

The critical importance of variation in tolerance has come into sharper focus over the past several years. A striking example comes from Bush and colleagues [17] — using a species distribution modeling approach which incorporated empirical estimates of variability heat tolerance, they found qualitatively different forecasts of vulnerability to climate change compared with models that excluded this variation. Specifically, for several of the

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