

Toward an integrated framework to assess climate vulnerabilities: Beyond the thermal tolerance in tropical insects

Zhong-Wen Jiang,^{1,*} Lin Zhang,² Bao-Jun Sun,³ and Jinlin Chen^{4,*}

¹School of Ecology, Shenzhen Campus of Sun Yat-sen University, Shenzhen 518107, China

²Hubei Shizhen Laboratory, School of Basic Medical Sciences, Hubei University of Chinese Medicine, Wuhan 430065, China

³State Key Laboratory of Animal Biodiversity Conservation and Integrated Pest Management, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

⁴Department of Ecology, School of Life Sciences, Nanjing University, Nanjing 210023, China

*Correspondence: zhongwen.jiang0522@gmail.com(Z.J.); jlchen@nju.edu.cn(J.C.)

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Climate warming is contributing to global biodiversity loss, with impacts varying across elevational and latitudinal gradients. Identifying the regions and taxa more vulnerable is crucial for developing conservation strategies, yet it remains a hotly debated challenge. By evaluating the thermal limits, adaptive potential, and climate sensitivities of ~2,300 insect species along elevational gradients across two continents, Holzmann and colleagues demonstrate that tropical lowland insects operate near their evolutionary thermal limits;¹ burdened by current heat stress, these species face a severely elevated risk of heat-induced mortality by 2100.

While this field-based study possesses several commendable strengths, one aspect deserves particular recognition for its contribution to the disciplines whose developments are based on field experiments, such as Ecology and Evolutionary Biology. The authors established intensive sampling transects along parallel elevation gradients in both Afrotropical and Neotropical regions. The identification and utilization of such natural systems across continents is exceptionally rare. Traditionally, such scientific questions have often been explored through meta-analyses or indoor factor-manipulated experiments. Studies conducted by field temperature-controlled experiments remain largely scarce, primarily due to the formidable logistical challenge of implementing extensive, comparative, and manipulative studies at such a large geographic scale. Holzmann et al. successfully amassed a robust dataset of over 8,000 samples.¹ Its design demonstrated that future investigations of broad-scale biogeographical patterns could incorporate cross-continental comparisons, which would also facilitate replicated validation. For instance, investigating latitudinal patterns of environmental adaptation or species vulnerabilities under climate change could involve empirical studies along gradients in Asia and Oceania, with comparable designs in North and South America.²

A striking contribution of Holzmann et al. is the demonstration that neither thermal tolerance nor plasticity of tropical insects increases (even maladapted in the case of plasticity) proportionally with environmental temperature along elevational gradients. This pattern is a fundamental insight that reshapes how we think about tropical biodiversity in a warming world. The consistency of the pattern suggests that lowland tropical insects are not there because they are exceptionally well-adapted to heat, but rather because they have been constrained to these environments — a perspective that resonates with several recent works on investigating the drivers of species distribution in the tropics.³ Their rich dataset and the patterns it reveals point to several future directions that are both biologically interesting and practically essential for understanding the future of the most diverse taxonomic groups residing in the world's most biodiverse regions (Figure 1).

PHYSIOLOGICAL LIMITS TO THERMAL EVOLUTION AND THE GENOMIC SIGNATURE

Holzmann et al. found that critical thermal maxima (CT_{max}) saturates in tropical lowlands, approaching an asymptote that aligns with the predicted melting temperature of the most heat-sensitive proteins (approximately 42°C). By integrating evolutionary modeling of trait optima with deep-learning-based genomic predictions, they revealed a striking convergence: the long-term evolutionary optimum for thermal tolerance perfectly mirrors the average melting temperature of the proteome's most thermally sensitive components.

This convergence provides compelling evidence that upper thermal tolerance is ultimately constrained by protein stability. Because this phylogenetic signal is rooted in lineage-specific protein structures, remodeling these

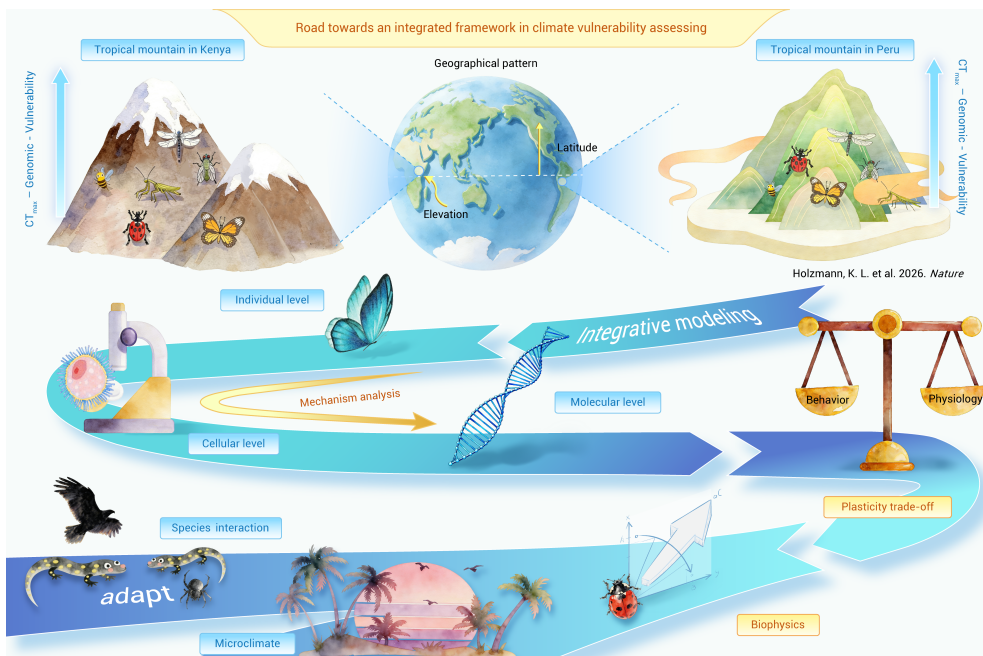


Figure 1. Road toward an integrated framework in climate vulnerability assessing Future work for assessing vulnerabilities can contain several important aspects, including illustrating the geographical pattern, analyzing mechanisms, balancing trade-off between behavior and physiology, and applying integrative models with considerations of biophysics, microclimate, and species interactions etc.

foundational biochemical networks to withstand higher temperatures would entail prohibitive evolutionary costs. This finding resonates with a growing body of literature suggesting that upper thermal limits are inherently conserved. What Holzmann et al. add to this understanding is the demonstration that natural populations in the warmest environments have already reached this limit.¹ The saturation of CT_{max} in tropical lowlands is not merely a theoretical possibility; it is an empirical reality documented across thousands of species, and it poses an immediate threat under ongoing warming.

THE PLASTICITY TRADE-OFF

Organisms face a fundamental choice: invest in "always-on" protection that provides immediate defense against predictable stressors or maintain flexible responses that can be upregulated when needed but may fail under extended and extreme challenges. The trade-off between constitutive tolerance and inducible plasticity has been a subject of theoretical interest for decades, and empirical evidence has seen mixed results. Holzmänn et al. provide possibly the most comprehensive evidence to date that the trade-off is real and general among tropical insects.¹ Their interpretation points to an important nuance: the capacity for plasticity depends not only on the presence of appropriate molecular mechanisms but also on the energetic reserves available to mount those responses. This suggests that plasticity is not simply a trait that species either possess or lack; it is a capacity that can be expressed only when resources permit. This explanation also fits the finding that lowland insects show reduced cold hardening capacity, suggesting that chronic heat stress may erode plasticity across multiple axes. That said, the connection remains correlative. Understanding the molecular basis of this trade-off could open a door to seeking ways to enhance performance through concurrent evolution and plasticity in a gradually warming environment with more frequent extremes.

MICROCLIMATE, BIOPHYSICS AND SPECIES INTERACTIONS

A notable feature of Holzmänn et al.'s data is the cross-continental geographic difference in thermal tolerance: Neotropical insects show lower CT_{max} values than their Afrotropical counterparts.¹ For small ectotherms, behavioral thermoregulation is often the first line of defense against heat stress. This strategy requires minimal physiological investment and allows organisms to maintain performance across variable conditions. However, its effectiveness depends critically on the availability of thermal gradients in microhabitats. Compared with the Afrotropical gradient, which is characterized by more open habitats, the continuous and vertically complex forest cover in the Neotropics provides abundant shade. In such environments, insects may have evolved to rely heavily on behavioral thermoregulation rather than pushing their physiological limits upward. This interpretation aligns with the broader principle that ectotherms face a fundamental choice: invest in physiological tolerance or rely on behavioral thermoregulation. Each strategy carries different costs and consequences for plasticity. More broadly, this highlights that the evolution of thermal tolerance requires considering the thermal heterogeneity of the environment. The availability of cool microhabitats may shape whether populations invest in physiological tolerance or behavioral flexibility—a trade-off with profound implications for vulnerabilities to climate change along with ongoing habitat degradation.

To quantify the climate-driven vulnerability, Holzmänn et al. developed a heat coma model to predict knockdown times relying on shaded air and surface temperatures as model inputs.¹ However, air temperature often fails to represent the realistic thermal state of an organism.⁴ In reality, the body temperature of an insect without physiological heat production and dissipation, defined as the operative temperature, is dictated by a complex biophysical interplay of ambient temperature, radiation, convection, and conduction. Therefore, relying solely on ambient temperature risks severely underestimating the actual thermal stress. We propose leveraging tools like NicheMapR to predict microclimates experienced by organisms and subsequent physiological responses. First, the extensive field-measured air temperatures from the study provide an ideal dataset to validate microclimate models. Crucially, by coupling these refined microclimate projections with insect-specific biophysical models that account for heat exchange, researchers can calculate the true operative temperatures. Inputting these operative temperature values into the dynamic heat coma model would yield a significantly more precise and biophysically realistic vulnerability assessment.

Furthermore, an organism does not exist in a vacuum. One significant gap in our understanding of thermal evolution is the role of species interactions. This complexity is evident when we consider the discrepancy between artificial selection experiments and evolution in natural contexts. It is worth noting that the observed CT_{max} of organisms is not simply a readout of their genetic potential, but already modulated by their history of species interactions.⁵

Selection on thermal tolerance acts on phenotypes that have been shaped by competition, parasitism, and other biotic pressures, meaning that the genetic information for thermal tolerance may not be directly visible to selection. Second, the constraints on thermal evolution may be more multidimensional than the heat-cold trade-off examined by the authors. Species interactions impose costs that are only apparent in community contexts. The multidimensional selective landscape means that selection rarely favors extreme specialization in any single trait. Understanding the pleiotropy and coevolution of multi-gene traits is thus crucial for assessing the potential for evolutionary rescue in realistic ecological contexts with complex eco-evolutionary feedback.

TOWARD AN INTEGRATED FRAMEWORK

The work of Holzmänn et al. provides a foundational baseline,¹ yet true climate vulnerability emerges from the interplay of exposure, sensitivity, and adaptation, modulated by microclimate, physiological trade-offs, and species interactions. Exposure concerns not ambient temperature but operative body temperature, governed by biophysical exchange, microclimate and behavior modulation in the presence of interacting species. This invites the hypothesis that insects in structurally complex forests will exhibit lower constitutive thermal tolerance but greater behavioral thermoregulatory capacity. Sensitivity reflects the decline in performance near physiological limits, shaped by the observed trade-off between standing tolerance and plasticity. The negative trade-off, especially the maladaptive plasticity in warm lowlands, requires mechanistic understanding on shared molecular pathways and competing energetic demands, alongside investigations into which abiotic and biotic contexts relax or reinforce this relationship. Adaptation concerns evolutionary potentials under these layered constraints. An open question remains whether biotic interactions further conserve expressed upper limits, and how biodiversity loss and restructuring might alter such constraints. Together, these implications position the Holzmänn et al. dataset as a platform for the next generation of hypotheses on climate vulnerabilities in tropical insects.¹

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AUTHOR CONTRIBUTIONS

Zhong-Wen Jiang and Jinlin Chen conceived the idea. Zhong-Wen Jiang and Jinlin Chen prepared the manuscript. Zhong-Wen Jiang, Jinlin Chen, Lin Zhang and Bao-Jun Sun revised the manuscript. All the authors have approved the final version of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.