COMMENTARY

# Biologically grounded predictions of species resistance and resilience to climate change

**Joseph Bernardo**[1]
*Department of Biology, Texas A&M University, College Station, TX 77843*

Cole (1) remarked [it is] "axiomatic that the reproductive potentials of existing species are related to their requirements for survival"; this logic applies to understanding species' capacities to respond to anthropogenic climate change. Extant species reflect the ghost of environments past: species traits such as physiological performance and tolerance are evolutionary products of environmental selection (2). They must also have had the right traits to weather previous cycles of climate change, a perspective generally lacking in the expansive literature exploring vulnerability to warming. Can these traits be useful in predicting relative vulnerability to ongoing climate change? The only way to know is to analyze such traits of many species in the context of current and projected climates. In PNAS, Sunday et al. (3) advance this approach with a suite of sophisticated analyses in the most comprehensive and biologically realistic assessment of organismal capacity to resist climate change to date.

To understand the significance of this work, consider a simple model of species' climate change responsiveness ($R$), which is a joint function of the magnitude of environmental change ($C_E$) and the organism's intrinsic sensitivity ($S$) to environmental stress. The response falls along a continuum with vulnerable at one extreme and facilitation at the other. Intermediate responses are resistance due to broad tolerances or behavioral lability and resilience, which is the capacity to rebound rapidly from demographic depression due to acute climatic stress events.

Estimates of $C_E$ should comport with microclimates that organisms experience, but most analyses have used 2-m air temperatures ($T_a$) (Table 1) measured at spatial scales that average $10^4$-fold coarser resolution than animal size (4). Sensitivity is determined by physiological species traits ($S_{PSTs}$) such as critical thermal maximum ($CT_{max}$), which is the highest nonlethal temperature an organism can tolerate; basal metabolic rate (BMR), which is a proxy for performance capacity; and acclimation capacity ($S_{plasticity\ PSTs}$), which is a measure of the plasticity of thermal tolerance or performance after exposure to short-term temperature changes. To this list, the new analysis (3) considers behavioral capacity to thermoregulate ($S_B$) by moving between microhabitats to avoid or moderate acute exposures to thermal extremes (Fig. 1).

**Fig. 1.** Animals behave: A dog, *Canis familiaris* (Eddie), moderates exposure by microclimatic selection.

Table 1 summarizes the progression of models to assess vulnerability. The oldest and still most widespread approach is to model $R = C_E$. These analyses conclude that temperate species are most vulnerable to warming. However, most of this literature ignores species biology as relevant to predicting organismal responses to climate change (5). Other studies have examined variation in $S_{PSTs}$ without addressing the interaction with $C_E$, and variation in $S_{PSTs}$ and $S_{plasticity\ PSTs}$ (Table 1).

A seminal analysis that first considered both $C_E$ and $S_{PSTs}$ (as $CT_{max}$) (6) (Table 1) introduced a metric called the thermal safety margin (TSM), which is a measure of the latent capacity of organisms to resist temperature extremes ($CT_{max}$ − environmental temperature). This study concluded that, although $C_E$ is expected to be smallest in the tropics, it is tropical, not temperate, taxa that are most at risk from warming because they are already living close to their tolerance extremes and that temperate species have large TSMs, indicating that they should largely be able to resist climate warming. These conclusions are opposite of those models considering only $C_E$ and they highlighted the importance of considering organismal sensitivity in assessing climate change vulnerability.

## Adding Microclimates and Behavior to the Mix

The study of Sunday et al. (3) is an advance on prior studies (Table 1) in two key ways. First, it uses an ecologically relevant estimate of $C_E$: operative temperature ($T_e$). Second, their model considers three factors simultaneously—$C_E$, $S_{PSTs}$, and for the first time, to the knowledge of this author, the potential for behavior ($S_B$) to moderate exposure—for a wide range of species across latitude.

Their first task was to compile georeferenced $CT_{max}$ data for 299 species of amphibians, reptiles, and insects. Next, they use a biophysical model (7) to estimate $T_e$ at these

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[1] E-mail: jbernardo@tamu.edu.

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**Table 1. Ontogeny of structural diversity of empirical attempts to assess relative vulnerabilities of species to climate change**

| Model | Estimator of $C_E$ | $S_{PSTs}$ analyzed and empirical examples | Conclusion |
|---|---|---|---|
| $V = C_E$ | $T_a$ | None [environmental niche modeling (13)] | Most species will have smaller ranges in the future and so are vulnerable to climate change |
| $V = S_{PSTs}$ | None | BMR (9) | Eurytherms are more resistant than stenotherms |
| $V = S_{PSTs}, S_{plasticity\ PSTs}$ | None | $CT_{max}$, acclimation capacity of $CT_{max}$ (10) | Restricted acclimation capacity of warm-climate species renders them more vulnerable compared with cool climate species |
| $V = S_{PSTs}, C_E$ | $T_a$ | $CT_{max}$, $CT_{min}$, $T_{opt}$, $T_b$ (14)<br>$CT_{max}$ (6, 15–17)<br>BMR (18) | Tropical species more vulnerable than temperate species because they have lower TSMs or elevated metabolic costs |
| $V = S_{PSTs}, C_E$ | $T_a$ | $CT_{min}$, $CT_{max}$, thermal sensitivity of fitness (19) | Both temperate and tropical species are near thermal limits |
| $V = S_{PSTs}, S_B, C_E$ | $T_a$ and $T_e$ | $CT_{max}$ (3) | Both temperate and tropical species are near thermal limits and require behavioral moderation of exposure to persist |

exact localities. $T_e$ is an organism's equilibrium temperature reflecting heat fluxes in and out of the body. It can differ dramatically from $T_a$ depending on passive (e.g., organismal shape, mass, reflectance, and other physical properties of its surface) and active (behavioral thermoregulation) influences of organismal traits. Hence, $T_e$ is a far more biologically realistic estimate of $C_E$. TSMs were then computed using both $T_a$ (as in ref. 6) and $T_e$, and latitudinal and elevational patterns in both were examined. This contrast indicated that $T_a$ grossly overestimates temperate species' TSMs and that most of these species also appear to be living near their thermal tolerance limits.

This finding prompted the next advance of this study: exploring the role of behavior. Behavioral responses include temporal shifts in activity to escape acute thermal stress (ATS) on both a daily and seasonal basis including shifts to nocturnality; fine-scale spatial shuttling between microhabitats with divergent microclimates (8); and large-scale movements to more equable sites. To do this, Sunday et al. estimated how $T_e$ varies across microhabitats (e.g., full sun, deep shade, burrows) and therefore the extent to which behavioral exploitation of microhabitat diversity can ameliorate the expected ATS captured by the TSMs. They concluded that behavior can adequately moderate ATS in most cases, provided that habitats are sufficiently intact to provide thermal heterogeneity.

One implication of this study is that some species may not need to track climate change spatially. Many empirical studies have compared recent and historical distributions to estimate the extent of "range shifting" that has occurred. Inevitably, it is concluded that species that have not range-shifted must therefore be more endangered and those that have moved are least vulnerable. However, without an objective expectation of which species need to move (e.g., they cannot achieve thermal balance even with behavioral thermoregulation) there is no way to exclude the alternative explanation: species that have not moved may not need to and those that have moved had no other option. The analytical approach of Sunday et al. provides a basis for reassessing these conclusions, and calibrating new analyses of tracking against biologically realistic predictions.

Another key finding is that different groups of organisms with different biological attributes (e.g., wet-skinned amphibians vs. dry-skinned reptiles) will respond differently to the same climate stressors—biology matters. Even closely related species (9, 10) may differ in meaningful ways, so broad generalizations about vulnerability of, say, frogs (11) should be viewed cautiously.

## Conclusions and Prospectus

Well-founded concerns about climate change are resulting in many papers purporting to "predict" the responses of species, communities and ecosystems to future climate scenarios. This study should give pause to authors and editors who seek quick, simple answers that ignore species biology and use ecologically questionable temperature data. The urgency to obtain answers does not obviate the need for good science. This study and the theoretical work that preceded it demonstrate the way forward.

This study with its roadmap of powerful analytical approaches should prompt the generation and analysis of new physiological data for a broader phylogenetic, geographic, and ecological spectrum of species. A conceptual reunification of physiological thinking into mainstream ecology (12) and more collaborations of ecologists and physiologists are routes to tackle this challenge. Finally, the overarching conclusion of this work is a familiar theme of conservation–the key to preservation of biodiversity in the face of anthropogenic climate change is to preserve intact habitats that conserve the microclimate diversity required for behavioral thermoregulation and spatial corridors for accessing equable microsites.

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