## Biophysical approaches to predicting species vulnerability

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Earth's climate is warming rapidly at rates which, by some estimates, exceed those of climatic niche evolution among vertebrate animals by >10,000-fold (Quintero & Wiens, 2013). Assessing this ubiquitous threat to biodiversity requires a variety of robust approaches to predict organismal responses to future climates. In this issue, Briscoe et al. (2022) provide a road map for using species' functional traits (morphological, physiological, and behavioral) and localized and global climate data to inform biophysical models that estimate the effects of specific climate scenarios on the energy balance and water economy of animals in the wild. Biophysical modelling approaches predict relationships between heat exchange, body temperature and behavior over wide ranges of environmental temperature from functional traits. Many of the direct impacts of climate change are consequences of supply-and-demand mismatches involving water or energy, the currencies of life. Biophysical modelling is uniquely well-suited for predicting these impacts and evaluating adaptation strategies available to conservationists, managers and policy-makers.

Biophysical models have long been of interest to physiological ecologists for understanding the responses of humans and animals to challenges imposed by their physical environments, and constraints on those responses (Winslow et al., 1937). One of the earliest and most influential animal models used a climate space and energy budget analysis approach to characterize the environment within which an animal can survive—a space bounded by air temperature, radiation, wind speed and humidity (Porter & Gates, 1969). Biophysical models use functional traits, (e.g., body size, plumage thickness, metabolic/evaporative responses to temperature, critical thermal tolerances, etc.) and climate/microclimate data to examine constraints on animal performance. These models are versatile enough to examine individual limits on performance via estimates of energy or water fluxes under specific climate scenarios for endotherms such as mammals or birds or produce body temperature estimates in ectotherms such as mammals. When mapped onto current and projected future climate data, well-parameterized biophysical models provide robust predictors of future species abundance and distributions.

Briscoe et al.'s (2022) goal is to introduce and increase the accessibility of the biophysical modelling approach to the broader global change research community. They start by introducing mechanistic biophysical models, which use animal functional traits as their bases and compare these to statistical or phenomenological models that correlate species distributions

with predictor variables. The authors highlight how biophysical models can describe spatial and temporal variability and account for complexity such as changes in environmental constraints across life-history stages. They then provide examples of how biophysical modelling can be applied to both ectotherms and endotherms. For ectotherms—such as reptiles, amphibians and arthropods—biophysical models and species' functional traits can be used to predict thermal constraints on offspring sex, the viability of developing eggs, and limits on daily activity and energy acquisition under any climate scenario. For endotherms, such as mammals and birds, the costs of maintaining a high stable body temperature can be quantified in terms of water and energy fluxes. High rates of energy and water exchange define endotherms and limit their performance and distribution, making limits on distributions intimately tied to species' traits associated with diet and energy as well as to water availability in the environment. Biophysical models have provided insights into individual performance and limits of species distributions, allowing researchers to identify functional bottlenecks or limits of species persistence.

Briscoe et al. (2022) present a vision for tackling global change problems that includes a new cohort of global change researchers proficient in biophysical modelling approaches with access to functional trait databases. As physiological ecologists, we suggest that limited access to taxon-specific functional trait data and a lack of in-depth knowledge of many organisms' natural history will continue to create a bottleneck in expanding the value and implementation of biophysical modeling approaches. As the authors note, however, the collection of empirical species-specific physiological data remains essential for parameterizing models and validating their predictions. Species-specific tolerance limits and thresholds can vary widely within taxa, making data on the upper and lower boundaries of physiological performance essential. Among southern African songbirds, for instance, body temperature associated with the onset of loss of balance and coordination varies by ~5°C and the threshold environmental temperature above which metabolic rate increases, primarily on account of muscle activity associated with panting, varies by ~12°C (Freeman et al., 2022).

Briscoe et al. (2022) also note that quantifying intraspecific variation in species functional traits is a prerequisite for accurately parameterizing biophysical models. Such variation can arise from local adaptation or phenotypic plasticity and, whereas morphological variation will often be apparent from natural history museum specimens, which serve as a vast repository for functional trait data, the same is not necessarily true for physiological and behavioral variation. For this reason, empirical data on intraspecific variation in physiology and behavior under natural conditions, acclimation/acclimatization experiments to elucidate the shapes and limits of reaction norms for phenotypically plastic traits, and common-garden experiments to detect local adaptation, remain essential for modelling responses to climate change.

The potential applications of biophysical models in ecology and conservation are vast. As climate change advances, many species may be expected to lose substantial portions of their current ranges and become ecological refugees in marginal habitats (Kerley et al., 2020). Under such conditions, biophysical modelling of energy and water fluxes may prove essential for population management. Similar approaches based on a detailed understanding of thermal tolerances are required for species-specific conservation interventions, such as the design of artificial nest boxes with appropriate thermal properties for cavity-nesting birds threatened by the loss of suitable natural nesting sites (e.g., Carstens et al., 2019). Biophysical modelling of the importance of microclimates provided by shady vegetation can be used to understand implications of vegetation management regimes in protected areas, particularly those with large

populations of megaherbivores such as elephants, for maintaining biodiversity in a hotter future characterized by increasingly frequent extreme heat waves.

At the United Nations Biodiversity Conference (COP15) in Ontario, Canada, in December 2022, Inger Anderson, executive director of the United Nations Environment Programme, identified the Climate Crisis as one of the "five horsemen of the biodiversity apocalypse". Against this backdrop, Briscoe et al. (2022) have introduced a tool for global change biologists in biophysical models which, if embraced, could provide insights into how novel climates of the future will shape future distributions and abundances for individuals, populations, and communities. With a million species at risk (IPBES, 2019), individually tailored biophysical models informed by functional trait data and microclimate data driven by sophisticated and accessible software provide a solution that is likely to provide some of the best information for understanding species responses and potential mitigation strategies to rapid climate change.

## DATA AVAILABILITY STATEMENT

No data were used in this commentary.

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