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REVIEW

Parameterizing mechanistic niche models in biophysical ecology: a review of empirical approaches

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ABSTRACT

Mechanistic niche models are computational tools developed using biophysical principles to address grand challenges in ecology and evolution, such as the mechanisms that shape the fundamental niche and the adaptive significance of traits. Here, we review the empirical basis of mechanistic niche models in biophysical ecology, which are used to answer a broad array of questions in ecology, evolution and global change biology. We describe the experiments and observations that are frequently used to parameterize these models and how these empirical data are then incorporated into mechanistic niche models to predict performance, growth, survival and reproduction. We focus on the physiological, behavioral and morphological traits that are frequently measured and then integrated into these models. We also review the empirical approaches used to incorporate evolutionary processes, phenotypic plasticity and biotic interactions. We discuss the importance of validation experiments and observations in verifying underlying assumptions and complex processes. Despite the reliance of mechanistic niche models on biophysical theory, empirical data have and will continue to play an essential role in their development and implementation.

KEY WORDS: Biophysics, Ecology, Mechanistic niche models, Prediction, Experiment

Introduction

Generating accurate predictions in ecology is one of the most effective ways to demonstrate a deep understanding of a system (Houlahan et al., 2017). In general, predictions in ecology are made through either correlative or mechanistic approaches (Buckley et al., 2010; Connolly et al., 2017). Both of these approaches have made important contributions to prediction in ecology by revealing the processes that structure species distributions and ecological responses to environmental change (Urban, 2015; Briscoe et al., 2022a; Pillet et al., 2022). Despite answering similar questions in ecology, correlative and mechanistic models are built using a wide variety of theoretical and empirical approaches and provide varying levels of insight into the underlying processes driving complex phenomena in ecology.

Mechanistic approaches to prediction are not as common as correlative approaches, but they can provide important insights into

underlying processes at multiple levels of organization. In ecology, correlative models have been used to improve our understanding of the statistical relationship between biological data (e.g. species richness, occurrences and phenology) and environmental variables (e.g. latitude, temperature and precipitation) to answer questions about global patterns of diversity (Li et al., 2023) and predict future ecological responses to environmental change (Pillet et al., 2022). Alternatively, ecological predictions can be made from a mechanistic perspective. For the purpose of this Review, we have narrowed our definition of mechanistic models to those that use theory from biophysical ecology to predict mass or energy balance of the focal organism(s) (Briscoe et al., 2022a). These mechanistic models rely on applying principles from thermodynamic theory to model the exchange of mass and energy between an organism and its environment (Fig. 1; Briscoe et al., 2022a; Kearney, 2013). When combined with detailed information on the microclimates that organisms experience (Meyer et al., 2023), mechanistic species distribution models are frequently used to predict many indices of fitness (e.g. growth, reproduction and survival) across the geographic range of the focal species (Kearney and Porter, 2009). Mechanistic models also predict performance through time or the relative performance of certain phenotypes and can be used to answer a wide variety of questions (Table 1, Fig. 2). Thus, we refer to these models more broadly as 'mechanistic niche models'.

Here, we review the empirical approaches that are frequently conducted by experimental biologists and often used to parameterize mechanistic niche models, helping to improve transparency and provide a guide for developing experiments to parameterize them. We focus on the physiological, morphological and behavioral experiments often conducted to parameterize these models (Table 2), and we briefly touch on the experiments used to parameterize evolutionary responses, phenotypic plasticity and species interactions. We also address empirical approaches in ectotherms and endotherms, but we note that models of endotherms can contain substantially more complex processes and traits (for further discussion, see Porter and Kearney, 2009; Kearney et al., 2021a; Conradie et al., 2023). This Review is not intended to be exhaustive, in part because the parameterization of these models is often question and system specific. Moreover, we also do not cover the theoretical approaches, assumptions or thermodynamic concepts in parameterizing mechanistic niche models (see Porter et al., 1994; Kearney and Porter, 2020; Kearney et al., 2021b). We also make distinctions between experiments and observational studies, both of which are often used to parameterize mechanistic niche models. Although we focus on niche models developed for animals, we acknowledge the rich body of literature on mechanistic niche models of terrestrial plants (Wright et al., 2017; Muir, 2019). Regardless, we hope this Review provides a useful resource for experimental biologists to design experiments that can be used to parameterize mechanistic niche models that answer fundamental questions in ecology and evolution.

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Glossary

Allometry
A biological concept that describes the dependence of a biological variable (such as metabolic rate) on mass or size.

Basal metabolic rate
The minimum amount of energy burned by an adult, non-reproductive endotherm at rest, within the thermoneutral zone, in a post-absorptive state while regulating body temperature during an inactive period (McNab, 1997).

Doubly labeled water
A technique used to measure the total energy expenditure of an organism for an extended period of time, typically spanning days to weeks. Organisms are provided with stable isotopes of water and, after a period of equilibration, samples from the organism are taken to estimate the rate of labeled water loss via respiration. These values are then used to estimate a metabolic rate over time.

Dynamic energy budget theory
A theoretical framework used to model the energy budgets and life history of organisms across their entire life cycle (Kooijman, 2010).

Emissivity
A physical property of an object that describes how efficiently it emits thermal radiation (Campbell and Norman, 1998).

Operative temperature
An equivalent blackbody temperature that combines air temperature, absorbed radiation, wind speed and the characteristic dimension into a single equivalent value (Campbell and Norman, 1998).

Resting metabolic rate
A more general term for the minimum amount of energy burned by an endotherm or ectotherm at rest in a post-absorptive state at a specified temperature (Arnold et al., 2021).

Sensitivity analysis
An approach that explores how different values of a model parameter affect a particular output variable. The model parameter values are often based on known or hypothetical variation in model parameters.

Standard metabolic rate
The minimum amount of energy burned by an adult, non-reproductive ectotherm at rest in a post-absorptive state during an inactive period at a specified temperature (McNab, 1997).

Standard operative temperature
An equivalent blackbody temperature that combines air temperature, absorbed radiation, the characteristic dimension, wind speed and interactions between wind speed and insulation into a single equivalent value (Campbell and Norman, 1998).

Metabolic rate and energetics

Mechanistic niche models require approximations of metabolic expenditure to estimate energy budgets and/or body temperature (Barlett and Gates, 1967). These models typically use one of three approaches for estimating metabolic rate: allometry (see Glossary), the dynamic energy budget theory (see Glossary) or experimental measures of metabolism (Sarà et al., 2011). These approaches vary in the level of experimental detail required to parameterize them, as well as their biological relevance.

Allometry is used to estimate metabolic expenditure based on the body mass of the focal organism and linear relationships between body mass and metabolic rate across a range of taxa that can incorporate some degree of thermal context (Barlett and Gates, 1967) or phylogenetic dependence (Uyeda et al., 2017). Allometric relationships of metabolic rate are generated from experimental measures of metabolism across many taxa. These relationships are sometimes used to estimate metabolic expenditure for ectotherms in mechanistic niche models but ignore the relatively strong thermal dependence of metabolic rate (Angilletta, 2009). Nevertheless, they have been used to approximate heat balance (Barlett and Gates, 1967). More often, allometric relationships are used for endotherms

to approximate basal metabolic rate (see Glossary; Kearney et al., 2016), which is insensitive to acute changes in environmental temperature at the level of the organism (McNab, 1997). Alternatively, mechanistic niche models can directly incorporate the thermal sensitivity of metabolic rate from respirometry experiments (Porter and Gates, 1969; Buckley, 2008). Traditionally, these experiments involve measuring metabolic rate of fasted animals at rest in a dark chamber during the inactive portion of their diel cycle, thereby quantifying minimum energetic demands (Dawson, 1958; Kleiber, 1975). These rates are typically referred to as standard metabolic rate (see Glossary) for ectotherms or basal metabolic rate for endothermic homeotherms (McNab, 1997). In mechanistic niche models, these measurements are made across a range of temperatures in a controlled laboratory setting to characterize the non-linear relationship between temperature and metabolic rate, such as the typical thermal performance curve for ectotherms or Scholander–Irving models for endotherms (Angilletta, 2006; Scholander et al., 1950; Dawson, 1958). These experiments are thus designed to measure the routine 'maintenance costs' of resting animals across a range of environmental temperatures. The experiments require careful design of the sequence and duration of temperature exposure and ecological context of the animal.

There are a variety of ways to design an experiment to measure the thermal sensitivity of metabolism, with some controlling for biases more than others. In 'ramping experiments', metabolic measurements are taken over a series of increasing temperatures with brief periods of rest between temperatures for the animal to come to thermal equilibrium (Smith et al., 2017; Shah et al., 2021). Ramping experiments might introduce acclimation biases because the animal may respond behaviorally, morphologically or physiologically in anticipation of further warming during the experiment; thus, some experiments attempt to minimize these ramping effects by randomizing the order of exposure to environmental temperatures (Wolf and Walsberg, 1996; Angilletta, 2001). Moreover, many studies measure physiological rates under constant temperatures, yet experiments have shown that constant temperatures may fail to predict performance under more realistic, variable temperatures (Niehaus et al., 2012). However, experiments should prioritize measuring metabolic rates under conditions that organisms experience in nature. For instance, constant temperatures may be more relevant for organisms that often experience stable temperatures underground, whereas fluctuating temperatures may be more relevant for surface-dwelling diurnal organisms that experience a broad range of temperatures. Thus, experiments intended to inform mechanistic niche models may consider carefully designing their experiments to capture the maintenance costs of animals in their current environment or environments they may experience in the future.

Ecologists have long appreciated that resting metabolic rates (see Glossary) are unlikely to describe the maintenance expenditure of active animals in nature (Niewiarowski and Waldschmidt, 1992; Mitchell et al., 2018). To account for the increase in energetic expenditure during activity (e.g. foraging, mating and digestion), mechanistic niche models often increase resting maintenance costs by an empirically defined constant derived from observation or experiments (Buckley, 2008; Gifford and Kozak, 2012). In some cases, the experiments were designed to measure the energetic costs of courtship behavior, aggression between conspecifics (Bennett and Houck, 1983) or the cost of activity in general (Bennett, 1982). Mechanistic niche models then adjust resting metabolic rates by incorporating the increase in energy consumption from digestion and foraging activity measured in laboratory and field experiments
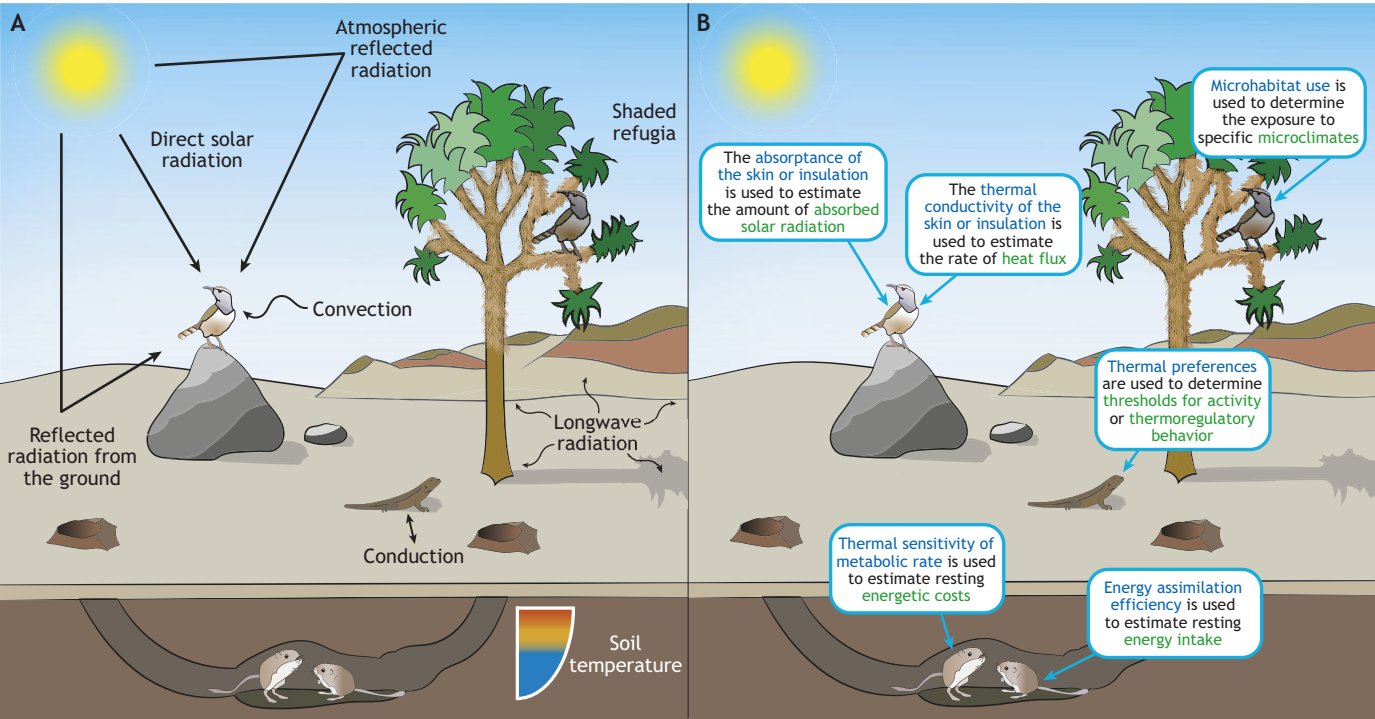
Fig. 1. Overview of the physical processes and empirical data used to parameterize mechanistic niche models. (A) An overview of the physical processes underlying predictions in mechanistic niche models. Animals are illustrated in commonly used microhabitats, but all processes are relevant for each animal. The soil temperature symbol indicates soil temperatures are usually warmer (red) and more variable (wider) near the surface relative to the cooler (blue), less variable (narrower) soil temperatures at deeper depths. (B) Examples of the empirical data (blue text) used to parameterize aspects of mechanistic niche models (green text). These only represent a small fraction of the experiments that are used to parameterize mechanistic niche models and many of the same measured traits are relevant for a wide variety of taxa.

(Levy et al., 2017). In theory, mechanistic niche models can use empirical estimates of field metabolic rates (Spotila and Standora, 1985); however, these rates represent static estimates and neither incorporate the thermal sensitivity of energy expenditure nor disentangle maintenance and active metabolic expenditure.

Developing an energy budget requires an estimate of energy intake in addition to energetic costs. The amount of energy an organism can allocate to reproduction, growth, maintenance and storage depends on prey encounter rates, handling time, the amount and type of food ingested and the rate of energy assimilation (Grant and Porter, 1992; Levy et al., 2017). Prey encounter rates can be estimated from movement rates of animals and prey density, which

can both be measured empirically (Buckley, 2008; Levy et al., 2017). Energy (or digestive) assimilation is defined as the process of absorbing and converting food to usable energy (Kooijman, 2010). In ectotherms, rates of energy assimilation typically vary with body temperature and can be described using a thermal performance curve (Clay and Gifford, 2017; Levy et al., 2017). The experiments usually consist of using a bomb calorimeter to quantify the amount of energy per gram of food and then carefully measuring the amount of food consumed and the amount of energy in the resulting fecal samples (Waldschmidt et al., 1986; Clay and Gifford, 2018). Alternatively, other assimilation experiments consist of feeding isotopes to the prey and then comparing the radiation content of the

Table 1. Questions that mechanistic niche models are typically designed to answer in ecology, evolution and global change

| Question	Example reference
Ecology	
How do physiological limits shape the geographic distribution of a species or population?	Riddell et al., 2017
How do physiological traits influence activity patterns and foraging behavior?	Levy et al., 2016
How do species interactions influence species abundance across a landscape?	Buckley and Roughgarden, 2005
Evolution	
What is the adaptive significance of variation in morphological traits?	Mason et al., 2023
How do phenotypic plasticity and adaptive evolution influence species distribution along climatic gradients?	Kingsolver and Buckley, 2017
How does evolutionary change of physiological traits influence population persistence during changing environmental conditions?	Kearney et al., 2009a
Global change	
How does behavior buffer organisms from climate change?	Sunday et al., 2014
How does acclimation buffer organisms from climate change?	Enriquez-Urzelai et al., 2020
Has recent climate change caused species declines by directly affecting physiological performance?	Riddell et al., 2021
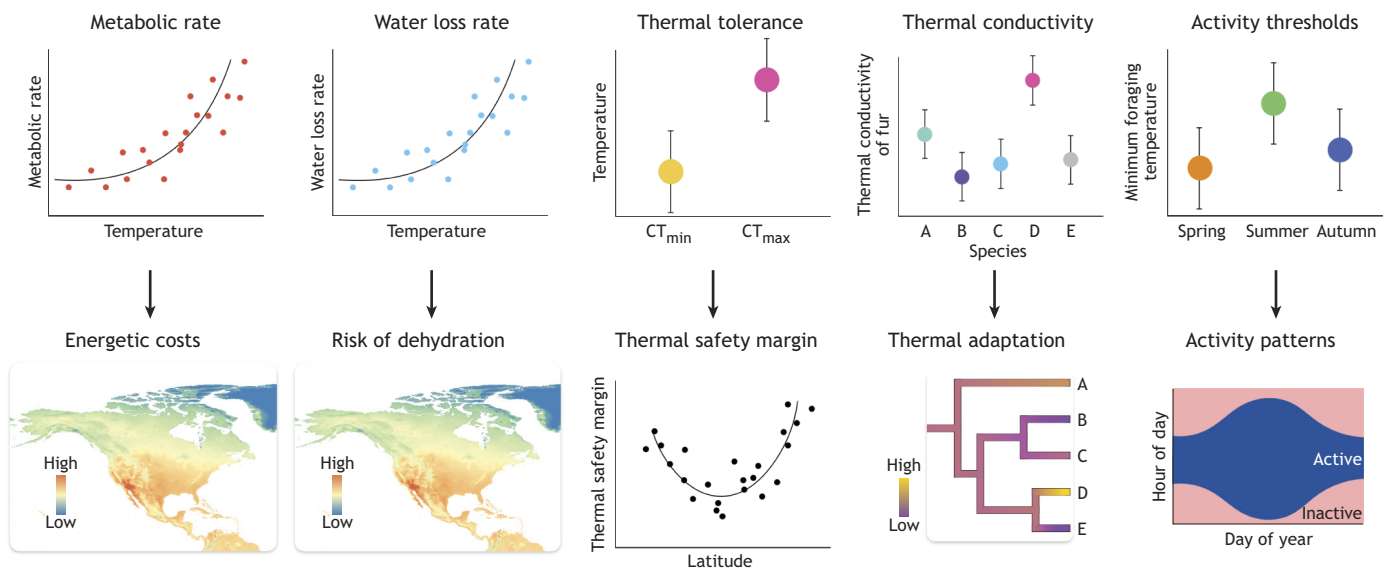
Fig. 2. Examples of empirical data that are often incorporated into mechanistic niche models to answer questions in ecology and evolution. The top row illustrates common types of empirical data that are collected by experimental biologists, and the bottom row provides a corresponding illustration of the type of analyses used to answer ecological and evolutionary questions. CT_{min}, critical thermal minimum; CT_{max}, critical thermal maximum.

prey and focal organism (Bobka et al., 1981). For endotherms, mechanistic niche models often assume a static assimilation efficiency (Porter et al., 2006; Briscoe et al., 2016) based on similarly designed experiments (Nagy and Martin, 1985), though future experiments might explore whether assimilation efficiency varies with body temperature or ambient temperature in endotherms. Regardless of the taxon, energy assimilation efficiency is dynamic and dependent on life history, activity and ecological context (Dunham et al., 1989). A greater emphasis on empirical work will improve the predictive capacity of mechanistic niche models to accurately simulate species-specific energy budgets.

Water balance physiology

The rate at which animals gain and lose water to their environment has a major impact on energy budgets (Tracy, 1976) and is sensitive to environmental conditions and the physiological state of the organism (Riddell et al., 2018). From the perspective of the environment, the primary factors that determine rates of evaporative water loss are wind speed and humidity, which increase and decrease evaporative water loss, respectively (Feder and Burggren, 1992). Higher temperatures can also indirectly amplify rates of evaporative water loss by increasing the saturation vapor pressure (Anderson, 1936), thereby increasing the diffusion gradient of water

Table 2. Experiments and observations used to parameterize mechanistic niche models

Category	Technique used	Example reference
Physiological		
Metabolic rate	Experiment	Buckley, 2008
Assimilation efficiency	Experiment	Gifford and Kozak, 2012
Water loss	Experiment	Riddell et al., 2018
Water intake	Experiment	Tracy, 1976
Body temperature	Experiment/observation	Ma et al., 2023
Morphological and physical		
Body size	Observation	Mathewson et al., 2020
Surface area	Observation	Kobelt and Linsenmair, 1995
Thermal conductivity	Experiment	Riddell et al., 2022
Reflectance or absorptance	Experiment/observation	Kingsolver and Watt, 1984
Behavioral		
Thermal preference or set point	Experiment	Sears et al., 2016
Microhabitat use	Observation	Moyer-Horner et al., 2015
Posture	Experiment/observation	Barton et al., 2014
Validation		
Microclimate	Observation	Maclean et al., 2017
Energy expenditure	Experiment	Fitzpatrick et al., 2015
Activity	Experiment/observation	Kearney et al., 2018
Evolutionary		
Selection gradients	Experiment	Kearney et al., 2009a
Heritability	Experiment	Kingsolver and Buckley, 2017
Biotic interactions		
Competition coefficients	Experiment/observation	Buckley and Roughgarden, 2005
Heat flux between plants and animals	Experiment/observation	Pincebourde and Casas, 2019

vapor. Therefore, experiments on the environmental sensitivity of water loss must carefully consider how each of these variables interacts with the physiological state of the organism. In general, water loss rates are measured using flow through water vapor analysis or gravimetric measurements across a range of thermal, hydric and convective conditions (Feder and Burggren, 1992). However, mechanistic niche models often do not rely on empirical data for parameterizing water balance.

Because of the sensitivity of water loss rates to multiple environmental factors, physiologists have developed metrics of water loss that account for the environmental factors and therefore isolate the resistance of the integument to water loss (Spotila and Berman, 1976). Rather than incorporating these empirically derived values, mechanistic niche models often assume a complete or partial 'free water surface' for the focal organism (Tracy, 1976), which represents the total proportion of the surface of the animal that loses water freely without any resistance to water loss (Porter et al., 2006; Gifford and Kozak, 2012; Caruso et al., 2014; Kearney et al., 2016, 2018). This single proportion includes the skin but also more permeable surfaces such as the eyes (Kearney et al., 2018). By using this value, rates of water loss vary as a function of the environment (i.e. the evaporative demand of the air known as the vapor pressure deficit), and the physiological resistance is assumed to be static across a wide range of environmental conditions. However, experimental physiologists have uncovered many examples of organisms changing how quickly they lose water in response to chronic and acute changes in temperature and humidity (Buttemer and Thomas, 2003; Senzano and Andrade, 2018; Riddell et al., 2018). As indicated by Campbell and Norman (1998), 'Little is known about the variability [in vapor conductance of the skin] or their dependence on environmental moisture or temperature'. To date, this statement is still generally true. Few mechanistic niche models have incorporated such physiological sensitivity into their simulations (Riddell et al., 2018; Newman et al., 2022). Thus, predictions made using mechanistic niche models can improve by investigating and incorporating the physiological flexibility of resistance to water loss, particularly given the importance of water balance under future warming scenarios (Lertzman-Lepofsky et al., 2020; Riddell et al., 2021).

Few mechanistic niche models have incorporated empirical data from water intake or gain from the environment. In nature, animals gain water from their environment through their food, by drinking or across their skin. For animals that rehydrate from soils (e.g. amphibians), mechanistic niche models have relied on experiments that measure the water potential gradient driving water exchange between the animal and its environment (Tracy, 1976). Specifically, such experiments estimate the water potential of the animal by determining the point at which no water is exchanged between the soil and the animal (i.e. the soil and animal have the same water potential). However, water potential changes dynamically with the soil and hydration state of the animal. Thus, more experiments on water intake or rehydration rates will be needed to understand these complex interactions. Animals also gain water from metabolic water, which is produced as a by-product of the catabolism of energy sources, such as carbohydrates and proteins. In ectotherms, this has been assumed to be negligible (Tracy, 1976) or has been estimated using dynamic energy budget theory (Kearney et al., 2018). Developing experiments on rehydration rates in nature will improve water budgets developed by mechanistic niche models.

Thermal limits
Predicting the ecological impact of environmental change on organisms usually involves empirical measurements of physiological limits, often in response to temperature (Sunday et al., 2014). For ectotherms, indices of thermal limits vary, but the limits that are typically incorporated into mechanistic niche models include (i) the body temperature at which organisms lose motor function (critical thermal maximum, CT_{max}; Sunday et al., 2014), (ii) the body temperature at which an organism experiences substantial declines in cardiac function (Liao et al., 2021) and (iii) the temperature at which a group of organisms experiences 50% mortality (Pinsky et al., 2019). Alternative indices related to survival and the duration of exposure to temperature extremes are also frequently measured in experiments (Ørsted et al., 2022), and these have been recently incorporated into mechanistic niche models (Camacho et al., 2023). These indices are then compared with estimates of potential body temperature from mechanistic niche models to quantify the exposure to lethal environmental temperatures across space and time (Sunday et al., 2014; Riddell et al., 2018; Pinsky et al., 2019; Enriquez-Urzelai et al., 2020). Discrete physiological tolerances are not as well defined or used for endotherms. Some studies have suggested using the maximum body temperature at which endotherms lose coordination or experience a rapid increase in body temperature (McKechnie and Wolf, 2019). To our knowledge, a mechanistic niche model has yet to incorporate these thermal limits for endotherms. Sub-critical limits have been increasingly considered as the basis for climate vulnerability because of the impacts of temperature on fitness occurring well before critical limits are reached (Braschler et al., 2021). Some mechanistic niche models have assessed climate vulnerability from these sub-critical limits based on stereotypic behaviors observed during ramping experiments (Riddell et al., 2023). Thermal limits have played an important role in predicting vulnerability to climate change and represent a relatively straightforward avenue for incorporating empirical data into mechanistic niche models.

Organismal size and shape
Body size impacts nearly every biological aspect of organisms and is therefore one of the most crucial parameters in mechanistic niche models. As with many other traits, body mass varies with age, sex, season and geography and can have important consequences for heat flux and energetics (Porter and Kearney, 2009). Recent efforts to aggregate biological data in databases (e.g. VertNet) have made it easier to access body mass data and incorporate sources of size variation into models (e.g. Riddell et al., 2019). Body shape dimensions, such as length, width and height of organisms, are also important aspects of size that affect heat exchange. For example, convective heat loss is affected by the characteristic dimension of the organism, usually defined as the distance that fluids (such as air) travel when passing over the organism (Porter et al., 2000). Organisms can effectively modify their characteristic dimension by changing their orientation or posture to prevailing winds (Wiersma and Piersma, 1994; Porter et al., 2000). Some authors have explored the consequences of this by altering the orientation of heated organismal models in wind tunnel experiments and measuring rates of convective heat loss (Kingsolver and Moffat, 1982). Such experiments, when combined with behavioral observations under natural conditions (e.g. Watt, 1968), may be especially helpful for parameterizing mechanistic niche models. The length, width and height of organisms have also been used to estimate their volume and shape, assuming a geometric shape (Lovelace et al., 2020), though other methods for estimating volume exist, such as weighing organismal replicas and dividing by the density of the casting material (Harley et al., 2009).

The surface area of an organism affects its potential for heat and water exchange with the environment and is thus another common size- and shape-related parameter incorporated into mechanistic niche models. A key consideration for endotherms is the difference in surface area between the skin and the insulating layer (e.g. feathers). Measurements of these surface areas have found that the skin has more surface area than the outer surface of the insulating layer, despite the expectation of the opposite (Walsberg and King, 1978). Furthermore, organisms can alter their surface area by changing their posture (Porter et al., 2000). Depending on the questions being asked, mechanistic models have incorporated empirical estimates of surface area to simulate specific mechanisms of heat and water exchange (e.g. convective/conductive surface area, surface area exposed to direct/diffuse solar radiation or evaporative surface area; Henwood, 1975; Tracy, 1976; Bartelt et al., 2010; Tracy et al., 2010). The approaches used to incorporate direct empirical measurements have included creating a replica of an organism with metal or plaster of Paris (Tracy, 1976; Erskine and Spotila, 1977; Porter and James, 1979), casting and tracing shadows (Kobelt and Linsenmair, 1995) or immersing a metal replica in an electrolytic bath to measure the electrical resistance from the replica (Tibbals et al., 1964). More recently (and commonly), more indirect methods are used to estimate surface area, such as allometric relationships (Porter and James, 1979; Roughgarden et al., 1981) or estimates from an approximate geometric shape (Van Damme et al., 1987; Porter and Kearney, 2009; Riddell et al., 2019). In some cases, studies assume a proportion of the total surface area is involved in specific mechanisms of heat and water exchange (Porter et al., 1973; Christian and Tracy, 1981; Scott et al., 1982) or apply these approaches to organismal appendages (Conley and Porter, 1986). Regardless of the approach, direct measurements of surface area can sometimes lead to surprising results (i.e. surface of skin versus the insulation layer; Walsberg and King, 1978) and may help inform more accurate predictions of heat flux.

Physical properties of the skin and insulation layer

The skin and insulation layers constitute the barriers to heat and water exchange between the organism and its environment and are thus essential considerations in mechanistic niche models. Key properties that have been used to parameterize mechanistic niche models include the thickness of fur (McClure and Porter, 1983), feathers (Porter et al., 2006), skin (Porter et al., 1973) and fat (Spotila et al., 1973), as well as the length, diameter and density of hairs and feathers (Steudel et al., 1994; Porter et al., 2006; Rogers et al., 2021). Together, these variables influence the thermal conductivity of the insulation layer, which can include the fat, skin, vasculature and pelage or plumage.

Mechanistic niche models either measure these variables to estimate thermal conductance (Rogers et al., 2021) or measure conductance directly in lab-based experiments (Riddell et al., 2022). These experiments often use heat flux transducers and thermocouples to measure heat flux (Boyles and Bakken, 2007; Chappell, 1980; Wolf and Walsberg, 2000; Riddell et al., 2021). These measurements are often recorded in controlled laboratory experiments on tissue removed from recently deceased animals or museum specimens (Cena and Monteith, 1975; Walsberg, 1988; Riddell et al., 2022). Experimenters might also consider accounting for seasonal and geographic variation in insulation and short-term plastic responses that may affect measurements of conductance (e.g. Conley and Porter, 1985). Therefore, it may be important to measure individuals from appropriate seasons and sites (Natori and Porter,

2007) or to conduct experiments that explore plastic responses to environmental variation (Hohtola et al., 1980) to parameterize models. Mechanistic niche models have also used laboratory experiments to understand the effects of human activities on the conductivity of insulation, such as the effects of oil on feathers (Mathewson et al., 2018). When data on conductivity are not available, niche models have used sensitivity analyses (see Glossary; Porter and Gates, 1969) or adopted conductivity values from previous estimates (McClure and Porter, 1983; Natori and Porter, 2007; Tracy et al., 2010), including those in humans (Porter and Gates, 1969; Porter et al., 2000).

One of the traits most commonly included in mechanistic niche models is the spectral reflectance of an organism's outer surface (either skin or the insulation layer). This is quantified by using a spectrophotometer to record the proportion of light reflected by the surface across various wavelengths and is used to estimate the amount of absorbed solar radiation. Reflectance values can be measured from different surfaces (e.g. dorsal versus ventral) or distinct integument patches (Mason et al., 2023). Most mechanistic niche models include reflectance measurements from ultraviolet (~300 nm) to near-infrared wavelengths (~2500 nm), which encompasses ~99% of solar irradiance hitting the Earth's surface (Medina et al., 2018). A common approach, especially for birds and mammals, is to take reflectance measurements from museum specimens (Natori and Porter, 2007; Fort et al., 2009; Medina et al., 2018; Riddell et al., 2019, 2021). In the absence of the expensive equipment required to take the measurements, some studies have made assumptions about reflectance based on partial reflectance curves (i.e. visible reflectance only) or close relatives (Gunderson et al., 2022). However, the reflectance properties can be difficult to predict. For instance, reflectance curves can change substantially after death (Henwood, 1975; Bakken, 1992). Furthermore, some organisms can change their reflectance properties in response to temperature variation, either by altering which integumentary surfaces are exposed to sun (Bakken, 1992) or by physiologically altering reflectance (Carey, 1978; Kobelt and Linsenmair, 1995). In at least some cases, these changes have been shown to significantly impact heat budgets (Kobelt and Linsenmair, 1995). Therefore, it may be worth conducting experiments that directly measure the thermal sensitivity of reflectance.

Other biophysical traits commonly incorporated into mechanistic niche models include emissivity (see Glossary) of the organism. Some authors have experimentally measured emissivity by heating live organisms above ambient air temperature and measuring air temperature a set distance away from the organism while simultaneously monitoring surface temperature with an infrared thermometer and a thermocouple (e.g. Kobelt and Linsenmair, 1995). More recent work assumes emissivity values between 97% and 100% based on previous work indicating that most organismal surfaces fall within this narrow range (Gates, 1980). Further experiments and observations on these traits may yield insight into climate vulnerability and species distributions.

Behavior

Behavior dictates how organisms interact with their environments, and so dynamically influences energy and heat balance. Understanding behavior, therefore, is key to making accurate predictions with mechanistic niche models (Kearney et al., 2009b, Sunday et al., 2014; Sears et al., 2016). Empirical studies on behavior can uncover the extent of behavioral thermoregulation, microhabitat use and other common behaviors that are used to modulate heat flux with their environment. Many mechanistic niche

models have integrated behavioral traits and these values or strategies are often based on laboratory or field experiments and observations.

Species vary in their use of thermoregulatory behavior to maintain a certain core body temperature, so the results from thermoregulatory experiments are often directly incorporated into mechanistic niche models. For ectotherms, laboratory experiments determine the range of preferred body temperatures (or set point temperature) in a continuous thermal gradient (Hertz et al., 1993). In these experiments, the animals are allowed to move freely across the thermal gradient to achieve a particular, species-specific body temperature (DeWitt, 1967). Body temperatures are then measured either using surgically implanted temperature loggers or via cloacal measurements (Sears et al., 2016). The range of preferred body temperatures is then based on the distribution of the data, such as the central 50% of mean body temperature (Sears et al., 2016). These values are then used to simulate thermoregulatory behavior in mechanistic niche models, such as shuttling between shade and sun or the probability of movement to achieve the preferred body temperature (Kearney et al., 2009b, Sears et al., 2016). Body temperature thresholds for basking and foraging may also be incorporated (Kearney et al., 2013). Few mechanistic niche models have included experiments related to behavioral thermoregulation of endotherms, likely because of the emphasis on physiological means for regulating body temperature (Angilletta et al., 2010). However, endotherms show clear patterns of behavioral thermoregulation in nature, such as the use of microhabitats with low shortwave radiation by mammals and birds (Cunningham et al., 2015; Milling et al., 2017; van de Ven et al., 2019; Briscoe et al., 2022a,b). Mechanistic niche models could therefore benefit from incorporating more experiments on behavioral thermoregulation in endotherms, especially with respect to thermal heterogeneity and preferred (standard) operative temperatures (Angilletta et al., 2010).

Experiments have also been used to parameterize processes related to foraging, such as those driving its temporal and spatial patterns (Levy et al., 2016). In a field experiment, researchers measured the quantity of seeds consumed by mice and then incorporated the food consumption into a mechanistic niche model using a 'harvest rate curve' to approximate the energy intake (Levy et al., 2016). Observations related to foraging have also been conducted to measure the abundance of prey items, such as insects (Gifford and Kozak, 2012). In these studies, sticky traps are deployed into the environment for a specific period of time to estimate prey abundance (Buckley and Roughgarden, 2005). This is then incorporated into foraging models to estimate the number of prey captured and energy intake.

Posture and basking behaviors also affect body temperature and have been assessed using field-based studies. In these experiments, temperatures are recorded of animal replicas or specimens placed in the environment at various angles and postures based on observations of the focal organism (Barton et al., 2014). These experiments can help developers of mechanistic niche models validate their predictions (see 'Validation of mechanistic niche models', below) or help them to understand the thermodynamic consequences of posture. In endotherms, similar field-based observations on microhabitat use have been used to examine posture and activity patterns in mammals (Briscoe et al., 2014) and birds (Dorr et al., 2020).

Observational studies have been used to study basking and posture behaviors, including the frequency at which animals bask or assume heat avoidance postures (Kingsolver and Watt, 1983). Mechanistic niche models have then incorporated these behaviors

into simulations to understand their thermoregulatory consequences (Wenda et al., 2021). These models have also incorporated behaviors that minimize exposed surface area, such as birds tucking appendages into insulation at night (Fitzpatrick et al., 2015). Observations are also used to determine the types of microhabitats that organisms use to buffer themselves from extreme temperatures (Fitzpatrick et al., 2019; Riddell et al., 2021; Briscoe et al., 2014) and regulate water balance (McEntire and Maerz, 2019). Some models estimate energetics based on movement patterns derived from GPS tags or collars in combination with local environmental data, such as temperature, cloud coverage, elevation, water availability, vegetation availability and concealment cover (Kearney et al., 2016; Levy et al., 2016; Long et al., 2014; Rogers et al., 2021). Behavioral observations have also been used to understand the general times of day and seasons under which activity occurs (Porter et al., 1973). These windows of activity can be used to parameterize mechanistic niche models or validate predictions of activity.

Validation of mechanistic niche models

Mechanistic niche models rely heavily on validation because they are built upon layers of interacting processes; for each component, experiments or observations can be used to verify that the underlying processes are realistic. Validation experiments are frequently used to corroborate the input data (such as the microclimatic conditions) or the output of the models (such as physiological rates, survival and reproduction). Regardless of the specific experiment or observation used, validations are crucial for assessing the accuracy and confidence of the model predictions.

Mechanistic niche models often validate the microclimatic conditions using field observations. For instance, environmental data loggers are deployed in microclimates associated with the focal organism to record the local environmental conditions (Mitchell et al., 2008; Kearney et al., 2016; Maclean et al., 2017; Newman et al., 2022). These microclimatic conditions can then be compared with ambient conditions, such as air temperature from local weather stations or collected with data loggers in solar radiation shields, to determine the difference between the microclimatic and ambient conditions. In some cases, air temperature can serve as an adequate proxy of the microclimate (Newman et al., 2022), but in other cases, ambient temperature can be 10–20°C greater or less than the microclimate (Gunderson et al., 2022). Others have used field measurements to correct large-scale environmental data (Kearney et al., 2016). Estimates of microclimates at global or regional scales have been verified using field-based observations from networks of weather stations or data loggers (Kearney et al., 2014; Maclean et al., 2017, 2019); however, these validations are often conducted at coarse spatial scales. Thus, field observations of microclimatic data can always improve confidence in the estimated microclimatic conditions in mechanistic niche models and remain an important part of model development.

Mechanistic niche models can produce estimates of body temperature, activity, survival, performance and reproduction (Briscoe et al., 2022a,b). Because these models are based on thermodynamic principles, many studies validate the models by ensuring they produce accurate predictions of body temperature at thermal equilibrium (Kearney, 2013). More specifically, the experiments are designed to measure operative temperature (see Glossary), which is defined as equivalent blackbody temperature and combines the air temperature and radiation into a single equivalent value (Campbell and Norman, 1998). The experiments typically consist of making a highly conductive replica of the animal

with similar absorptance (Dzialowski, 2005) or, in cases when the mass of the focal organism is very small (such as in some insects), can use specimens of the focal organism (Barton et al., 2014; Riddell et al., 2023). The experiments then record ambient conditions that are incorporated into the mechanistic niche model to generate predicted values of operative temperature for comparison with the observed values (Szathmary et al., 2009; Kearney, 2013; Riddell et al., 2023). Similar approaches are also used to validate predicted values of body temperature against observed values, assuming either operative 'steady-state' temperature (Henwood, 1975; Kearney et al., 2018; Riddell et al., 2023) or transient body temperature (Malishev et al., 2018). These methods apply to both ectothermic and endothermic taxa (Riddell et al., 2021), with the primary difference being that standard operative temperature (see Glossary) is used for endotherms because it incorporates interactions between insulation and wind (Bakken, 1980). Operative temperatures also have consequences for physiological values that are estimated with mechanistic niche models.

Mechanistic niche models frequently rely on field and laboratory experiments to validate model predictions of physiological traits. In one of the more common validations, these models compare estimates of the thermal sensitivity of metabolic rate with observed values from controlled laboratory experiments (Porter et al., 2006; Kearney et al., 2018; Riddell et al., 2019, 2021; Rogers et al., 2021). Similar validations have also been performed for body temperature (Kobelt and Linsenmair, 1995; De Jong et al., 1996; Mathewson et al., 2018, 2020), evaporative water loss rates (Riddell et al., 2019; Ma et al., 2023; Conradie et al., 2023), lower critical temperatures of metabolic rate (Porter and Kearney, 2009) and growth rates (Kearney et al., 2018). Validations of energy expenditure in a field setting are rare but are important for progressing mechanistic niche models. Experiments have used techniques involving doubly labeled water (see Glossary) to validate energy expenditure in field settings (Fitzpatrick et al., 2015). Doubly labeled water measurements can be challenging because they require taking blood samples from the same individual over a relatively short time scale (Speakman, 1998); however, the measurements can provide a rigorous approach for validation of mechanistic niche models, especially when paired with behavioral observations (Fitzpatrick et al., 2015). Similarly, some models have validated predictions of energy requirements using observations of food consumption in the field (Göktepe et al., 2012) or in more controlled laboratory settings (Homan et al., 2011).

The goal of many mechanistic niche models is to predict seasonal and diurnal patterns of activity; thus, studies that use these models also frequently validate their predictions of activity (Porter et al., 1973; Buckley, 2008; Kearney, 2013). Observations of activity in the field can be compared with predicted windows of activity to assess model performance (Porter et al., 1973; Kingsolver, 1983; Kearney et al., 2018). Some mechanistic niche models calculate the total proportion of time in which the predicted state of activity coincided with observed periods of activity (Kearney et al., 2018), while others have used field-based observations for more qualitative validations of predicted windows of activity (Kingsolver, 1983) or overheating risk (Thomson et al., 1998; Moyer-Horner et al., 2015). Predicted estimates of activity have also been verified using photographs from camera traps (Fitzpatrick et al., 2015). In general, there are many ways of assessing whether mechanistic niche models accurately predict activity, and verifying these predictions is especially important because restrictions on activity have been suspected to represent the basis for ecological responses to environmental change (Sinervo et al., 2010).

Many studies that focus on range shifts or species geographic distributions validate the output from mechanistic niche models using species occurrence data or species distributions (Buckley, 2008; Briscoe et al., 2016). Thus, they incorporate observations of species occurrence (i.e. coordinates associated with the presence of a focal organism) to validate niche models that predict the spatial distribution of suitable habitat (Riddell et al., 2017; Fordham et al., 2018). In some cases, habitat is considered suitable if the organism is predicted to obtain sufficient energy for reproduction (Buckley et al., 2010; Riddell et al., 2018) or if it can maintain life-sustaining processes such as homeothermy (Briscoe et al., 2016). These studies then assess the degree to which occurrences fall within or outside of the predicted suitable habitat. More quantitative validations include calculating sensitivity and specificity indices, which incorporate occurrences and absences, respectively (Buckley, 2008; Buckley et al., 2010). Validations that use species distributions or occurrences are important for improving the confidence of predictions for mechanistic niche models, though validations at the species distribution level do not assess the validity of the underlying assumptions. Moreover, some species only occupy a small portion of their fundamental niche as a result of species interactions, making occurrence data unhelpful for evaluating the performance of these niche models (Buckley, 2008; Newman et al., 2022). Thus, developers and users of these models should interpret results cautiously without using validations at multiple levels of inference. Of the most recent 30 studies that use mechanistic niche models (see appendix S2 in Briscoe et al., 2022a,b), 22 (73%) reported some type of validation. However, the type of validation was variable among studies: 10 (33%) with microclimate validations, 11 (37%) with physiological validations and one (3%) with species distribution validations. As mechanistic niche models become more accessible, validations will likely become critical to building confidence in this approach; thus, we encourage users to validate model input and output, especially if the models are applied to novel environments or organisms.

Evolution and phenotypic plasticity
A general limitation of mechanistic niche models is that parameters are often treated as static values, rather than features that can shift across space and time as a result of plasticity and evolution. These models do not often incorporate empirically derived values related to evolutionary change (e.g. selection coefficients and heritability) because of the complexity involved in linking heat balance models with simulations of phenotypic change across generations. However, there are two examples in which mechanistic niche models have simulated phenotypic responses to selection across generations (Kearney et al., 2009a; Kingsolver and Buckley, 2015). In these studies, researchers used empirically derived heritability and selection gradients from full-sibling breeding experiments (Ellers and Boggs, 2002) and survival experiments (Falconer and Mackay, 1996). In other cases, mechanistic niche models have explored the adaptive consequences of phenotypic variation for performance or survival (Kingsolver and Moffat, 1982). There are also many examples in which either observed or hypothetical phenotypic variation was integrated into niche models to understand the adaptive significance of a variety of traits (Steudel et al., 1994; De Jong et al., 1996; Mitchell et al., 2008; Finke et al., 2009; Riddell et al., 2022). Some niche models also integrate optimality models to predict optimal combinations of phenotypes, which are then compared with observations from nature (Kingsolver and Watt, 1984). Similar approaches have also been used to understand the effects of phenotypic plasticity.

Mechanistic niche models represent an effective way to incorporate and understand the ecological consequences of phenotypic plasticity measured in experiments (Kobelt and Linsenmair, 1995). These models typically incorporate plastic responses from a variety of physiological and morphological phenotypes from experiments or observations. Studies often conduct acclimation experiments to understand how an organism adjusts a trait (e.g. water loss rate, metabolic rate, thermal tolerance, coloration or reflectance) in response to environmental variables (often temperature) in a controlled laboratory setting (Riddell et al., 2018; Enriquez-Urzelai et al., 2020). These values are then incorporated into mechanistic niche models such that the physiological value is a function of the environmental cue, such as temperature (Kingsolver and Buckley, 2017; Newman et al., 2022), or comparisons can be made between models with the different phenotypic values from the experiments (Riddell et al., 2018; Enriquez-Urzelai et al., 2020). Reaction norms that capture the observed phenotypic plasticity have also been integrated with quantitative genetic models to predict phenotypic variation of coloration across latitude and elevation (Kingsolver and Buckley, 2017) or to predict whether organisms have the capacity to limit overheating risk by changing skin reflectivity (Kobelt and Linsenmair, 1995). However, relatively few models have incorporated evolutionary and plastic responses from experiments into their predictions, and such approaches are poised to improve predictions of phenotypic responses to environmental change.

Biotic interactions

Species interactions can limit the fundamental niche, shaping and ultimately determining a species' realized niche (Matthiopoulos, 2022). Thus, mechanistic niche models have begun to incorporate biotic interactions to provide further insight into the factors influencing the niche (Tylianakis et al., 2008; Buckley, 2013). Prey availability, competition and mutualistic interactions may affect geographic distributions, and ignoring these interactions may lead to less accurate predictions of species ranges (Buckley, 2013). Most examples of mechanistic niche models including biotic interactions involve theory (Buckley and Roughgarden, 2005; Buckley, 2008; Gifford and Kozak, 2012; Gutiérrez et al., 2014; Levy et al., 2016; Stephenson et al., 2022), yet experiments can also be used. For example, competition coefficients in the Lotka–Volterra model have been approximated as the ratio of observed interspecific to intraspecific aggressive encounters (Buckley, 2013). In these experiments, the focal organism is placed in a natural environment and once it establishes a territory, another individual is introduced (Hess and Losos, 1991). The experiments then quantify the intraspecific or interspecific interactions using ethograms to measure agonistic behaviors, such as aggressive interactions, competition for resources or territorial displays. To our knowledge, Buckley (2013) represents the only study to date that has explicitly included empirical estimates of competition in mechanistic niche models, likely because of the complexity necessary to couple heat flux simulations with demographic models. Despite the lack of examples, there are several experimental approaches that may be suitable for parameterizing mechanistic niche models.

Observational studies measure encounters within or between species using ethograms or annotations specifying the types of interactions that occur and can include competition (Wallace and Temple, 1987), mutualism (Pick and Schlindwein, 2011) or predation (Simon, 1975). These interactions can then be grouped into intraspecific and interspecific competition and used to calculate a competition coefficient (Cunningham et al., 2009). In addition, Lotka–Volterra models are also used to simulate predator–prey interactions (Obaid, 2013), where coefficients can be estimated based on the frequency of encounters or population demographics. Moreover, some mechanistic niche models have started to incorporate biophysical interactions between plants and animals. For instance, leaf temperature affects the microclimates that many insects experience (Pincebourde et al., 2021), and models that incorporate the physiological and physical characteristics that determine leaf temperature (i.e. stomatal conductance) are likely to play an important role in exposure to lethal temperatures for many insects (Pincebourde and Casas, 2019; Riddell et al., 2023). Models that account for these interactions may produce more rigorous predictions of species distributions, activity and energy budgets and could better estimate the effects of changing environments on organismal performance and fitness.

Conclusions and perspectives

Mechanistic niche models are used to answer a wide range of questions in ecology, evolution and global change – from the adaptive benefits of phenotypic variation (Riddell et al., 2022) to the traits that influence climate vulnerability (Briscoe et al., 2022a). In our Review, we describe the sources of empirical data that are often used to parametrize mechanistic niche models in biophysical ecology. These sources often involve experiments or observations on the physiological, behavioral and morphological sensitivity of organisms to the environment, with a particular emphasis on temperature. Moreover, empirical data are often used for ground truthing predictions from these models. We note that mechanistic niche models do not necessarily require empirical data and often rely heavily on theory (especially physical principles) for parameterization (Porter et al., 1994). Species-specific empirical data may also not be necessary in cases when questions are based on general mechanisms or patterns across broad spatial scales. Moreover, sensitivity analyses on species-specific data may provide insight into how predictions change for species with different trait values. Theory helps to speed the development of these models and incorporate increasingly complex processes into mechanistic niche models (Kearney et al., 2021b). Nevertheless, theory does not provide a surrogate for validations or capturing the observed variation in functional traits among populations and species. Rather, empiricism and theory complement each other through a reciprocal exchange of ideas and information (Angilletta, 2009), and mechanistic niche models can be viewed as the vehicle by which the exchange occurs. The future development and implementation of mechanistic niche models will continue to rely on empirical data to answer some of ecology's most pressing questions, especially with the emergence of more efficient data automation to study animal behavior and physiology (Kays et al., 2015). Integrating mechanistic niche models with ecological data on long-term species responses to environmental change and global networks of environmental data will also continue to reveal the processes driving the climate vulnerability of species (Riddell et al., 2021). By unifying theory and empiricism, mechanistic niche models are poised to enhance ecological forecasting by providing a process-based foundation for prediction.

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