



SYMPOSIUM

Fundamental Flaws with the Fundamental Niche

Michael J. Angilletta Jr,^{1,*} Michael W. Sears,[†] Ofir Levy,[‡] Jacob P. Youngblood^{*} and John M. VandenBrooks[§]

^{*}School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA; [†]Department of Biological Sciences, Clemson University, Clemson, SC 29634, USA; [‡]School of Zoology, Tel Aviv University, Tel Aviv, 69978, Israel; [§]Department of Physiology, Midwestern University, Glendale, AZ 85308, USA

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¹E-mail: ma@asu.edu

Synopsis For more than 70 years, Hutchinson’s concept of the fundamental niche has guided ecological research. Hutchinson envisioned the niche as a multidimensional hypervolume relating the fitness of an organism to relevant environmental factors. Here, we challenge the utility of the concept to modern ecologists, based on its inability to account for environmental variation and phenotypic plasticity. We have ample evidence that the frequency, duration, and sequence of abiotic stress influence the survivorship and performance of organisms. Recent work shows that organisms also respond to the spatial configuration of abiotic conditions. Spatiotemporal variation of the environment interacts with the genotype to generate a unique phenotype at each life stage. These dynamics cannot be captured adequately by a multidimensional hypervolume. Therefore, we recommend that ecologists abandon the niche as a tool for predicting the persistence of species and embrace mechanistic models of population growth that incorporate spatiotemporal dynamics.

Introduction

Every introductory textbook in biology defines the concept of a fundamental niche and discusses its role in setting the distributions of species. What started as concluding remarks by Evelyn Hutchinson about a symposium on quantitative biology (Hutchinson 1957) was destined to guide research on organisms, populations, and communities for decades to come (Chase and Leibold 2003; Holt 2009; Schoener 2009; Kearney et al. 2010a). Hutchinson defined the niche as a set of points in an abstract n -dimensional space—a hypervolume of environmental states that enable a species to exist indefinitely. This perspective enabled researchers to quantify dimensions such as a thermal, hydric, or dietary niche. In theory, the breadth of the niche in each dimension evolves according to a simple tradeoff: a jack-of-all abiotic conditions is a master of none (Levins 1968; Lynch and Gabriel 1987; Kassen 2002). Furthermore, interactions with other

species feed back to shape the fundamental niche through coevolution. The breadth of the niche along each of these dimensions limits the environments in which we can expect to find an organism. Therefore, ecologists use models of the niche to predict many patterns, such as where a rare species will occur, how far an invasive species will spread, and whether species will persist in a changing environment.

Unlike previous concepts of the niche (Grinnell 1917; Elton 1927), Hutchinson’s hypervolume offers the mathematical framework to represent interactions among environmental variables that influence the fitness of an organism (Fig. 1). For example, the optimal temperature of an organism depends on the quantity or quality of food in its environment; the more food an organism consumes, the higher the temperature it needs to maximize growth (Brett 1971; Elliott 1982; Huey 1982). Similarly, the lethal temperature of an organism may depend on its supply of energy, water, or oxygen (Pörtner 2001;

(Santos et al. 2011; Verberk et al. 2016). These empirical patterns illustrate the advantage of a multivariate model of the niche, which describes how two or more environmental variables interact to affect the fitness of an organism. For example, consider this model of a niche with three dimensions:

$$F = \alpha + \beta_1 X_1 + \beta_2 X_2 + \beta_3 X_3 + \beta_4 X_1 X_2 + \beta_5 X_2 X_3 + \beta_6 X_1 X_3 + \beta_7 X_1 X_2 X_3 + \epsilon,$$

where F is fitness estimated as a rate of population growth, α is the intercept of the model, X_i is abiotic factor i , β_i is the effect of abiotic factor i , and ϵ is the expected error. The parameters β_4 through β_7 describe the curvature of the hypervolume in three-dimensional space, which leads to potentially surprising predictions about where the species would occur in nature. We can estimate the parameters of this model experimentally by manipulating the three variables (X_1 , X_2 , and X_3) in a factorial design and measuring rates of population growth (Birch 1953a). As you can imagine, such experiments become unwieldy for more than a few dimensions, and even a simple factorial experiment would be impractical for many species. Alternatively, many ecologists use the geographic distribution of a species to approximate the fundamental niche; the model fitted like the one listed above would be fit to presence or absence of species at locations with the relevant abiotic variables (X_1 , X_2 , and X_3), such as temperature, precipitation, and humidity (Guisan and Zimmermann 2000; Pearson and Dawson 2003; Elith et al. 2006; Pearson et al. 2006). Of course, the resulting model describes only a subset of the fundamental niche referred to as the realized niche, because geographic distributions depend on interactions between species (Guisan and Zimmermann 2000; Hampe 2004; Araujo and Guisan 2006). Nevertheless, such a model has value when applied cautiously in cases where one cannot obtain experimental data (Franklin 2009).

In using the niche as an organizing concept for research and teaching (Angilletta and Sears 2011; Angilletta 2014), we have come to realize that a fundamental niche is easy to discuss in principle but difficult to quantify in practice. At a minimum, one must define the relevant environmental variables of the n -dimensional hypervolume and relate these variables to a metric of fitness. In doing so, three challenges stand in the way. First, the hypervolume must account for the frequency, duration, and sequence of abiotic stresses over time. Second, the same hypervolume must reflect the spatial structure of the abiotic environment as well as its temporal

structure. Finally, this hypervolume must change as development and acclimatization changes the phenotype of the organism. In this article, we explore these challenges and present a case for abandoning the niche as a quantitative paradigm in ecology. We are not the first to criticize the concept (Holt 2009) or even to call for its dismissal (McInerny and Etienne 2012). However, we offer a unique perspective as researchers engaged in mechanistic niche modeling—namely, that ecologists would benefit from abandoning Hutchinson's concept of the n -dimensional hypervolume in favor of individual-based models of population growth that incorporate temporal and spatial variation.

Niche boundaries are fuzzy

Environmental variation has always been a central focus of niche models. Levins (1962) assumed that environments varied only among generations, while Lynch and Gabriel (1987) extended the theory to add variation within generations. In both cases, variation over space effectively resulted in variation over time caused by movement or dispersal. These models assume that one can ignore the order of environmental states when calculating the fitness of the organism. In other words, an organism that experienced 25°C for the first half of its life and 30°C for the second half would have the same fitness as an organism that fluctuated between these temperatures daily. However, real organisms have a physiological memory that results in either cumulative stress or acquired resistance.

The frequency, duration, and sequence of abiotic stress often matter as much as the magnitude. Nothing illustrates this point better than the following observation: a condition that enhances growth or development over short periods could cause death over longer periods. For example, lizard embryos exposed to a constant temperature of 34°C suffered 100% mortality, but even higher temperatures promote survival and development when experienced for just a few hours a day (Fig. 2). Similarly, insects survive repeated exposures to low temperatures that cause death during chronic exposure (Marshall and Sinclair 2010). The effects of duration on survivorship and performance extend to other abiotic stresses, such as relative humidity (Arlian et al. 1998). These temporal effects introduce substantial error when predicting the performance of organisms in fluctuating environments from their performance in constant environments (Niehaus et al. 2012). The development of phenotypes can also depend on how often an abiotic factor fluctuates

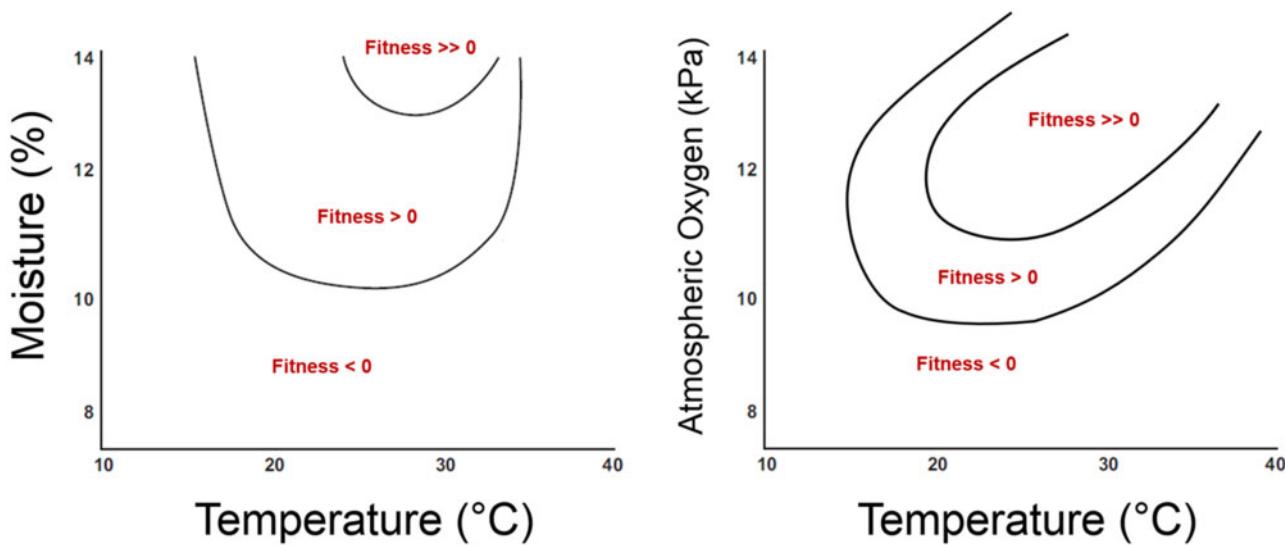


Fig. 1 A fundamental niche relates the fitness of a genotype to one or more dimensions of the abiotic environment, such as temperature, moisture, or oxygen concentration. Left: The fundamental niche of a species of beetles, *Calandra oryzae* (Birch 1953b). The contours show the relative fitness as estimated by the finite rate of increase (λ). The two abiotic variables, temperature and moisture, do not interact strongly to influence fitness. Right: A hypothetical niche for a species of aquatic insects, depicting the common interaction between temperature and oxygen concentration.

(Czarnoleski et al. 2015). Frequent fluctuations, without a change in the mean or variance of temperature, enhanced survivorship but decreased fecundity of *Drosophila melanogaster*, leading to a complex effect on fitness (Marshall and Sinclair 2010).

The boundaries of a fundamental niche are clearly fuzzier than Hutchinson imagined, but do we really need to abandon his concept altogether? Some might warn us not to throw out the baby with the bathwater. Indeed, Hurlbert (1981) suggested decomposing each abiotic factor into several dimensions to account for temporal variation. For example, temperature can be divided into mean temperature, the standard deviation of temperature, minimal temperature, and maximal temperature. Hurlbert's approach has been used extensively when building statistical models of the niche from climatic data (Franklin 2009). These models decompose a thermal niche into many variables, such as monthly mean temperatures, minimal annual temperature, and maximal annual temperature. Each of these variables represents a dimension of the n -dimensional niche. Clearly, some dimensions are more relevant than others, but these dimensions might also interact. For example, a high standard deviation of temperature positively affects fitness when the mean temperature is low but negatively affects fitness when the mean is high (Siddiqui et al. 1973; Siddiqui and Barlow 1973; Martin and Huey 2008; Bozanic et al. 2011).

Even if we decompose each abiotic factor into statistical parameters such as the mean and the

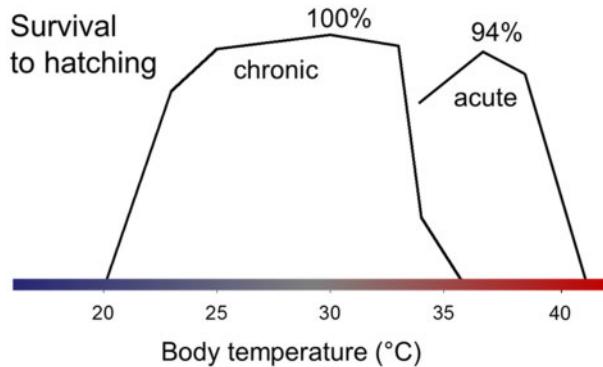


Fig. 2 How well an organism tolerates a temperature depends on how long it experiences that temperature. For example, lizard embryos can survive daily exposure to temperatures that would cause death during prolonged exposure. Rates of survival at constant temperatures (chronic) were taken from Angilletta et al. (2000) and Andrews et al. (2000). Rates of survival at fluctuating temperatures (acute) were taken from Levy et al. (2015).

variance, we still should account for the duration of exposure to extreme conditions. Some biologists have proposed that complex indices of environmental tolerance replace simple thresholds such as lethal limits. Cooper et al. (2008) accounted for the duration of stress when predicting heat tolerance. Rezende et al. (2014) expanded this perspective to develop the concept of a tolerance landscape, which relates the survivorship of an organism to the magnitude and duration of stress (Jørgensen et al. 2019). However, this approach quickly becomes unwieldy when the frequency, timing, and duration of stress

matter for many abiotic factors. The resulting fundamental niche would be a ridiculously complex hypervolume.

Abiotic conditions reside in a landscape

An abiotic environment has a texture, in the sense that abiotic conditions vary over space to create a visible structure (Porter et al. 2010). We refer to this structure as the abiotic landscape—a spatially explicit map of relevant variables such as temperature, radiation, pressure, wind speed, and humidity. Importantly, an organism experiences an abiotic landscape on a scale determined by its size, shape, and mobility. A larger animal heats more slowly in a location and likely moves more quickly between locations. To account for the way that each organism interacts with its abiotic environment, ecologists must infer operative environmental conditions. For instance, an operative temperature defines the way that air temperature, radiation, and wind speed combine to change the body temperature of an organism, given its physical properties. With a landscape of operative temperatures, one can quantify the change in body temperature as the organism moves through the landscape.

The spatial structure of the abiotic landscape adds another challenge when quantifying a fundamental niche: accounting for constraints and costs associated with homeostasis. When deciding whether a species can persist in an environment, we presume that Hutchinson would have us account for the organism's capacity to regulate its internal state. If so, each axis of a niche represents abiotic conditions as experienced by the organism, because the abiotic state of the organism likely differs from the abiotic state of the environment (Kearney 2006). The magnitude of this difference depends on the extent to which an organism can balance its exchange of matter and energy with its environment.

Using behavioral thermoregulation as an example, we can understand the difficulty of factoring homeostasis into the fundamental niche. When possible, an animal moves through its environment to keep its body temperature within certain bounds. Even a mammal or bird, which produces copious amounts of heat through cellular respiration, will seek solar radiation to offset heat lost to the air or ground (Angilletta et al. 2010). Similarly, an animal might press against a warm surface to speed conduction or seek shelter from wind to avoid convection. A neural thermostat coordinates movements between these microclimates to remain within a preferred range of body temperatures (Angilletta et al. 2019). With

each decision, an animal spends energy to move, or misses an opportunity to behave differently. In this way, thermoregulation imposes costs that reduce the net benefit of homeostasis.

The exact cost of thermoregulation depends on the spatial distribution of microclimates (Fig. 3). Simulations have shown that patchier distributions of microclimates enable animals to thermoregulate with less movement (Sears et al. 2011; Sears and Angilletta 2015), saving energy. When an animal must move between sun and shade too frequently, the cost of thermoregulation will exceed the benefit (Huey and Slatkin 1976), causing the animal to stop shuttling (Withers and Campbell 1985). Thus, a patchier distribution of sun and shade should enhance an animal's opportunity and willingness to thermoregulate. By doing so, a patchy distribution increases the chance of surviving in an environment where an animal must behaviorally thermoregulate.

Current niche models ignore the cost of searching for and moving between microclimates. When fitting a statistical model of the niche, the parameter for residual variation subsumes any effect of spatial configuration on the rate of a population's growth or the chance of species' presence. This problem can be solved by adding a dimension of the niche to describe the spatial configuration. For instance, one might include the fractal dimension of operative temperatures as an independent variable in a niche model; the fractal dimension has been shown to adequately capture the spatial configuration of operative temperatures (Sears et al. 2011). However, further proliferation of niche dimensions seems impractical for two reasons. First, we rarely know the spatial configuration of abiotic conditions at the scale and extent of the regions in which we intend to apply the niche model. Second, even if the spatial configuration were known, would we really choose to visualize its influence on an organism as a dimension of a hypervolume? The proliferation of niche dimensions from simple abiotic variables to complex indices of abiotic variation becomes a cumbersome exercise needed only to conform to a flawed concept.

A more transparent approach would be to simulate the behavior and energetics of an animal in an abiotic landscape (Sears et al. 2011). Such simulations generate a sequence of body temperatures for use in a lab experiment or a niche model. To develop a realistic sequence, one must use the spatial distribution of microclimates and the properties of an animal to compute a landscape of operative temperatures (Sears et al. 2016). Then, by simulating the warming and cooling of an animal as it moves through this landscape, we generate an expected

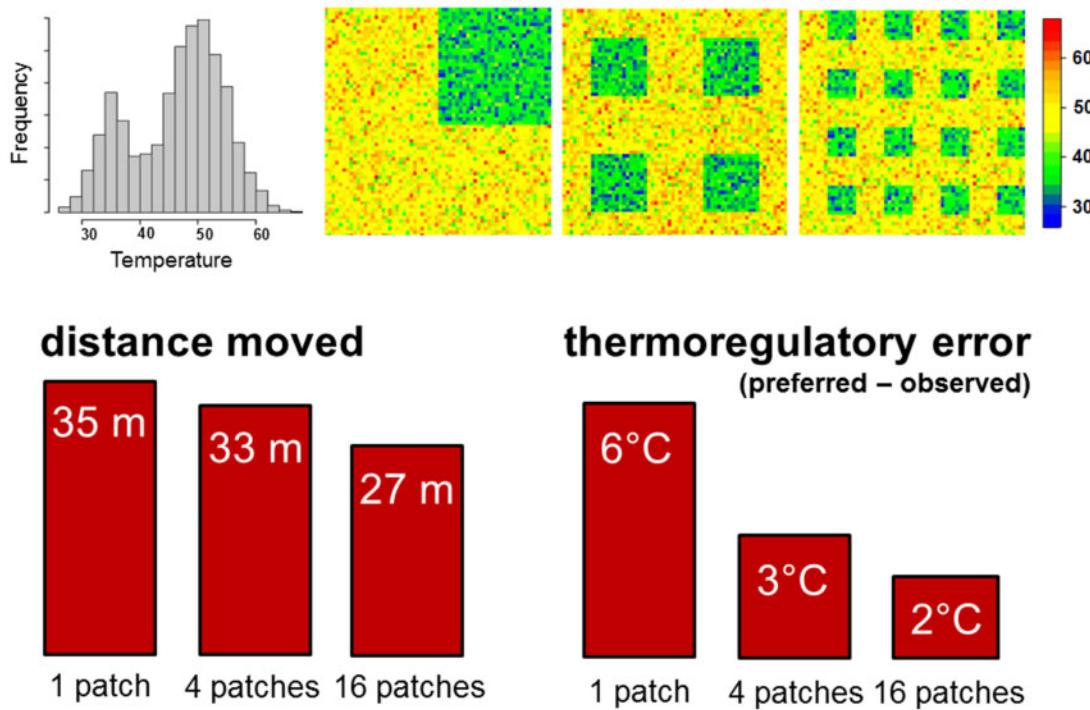


Fig. 3 The spatial configuration of operative temperatures determines the energetic cost of and the environmental constraint on thermoregulation. Sears and Angilletta (2015) illustrated this point by simulating a lizard moving through different landscapes while trying to keep its body temperature within a preferred range. The landscapes (top right) differed in the spatial distribution of cool patches (1, 4, or 16), while having the same statistical distribution of operative temperatures (top left). On average, greater patchiness decreased the movement required to thermoregulate and the resulting error in thermoregulation, estimated as the actual body temperature minus the preferred body temperature.

sequence of body temperatures for any type of animal (Sears and Angilletta 2015). Such simulations produce more realistic sequence of body temperatures than those commonly used by researchers interested in niches. For instance, Deutsch et al. (2008) computed the fitness of each species of insects from its thermal niche and a sequence of air temperatures recorded by weather stations. In doing so, they assumed that the organism remains in shade at a height of 2 m above ground, the meteorological definition of air temperature. This behavior deviates greatly from that of most species, including the insects considered by Deutsch and colleagues. Regardless of how one chooses a sequence of temperatures, this choice implies a certain combination of abiotic landscape and thermoregulatory behavior, stemming from the movement of an animal in its environment.

The configuration of spatial variation can be just as important as the magnitude of abiotic variation over space. For example, the patchiness of operative temperatures can affect the energy needed to thermoregulate as much as the mean and standard deviation of operative temperatures do (Sears and Angilletta 2015). Moreover, temperature covaries

spatially with other abiotic variables, which may create tradeoffs when choosing microhabitats. This spatial covariation has only recently been explored experimentally; Rusch (2017) showed that a negative spatial correlation between thermal resources and food resources reduced the performance of lizards in patchy landscapes. If similar phenomena occur when other environmental factors covary, ecologists cannot ignore spatial variation when modeling the persistence of a species. Yet, we see no obvious way to account for spatial covariance between environmental factors that make up the dimensions of a niche.

A genotype has multiple niches

As an organism develops from one life stage to the next, major changes to its morphology, physiology, and behavior will alter the resources and conditions needed to survive and grow. For instance, adults of a species tolerate very different abiotic conditions than a larvae or an embryo. Similarly, the type and abundance of food needed by each life stage differs radically. Development alters not only the boundaries of a niche dimension but also the interactions between

dimensions. For example, the thermal tolerance of embryonic lizards (*Sceloporus tristichus*) depends on the oxygen concentration of their environment, but no such interaction exists for adult lizards from the same population (Fig. 4). Likewise, the tolerance of a species at a given life stage depends on abiotic conditions experienced at previous stages (Niehaus et al. 2012) or in previous generations (Gilchrist and Huey 2001). This phenotypic plasticity results from neural and endocrine systems that regulate development in response to environmental cues (DeWitt et al. 1998). Predictable variation in abiotic conditions over space and time select for genotypes that can shift their environmental tolerance accordingly (Gabriel and Lynch 1992; Gabriel 1999, 2005, 2006; Le Vinh Thuy et al. 2016).

We cannot tell whether Hutchinson recognized how development and plasticity relate to his model of the niche. On page 417, he stated that “the model refers to a single instant of time (Hutchinson 1957).” However, he then goes on to explain that “the model” refers to how species use their environment given their fundamental niche. For example, Hutchinson states that “a nocturnal and a diurnal species will appear in quite separate niches, even if they feed on the same food, have the same temperature ranges etc.” Thus, we believe that Hutchinson failed to appreciate that a fundamental niche must change during the life of an organism. Otherwise, we have to wonder how Hutchinson envisioned a niche as an “environmental state permitting the species to exist indefinitely.” Ecologists have interpreted this statement to mean a stable or growing population can exist in that set of environmental conditions (Sibly and Hone 2002; Holt 2009). This interpretation translates to inferring the indefinite existence of a species from a positive rate of population growth ($r > 0$) or a positive carrying capacity ($K > 0$) in a given environment. Yet, a single organism, let alone a single life stage, does not have such a property! So how can we logically define a fundamental niche at each life stage? In other words, one cannot define the niche as an instantaneous property of an organism because its dependent variable (fitness) depends on the interactions between a genotype and its environment throughout a life cycle (i.e., $G \times E \times E$).

Arguably, we could solve this problem by defining a fundamental niche as the set of environmental states tolerated by all life stages. But the timing of birth, the rate of development, and the phenotype at each life stage determines the operative environmental conditions experienced by an organism (Levy et al. 2016b). And this definition would still not capture the potential for plasticity of environmental

tolerance between life stages. To be blunt, we see no way to portray the development and plasticity of environmental tolerance in Hutchinson’s fundamental niche. If phenotype at a given stage depends on the sequence of environmental conditions experienced at previous stages, no one-to-one mapping of fitness onto environmental space exists to depict as a hypervolume.

Modeling population dynamics without the niche

We have argued that Hutchinson’s fundamental niche fails to capture the spatiotemporal structure of the environment and the developmental trajectory of an organism. In spite of our argument, the concept of the fundamental niche seems alive and well in ecology, as evidenced by the flourishing literature on mechanistic niche modeling (Kearney and Porter 2009; Buckley et al. 2010; Kearney et al. 2010a). A mechanistic niche model connects the behavior and physiology of organisms to the demographics of a population. Such a model predicts the abiotic conditions or the geographic locations where a species can persist (Robertson et al. 2003; Crozier and Dwyer 2006; Buckley 2008; Kearney et al. 2009). Unlike statistical niche models, mechanistic ones account for temporal variation of the environment and developmental changes of the organism (Kearney et al. 2012; Levy et al. 2015, 2016b). Thus, these models have benefitted greatly from recent efforts to downscale climates to a spatiotemporal scale experienced by organisms (Potter et al. 2013; Kearney et al. 2014; Levy et al. 2016a). Given the thriving industry of ecological niche modeling, how can we assert that the fundamental niche no longer holds a useful place in ecological theory?

Upon closer inspection, mechanistic niche modeling has less to do with Hutchinson’s concept of the niche than one might think. The models emerging in recent years have roots in the theories of three disciplines: (1) biophysical ecology, which describes how an organism exchanges mass and energy with its environment (Gates 1980; Bakken et al. 1985; Porter et al. 1994; Campbell and Norman 1998); (2) physiological ecology, which describes how an organism survives and reproduces under abiotic stress (Feder and Block 1991; Huey 1991; Karasov and Martínez del Rio 2007), and (3) population ecology, which describes how births and deaths cause a population to grow (Renshaw 1991; Turchin 2003). These theories came together gradually over four decades. Between the 1970s and the 1990s, Porter and his collaborators pioneered the use of these

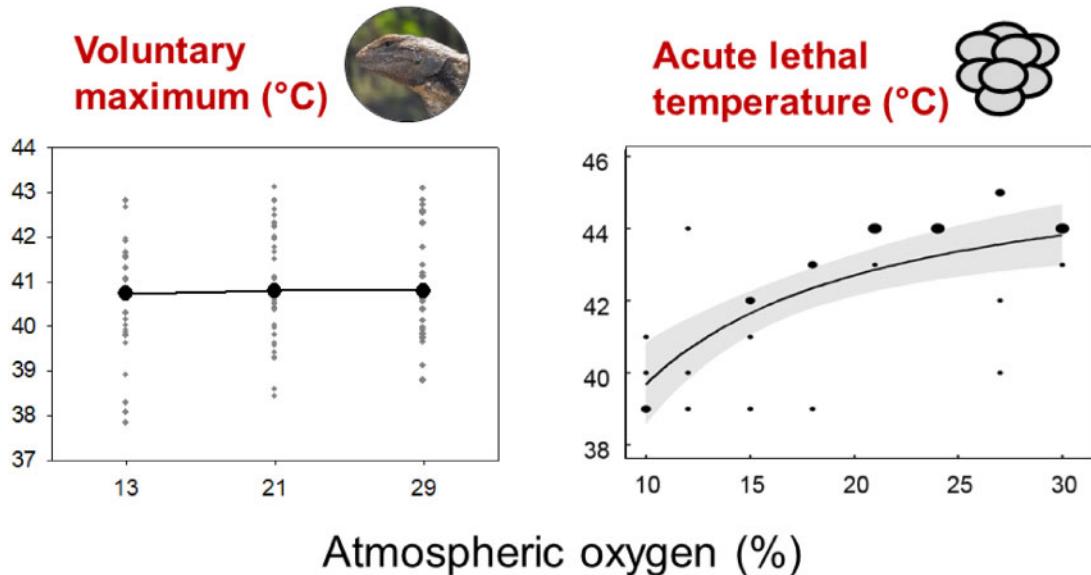


Fig. 4 The multivariate boundaries of the niche change throughout the life cycle of a lizard, *S. tristichus*. Left: During controlled warming, adult lizards avoid heating beyond 41°C, regardless of the oxygen concentration of their environment (Camacho et al. 2018b). This behavioral limit of thermal tolerance lies within 1°C of the physiological limit referred to as the critical thermal maximum (Camacho et al. 2018a). Right: During controlled warming, embryos survived temperatures >41°C when the oxygen concentration of their environment exceeded 13% (Smith et al. 2015).

biophysical models to predict as to when and where species can survive and function (Porter et al. 1973, 2010), eventually putting biophysical ecology in the context of geographic ranges (Adolph and Porter 1993; Porter et al. 2002). A turning point for this work occurred when Kearney and Porter (2004) combined climate and physiology to model the performance of a species over an entire continent. In doing so, these researchers rebranded this type of work as niche modeling by framing their study in the context of the fundamental niche. However, one does not need the concept of a fundamental niche to appreciate what Kearney and Porter did, or what Porter had done previously. Indeed, their models were far more complex than anything that Hutchinson's view could assimilate. Kearney went on to connect biophysics to population dynamics by modeling behavior, physiology, and life history (Kearney et al. 2010b; Kearney 2011, 2013), widening the gap between mechanistic niche modeling and the simple notion of an n -dimensional hypervolume. This body of ecological theory has moved past the point where Hutchinson's concept adds value. To avoid confusion and give credit where credit is due, ecologists should refer to this research as mechanistic population modeling, given its focus on mechanisms of population growth.

Abandoning the fundamental niche would encourage ecologists to move toward a theory that

integrates spatiotemporal dynamics across scales. Current models map spatial patterns of population growth among sites while ignoring spatial processes driving population growth within sites (Heffernan et al. 2014). For example, when modeling the activity of animals in an abiotic landscape, one generally ignores the cost of movement or treats this cost as a constant (Buckley et al. 2015). This practice misses potential impacts of movement of an organism on its energetics and life history (Adolph and Porter 1993; Werner and Anholt 1993; Anholt 1997; Sears and Angilletta 2015). To overcome this problem, many ecologists have turned to individual-based models (DeAngelis and Gross 1992; Judson 1994; Grimm 1999), which enable one to simulate population dynamics resulting from interactions between organisms (Grant and Porter 1992; Van Winkle et al. 1993; DeAngelis and Mooij 2005). Because an individual-based model can incorporate a spatially explicit landscape (Pacala and Silander 1985; Dunham 1993; McCauley et al. 1993), they offer a chance to see how the spatial structure of the landscape affects the fitness of an organism. Other approaches to population modeling, such as matrix models or integral projection models (Ellner and Rees 2006; Merow et al. 2014), can account for spatiotemporal dynamics in several ways (Hooten and Wikle 2008; Wikle and Hooten 2010; Jongejans et al. 2011). Still, individual-based models enable one to

incorporate an organism's interactions with its abiotic landscape over time, which underlie the plasticity of environmental tolerance.

For those who have a hard time letting go of classic models, consider the fact that a fundamental niche never really existed in the first place. The niche is only a property of life that we have learned to imagine through training. Organisms and their environments exist, but the niche is simply how we imagine those organisms would perform if we could place them in an infinite set of environments (which likely do not exist, despite what proponents of a quantum universe would argue). In their book about modeling, [Box and Draper \(1987\)](#) cautioned us to "remember that all models are wrong; the practical question is how wrong do they have to be to not be useful." In this spirit, we should ask whether Hutchinson's concept of the fundamental niche has outlived its use to ecologists. Clearly, we believe it has done so, although we understand the desire to connect current research to foundational concepts. Still, any connection between the fundamental niche and mechanistic models of population growth seem too strained to have value. The n -dimensional hypervolume that Hutchinson offered as a model of the niche cannot be quantified given environmental variation and phenotypic plasticity. Any relationship that we can quantify would be more accurately described as a performance curve or a tolerance curve, which applies to acute environmental stresses and specific life stages. Moreover, in trying to fit a mold created by Hutchinson, we must design experiments that have little bearing on spatiotemporal patterns of stress that occur outside of the laboratory. For these reasons, fundamental niches are like black holes: you can believe they exist if you want to, but you will never observe one directly. Until we come to grips with this reality, the niche will remain a concept that distracts ecologists from building a theory that solves meaningful problems.

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