



GRAND CHALLENGES

Coordinating Theoretical and Empirical Efforts to Understand the Linkages Between Organisms and Environments

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Synopsis Schwenk and colleagues challenged biologists to develop a deeper understanding of the linkages between organisms and environments. These linkages are captured by the concept of the niche, which has guided theoretical and empirical research in ecology for decades. Despite this research, we still cannot explain or predict much of the variation in niches over space and time. This shortcoming hinders efforts to forecast biological responses to environmental change. We believe that progress has been slowed by poor coordination between theoretical and empirical efforts to understand the evolution of niches. Therefore, progress should be sped by research programs that integrate modeling and experiments. Such research programs should focus on the structures of environmental variation, the constraints on phenotypes, and the relationships between phenotypes and fitness.

Theodosius Dobzhansky: Does theoretical, mathematical investigation make sense unless it leads to experiments or interpretation?

Richard Lewontin: Obviously not. After all, we are concerned with a contingent world and not the world of poetry. . . . However, almost always after the mathematics is done, the answer comes out in a very simple form that the experimentalist usually can read if he's willing to ignore the machinery and look only at the conclusions.

—Dialogue excerpted from Lewontin (1980, pp. 66–7)

Introduction

In 1900, the renowned mathematician David Hilbert challenged his peers to solve a lengthy list of problems, thereby setting the stage for mathematics in the 20th century and influencing the course of this discipline to the present day (du Sautoy 2003). In the same vein, Schwenk et al. (2009) recently challenged biologists to tackle a set of their own problems. These problems in biology, although more loosely defined than mathematical problems, were

summarized as follows: (1) understanding the linkages between organisms and environments, (2) utilizing the functional diversity of organisms, (3) integrating analyses of living and physical systems, (4) understanding how genomes produce organisms, and (5) understanding how organisms balance stability and change. One can hardly overstate the potential impact of such calls to action. Indeed, the 20th century witnessed mathematicians solving many of the problems on Hilbert's list. We should hope that biologists will perform equally well in dealing with their own set of problems. Yet to effectively solve the problems defined by Schwenk

and colleagues, we must first examine the issues underlying each problem and the strategies required to tackle these issues. In doing so, we should also consider how these problems have been approached in the past and why they remain unsolved today.

In this essay, we focus on the first problem on the list: understanding the linkages between organisms and environments. As do many scientists, we judge our understanding of these linkages by our ability to predict relationships between organisms and environments over space and time. Making such predictions requires a theory—a collection of models that describe *how* organisms interact with their environments and *why* they interact with their environments in these particular ways. One concept has been essential to the development of such a theory: the concept of the fundamental niche. Based on the influential remarks of Hutchinson (1957), ecologists often define a fundamental niche as the set of environmental conditions under which a genotype can persist. This concept enables biologists to connect ideas about processes that occur at all levels of biological organization. At lower levels, biochemical and physiological processes constrain organismal performance in particular environments (Mitten 1997; Hochachka and Somero 2002; Angilletta 2009). At higher levels, the performances of organisms determine the spatial and temporal dynamics of populations and communities (Chase and Leibold 2003). In the middle of this hierarchy of processes lies the niche, which characterizes the performance of a genotype (or species) over a range of environmental conditions (Holt 2009). The power of the niche concept can be inferred from its pervasive role in the development of community ecology (Roughgarden 1972; Colwell and Fuentes 1975; Werner and Gilliam 1984; Cornell and Lawton 1992; Amarasekare 2003; Silvertown 2004; Leibold and McPeck 2006; Tang and Zhou 2011), as well as its growing role in models of population dynamics and species' distributions (Guisan and Zimmermann 2000; Guisan and Thuiller 2005; Pearman et al. 2008; Kearney and Porter 2009;

Calosi et al. 2010; Kearney et al. 2010). In fact, niche-based approaches are now being widely used to predict the biological impacts of environmental change, such as anthropogenic warming (Crozier and Dwyer 2006; Angilletta et al. 2008; Deutsch et al. 2008; Kearney et al. 2008; Buckley et al. 2010) and species invasions (Daleo et al. 2009; MacDougall et al. 2009). Thus, understanding the linkages between organisms and environments effectively boils down to establishing a predictive theory of the niche (Chase and Leibold 2003).

Here, we pose two arguments about our understanding of niches. First, we argue that current models fail to explain variation in fundamental niches within and among species. This failure indicates a need to improve our knowledge of the evolutionary processes that determine niches. Second, we argue that progress toward a predictive theory has been slowed by poor coordination between theoretical and empirical activities. This disconnect has allowed some ecologists to develop a theory of the niche that conflicts with empirical data, while other ecologists have conducted experiments without reference to the theory. Consequently, despite decades of intensive research, we have little hope of accurately predicting how populations, communities or ecosystems will respond to environmental change. We support these arguments with examples from studies of thermal niches, which reflect our primary area of expertise. Nonetheless, we believe that our main points hold for studies of niches in general.

The discord between models and observations

Ultimately, our understanding of the linkages between organisms and environments must be assessed by the generality of our theory (Prosser et al. 2007). A general theory captures mechanisms that apply to a wide range of systems and makes useful predictions about the dynamics of these systems (Dunham and Beaupre 1995). In this section, we show that the evolutionary theory of the niche fails on both counts.

One need only consider the most robust prediction of evolutionary niche theory to appreciate the rift between the models and observations. The current theory traces back to Levins (1968), who presented a series of models to describe natural selection operating on a unidimensional niche (Fig. 1). This dimension captured continuous variation in an environmental factor, such as temperature, humidity, or light. By relating this environmental factor to some measure of fitness, Levins defined the range of environmental conditions that led to a positive fitness (niche breadth) and the condition that led to maximal fitness (optimal environment). To constrain adaptation, Levins assumed that the integral of the niche remained constant during evolution. Consequently, a specialist—which persists over a narrow range of conditions—would enjoy greater fitness in its optimal environment than would a generalist (Fig. 1). This hypothetical constraint has been referred to as a specialist–generalist tradeoff (Kingsolver et al. 2001; Angilletta et al. 2003), which is a technical way of saying that a jack of all environments is a master of none. Given this tradeoff, the model predicts that the position of the niche should correspond to the most frequent condition of the environment.

Since Levins' work, the theory of the niche has expanded greatly. Subsequent models have considered the coadaptation of the niche's position and breadth during stochastic or directional change in the environment (Lynch and Gabriel 1987; Gabriel 1988; Huey and Kingsolver 1993; Lynch and Lande 1993; Gilchrist 1995, 2000). More complex models have examined the selective pressures on plasticity of the niche (Gabriel and Lynch 1992; Gabriel 2005) and the selective pressures caused by interactions within and among species (Gavrilets 1997; Ackermann and Doebeli 2004; Kopp and Gavrilets 2006). Niche models have also considered how ecological and evolutionary mechanisms combine to limit the geographic ranges of species (Pease et al. 1989; Kirkpatrick and Barton 1997; Atkins and Travis 2010). In all of these aspects of the theory,

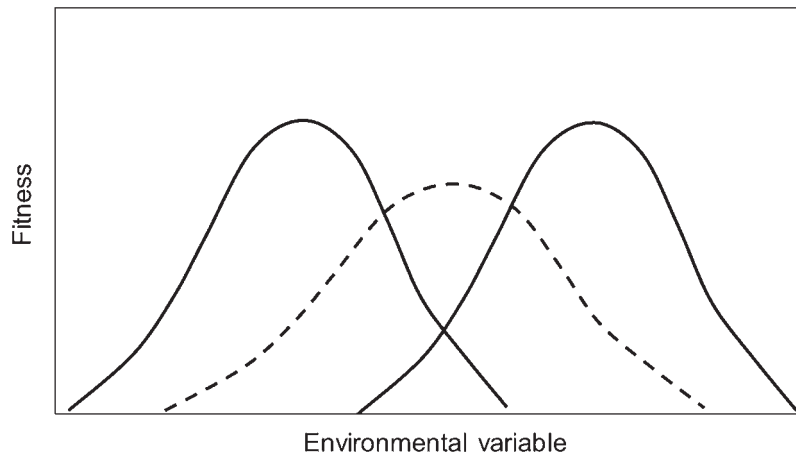


Fig. 1 Ecological niches are often modeled as a function relating the fitness of a genotype to a continuous environmental variable. The integral of this function is assumed to remain constant during evolution. Consequently, a greater breadth of the niche comes at a cost of fitness in the optimal environment, as depicted by these curves.

Levins' constraint on the evolution of the niche has been preserved (Chevin et al. 2010). Consequently, these models bolster Levins' prediction that the position of the niche should vary according to the conditions of the environment.

Despite the robust prediction that niches should correspond to environmental conditions, empirical data often deviate from this pattern. Consider examples from studies of thermal niches. Based on the theory, genotypes from colder environments should achieve their greatest fitness at lower temperatures—a shift in the position of the niche. Nevertheless, comparisons of thermal niches along altitudinal or latitudinal clines have often revealed a different pattern (Fig. 2A). Genotypes from some environments survived, developed, grew, or reproduced better than other genotypes over the entire range of temperatures (e.g., see Ayres and Scribner 1994; Yamahira and Conover 2002; Cooper et al. 2010; reviewed by Angilletta et al. 2002 and Angilletta 2009). This variation in the breadth of the niche, as opposed to variation in position, contradicts our expectation from the theory.

Even when the position of the niche does vary along thermal clines, another pattern in the data calls the theory into question: the integral (or area) of the niche varies among genotypes. A strict specialist–generalist tradeoff, as

depicted by most models, implies that the integral of the niche cannot evolve (Fig. 1). If that were the case, genotypes adapted to a low temperature and those adapted to a high temperature would be equally fit in their respective environments (compare the heights of the two solid curves in Fig. 1). Instead, genotypes adapted to high temperatures generally enjoy greater fitness at their optimal temperatures than do genotypes adapted to low temperatures (Fig. 2B). This phenomenon was first documented shortly after Levins' published his theoretical work (Eppley 1972) and formed the basis of early debates about the importance of thermodynamic constraints (Hamilton 1973; Heinrich 1977; Huey and Kingsolver 1989). Yet, the evolutionary theory of the niche continued to accumulate models that focus solely on a specialist–generalist tradeoff, ignoring the possibility that constraints on the niche might depend on other factors (but see Asbury and Angilletta 2010). Given our inability to predict current patterns of thermal niches, we should be wary of predictions about adaptation to thermal change, such as the warming caused by human activities on a local or global scale (Walther et al. 2002; Grimm et al. 2008).

Our inability to predict spatial variation in the thermal niche casts serious doubts on our understanding of the fundamental niche and its capacity to evolve. This doubt is reinforced by

experimental evidence against a key of assumption of the theory—that a specialist–generalist tradeoff pervades biological systems. Kassen (2002) reviewed the outcome of selection experiments that included constant and fluctuating environments. In contrast to the theory, evolution in a fluctuating environment generally increased the mean fitness over all environmental conditions. In other words, jacks of all environments somehow avoided becoming masters of none. Subsequent experiments involving a diverse array of environmental factors have confirmed these counter-intuitive results. (Turner and Elena 2000; Cuevas et al. 2003; Barrett et al. 2005; Hughes et al. 2007; but see Legros and Koella 2010). Although adaptation to a constant condition often resulted in a loss of fitness in other conditions (Kassen 2002; Hughes et al. 2007, Saxer et al. 2010), this pattern could reflect genetic drift rather than a specialist–generalist tradeoff (Hoffmann 2010). The prominence of the specialist–generalist tradeoff in the theory of the niche, despite abundant empirical evidence to the contrary, underscores a serious disconnect between the theoretical and empirical activities of ecologists.

Bridging the gap between theoretical and empirical research

If the current theory offers little hope of accurate prediction, how can we improve our understanding of ecological niches and their evolutionary dynamics? As illustrated above, the discord between theoretical predictions and empirical observations results from a failure to coordinate modeling and experiments. Therefore, future progress hinges on integrating these activities. If we are correct, the current state of affairs reflects an unfortunate irony. Levins opened his book by arguing that some areas of biology “suffered from an indigestion of facts, while data was [sic] collected without reference to problems. In these circumstances, theoretical work often diverged too far from life and became exercises in mathematics inspired by

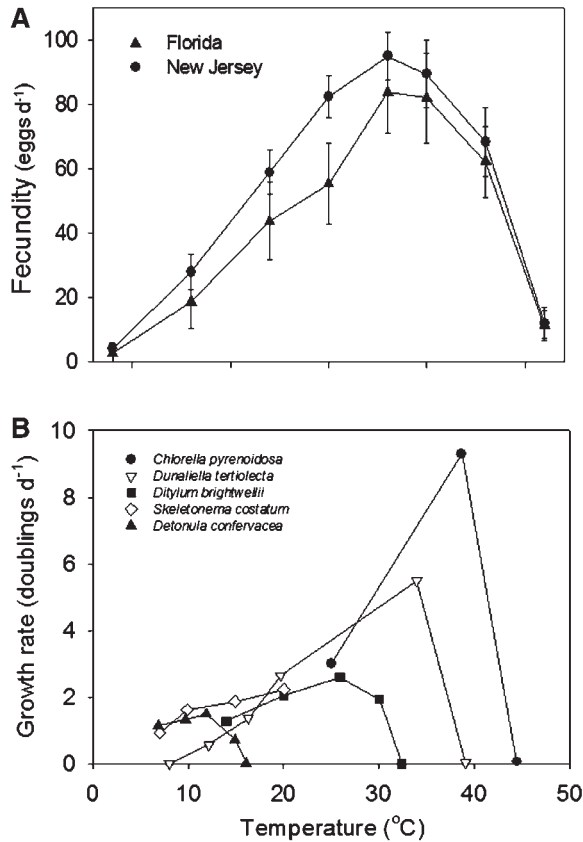


Fig. 2 Variation among thermal niches does not generally follow the patterns predicted by the theory. **(A)** Sometimes generalists outperform specialists over a wide range of temperatures. In this case, genotypes of *Drosophila melanogaster* from a population in New Jersey outperformed genotypes from a population in Florida, regardless of the temperature used in the experiment. Adapted from Cooper et al. (2010) with permission from John Wiley & Sons. **(B)** Often the integral of a thermal niche depends on its position along the thermal axis. In this example, the maximal fitness of a species depends on its optimal environmental temperature. Adapted from Eppley (1972) with permission from the National Marine Fisheries Service.

biology rather than an analysis of living systems” (Levins 1968, pp. 4–5). In his opinion, biology could profit greatly from interplay between models and experiments. Levins’ models of evolution in changing environments, along with a growing body of theory in other areas of biology, were supposed to set the stage for this transformation. In fact, Levins went so far as to predict that modeling would ultimately become part of the general practice, eliminating the need to consider theoretical biology as a distinct discipline.

A random sample of introductory texts in biology might convince readers that Levins was correct. These texts describe how biologists employ the scientific method to generate, evaluate, and refine theories about the processes of

life (Fig. 3). In the scientific method, one starts with some observations and constructs a verbal, graphical or mathematical model describing a mechanism that could account for these observations. With this mechanistic model in hand, one can predict a range of phenomena, including some phenomena not yet observed. One then tests these predictions empirically by manipulating and controlling certain variables and by observing their effects on other variables. Statistical modeling of the data enables one to infer the direction and magnitude of relationships between these variables. If the best statistical model accords with the predictions of the mechanistic model, one concludes that the data support the mechanistic model. If not, one

contemplates the cause of the discrepancy and refines the mechanistic model accordingly. In the words of the biologist John Moore (1993, p. 93), “this constant interplay of induction, hypothesis formation, deduction, and testing leads to improved understanding of the phenomenon being explored.”

This cycle of induction and deduction is how we describe the biological sciences to our students, but it probably describes the *minority* of research programs in organismal biology. More often, some researchers focus their efforts on theoretical investigations, while others focus their efforts on empirical investigations. Researchers often create mathematical models without collecting the data needed to test these models, while others conduct experiments without referring to hypotheses derived from theory (O’Connor 2000; Swihart et al. 2002). Both practices limit our progress toward understanding. Even when researchers actively combine inductive and deductive reasoning, they often rely on verbal models rather than on mathematical ones. Verbal models contain hidden assumptions and might not support the deductions claimed by their proponents (Angilletta 2009; Roff 2010). Moreover, verbal models make qualitative predictions, precluding the use of strong inference when multiple models predict similar relationships. To understand and predict linkages between organisms and environments, we must combine mathematical models and critical experiments in the way that has worked for other biological disciplines (e.g., see Dickinson et al. 2000; Stephens et al. 2007).

Some might argue that we exaggerate the problem. After all, the scientific method often comes to life as a collective enterprise among researchers with different interests, skills, and agendas. Theorists generate models that are then tested by empiricists. The results of these tests prompt theorists to revise their models. The interplay between these two groups of researchers completes the cycle of induction and deduction. Although we acknowledge this point, we still believe that our understanding of nature progresses more

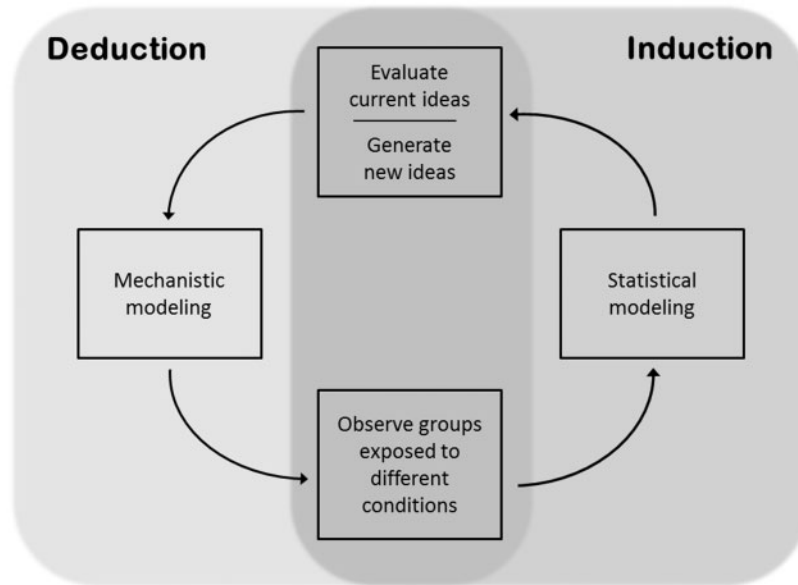


Fig. 3 The scientific method involves a cycle of induction and deduction. Observations lead a researcher to formulate a mechanistic model, which can predict a range of phenomena. A subset of these predictions is tested by fitting statistical models to experimental or comparative data. The outcome of this test can suggest a need to revise the mechanistic model, hopefully leading to an improved ability to predict future observations.

rapidly and more efficiently when a formal coordination exists between theoretical and empirical activities. Consider thermodynamic constraints on the evolution of thermal niches (Frazier et al. 2006), which we discussed in the previous section. More than 30 years passed before empirical observations by some researchers were used to develop a mathematical model by other researchers (reviewed by Angilletta et al. 2010). Who knows how long will pass before someone tests the predictions of the model? The progress of a loosely coordinated group will rarely match that of a team with a common agenda.

To bridge the gap between theoretical and empirical research, we must identify the reasons why many biologists (including ourselves) fail to integrate the two endeavors. The causes undoubtedly vary among individuals, but we propose four possibilities based on our experiences. First, rarely does one person possess the combination of skills required to complete all phases of the scientific method. Specialization begins during graduate education and intellectual inertia can be difficult to overcome. Given a finite period of time, one must trade off acquiring skills for theoretical research with acquiring skills for empirical research. If

one's graduate mentor focuses on empirical research, one likely receives extensive training in statistical modeling but little training in mechanistic modeling. The converse is true for those mentored by theorists. Even within the realm of modeling, universities typically divide mechanistic modeling and statistical modeling between courses, which undermines their complementary role in science (Hobbs and Ogle 2011). Second, one can become bored with old problems or distracted by new ones before completing a cycle of induction and deduction. This problem might explain why some researchers engage in both theoretical and empirical research without effectively linking the two. Third, one can publish more papers by focusing on a particular type of activity; juggling different activities, such as modeling and experimentation, likely slows the process (a specialist-generalist tradeoff!). In an environment in which administrators reward quantity over quality, researchers benefit by specializing in either theoretical or empirical work despite the cost to their discipline. Finally, one often cannot sustain funding to investigate a particular problem for a sufficient period of time. In an unstable economy, the best course of action to maintain financial

support might differ from the best course of action to solve a biological problem. By recognizing these and other extraneous factors that influence the nature of our research, we can consciously work to overcome their negative effects on scientific progress.

Further issues regarding the niche

Thus far, we have argued that ecologists must better integrate models and experiments to understand variation in fundamental niches. In constructing this argument, we focused on a nearly universal assumption about evolutionary constraints on the niche: the specialist-generalist tradeoff. Yet, ecologists should reconsider other aspects of the theory as well. In this section, we consider three key issues concerning fundamental niches: the structure of the environment, the constraints on performance, and the relationship between performance and fitness. For each issue, we highlight ways in which greater knowledge would help ecologists to advance the current theory.

Characterizing environmental variation as perceived by organisms

Despite their weaknesses, current evolutionary models have conclusively shown that patterns of environmental variation over space and time dramatically affect selective pressures on the niche. Expanding on Levins' work, other researchers (Lynch and Gabriel 1987; Gabriel and Lynch 1992) confirmed the need to consider environmental variation on two temporal scales: within generations and among generations. But how much do we know about these variations in real environments? Often comparisons of niches among populations are made without reference to the temporal structure of environmental variation (but see Cooper et al. 2010). Furthermore, real organisms inhabit complex environments, meaning that we must also consider the covariances between environmental variables over space and time. These covariances could impose unique selective pressures, especially if adaptation to one

environmental factor trades off with adaptation to another (see below). Thus, our ability to predict the evolution of niches would benefit from spatially explicit measurements of environmental conditions at a resolution germane to organisms (Bell et al. 1993; Helmuth et al. 2010; Sears et al. 2011).

Relating environmental measurements to the theory requires information about organisms, because the characteristics of a species determine whether it experiences environmental variation within or among generations (Levins 1968). The life history interacts with diel and seasonal cycles of the environment. Also, behavior has a major impact on the variation experienced by an organism (Sih et al. 2010). For example, the capacity for movement and the structure of the environment determine how spatial variation translates to temporal variation. If the environment varies on a microscale and individuals choose microclimates carefully, organisms could experience less variation than one would expect from physical measurements of the environment. Thus, behavioral strategies can relax selective pressures on the niche and slow the divergence of niches among populations (Wiens and Graham 2005), a phenomenon referred to as niche tracking by some (Labra et al. 2009) and behavioral inertia by others (Huey et al. 2003). Yet, behavioral strategies of homeostasis are not without costs. Existing theory could be extended to consider the coevolution of behavioral strategies and niche breadth (Angilletta et al. 2006; Angilletta 2009).

We have been discussing the niche in terms of an abiotic factor (temperature), but each organism resides in a landscape of competitors, predators and parasites. These biotic factors further constrain the distributions of genotypes. For example, the presence of a competitor or a predator can prevent a genotype from persisting in a region where abiotic conditions would otherwise permit persistence (Sexton et al. 2009). Empirical examples of this phenomenon underscore the need to distinguish between a fundamental niche and a realized niche—the realized niche being that part of the fundamental niche which remains unaffected by

interactions with other species (Hutchinson 1957). Community ecologists have spent decades trying to understand how biotic factors transform fundamental niches into realized niches (reviewed by Chase and Leibold 2003). Yet, the interactions between species do more than shape the realized niche; these interactions also affect the evolution of the fundamental niche. For example, Mitchell and Angilletta (2009) showed that interactions with predators can alter the optimal thermoregulatory behavior of prey, which in turn affects selective pressure on the thermal niche. Other models describe how the niches of competitors or mutualists might co-evolve (Gavrilets 1997; Ackermann and Doebeli 2004; Kopp and Gavrilets 2006). An integration of theoretical and empirical research in this area would facilitate progress. On the empirical side, novel predictions about the evolution of the niche during species interactions have yet to be tested experimentally or comparatively. On the theoretical side, empirical tests would be easier if the models were tailored to specific systems, incorporating known properties of environments and species.

Defining constraints on the niche

Originally, Levins (1968) envisioned the specialist–generalist tradeoff as a plausible, if not necessary, constraint on the evolution of the niche (Fig. 1). The underlying mechanism for this tradeoff was the allocation of limited resources to traits that enhance fitness in different environments. Yet, populations in fluctuating environments sometimes evolve broader niches without suffering an obvious cost (Kassen 2002). So, if a specialist–generalist tradeoff does not exist universally, what does constrain the niche?

The most important tradeoffs might occur *between* dimensions of the niche rather than *within* dimensions. A wide breadth along one dimension of the niche (e.g., temperature) might impose a cost along another dimension (e.g., humidity). Since most selection experiments involve only a single environmental factor, they can neither confirm nor refute the existence of tradeoffs between niche dimensions. In a particularly intriguing experiment,

however, MacLean et al. (2004) studied bacteria that had adapted to spatial variation in their environment. Within a few days, the populations consisted of typical genotypes that grew within the broth as well as mutant genotypes, which grew at the oxygen-rich interface between broth and air. However, the mutants exhibited catabolic deficiencies that prevented them from using many nutrients that could be used by the ancestral genotype. Thus, a shift in one component of the niche was accompanied by a shift in another component. Surprisingly, most of the catabolic deficiencies disappeared within a few weeks, suggesting that subsequent adaptations compensated for the initial tradeoff (MacLean et al. 2004). Perhaps even this compensatory adaptation involved a loss of fitness along some unquantified dimension of the niche.

Tradeoffs between fundamental and realized components of the niche should also constrain adaptation, especially considering a common way that genotypes expand their fundamental niche. Here again, a consideration of thermal niches drives the point home. In some species, thermal niches have diverged among populations such that certain genotypes grow rapidly over a wide range of temperatures. To accomplish this feat, these genotypes have increased their frequency of feeding relative to that of genotypes with narrower niches. Nevertheless, this strategy imposes a tradeoff that ultimately limits the evolution of the niche, such as a greater the probability of being injured or killed by predators (Angilletta et al. 2003). For instance, Billerbeck et al. (2001) showed that rapidly growing genotypes of fish swam slower than did slowly growing genotypes. As one might expect, slower fish suffered a greater risk of predation in staged encounters with predators. In contrast to a specialist–generalist tradeoff, this acquisition tradeoff would only be perceived when comparing realized niches among genotypes.

Linking phenotypes to fitness

Ideally, one would investigate the fundamental niche by directly measuring the relationship between environmental

conditions and genotypic fitness. However, this approach suffers from practical drawbacks when predicting how species will respond to environmental change. For example, researchers have estimated thermal niches by measuring the fitness of similar genotypes raised at constant temperatures. By fitting a statistical model to the data, one can estimate the position and breadth of the niche along the thermal axis. Thermal niches estimated in this way have been used to infer the impacts of climate change on regional and global scales (Deutsch et al. 2008). In doing so, however, one assumes that the fitness of a genotype at a constant environment equals its fitness in a fluctuating environment with the same mean temperature. We know that this assumption does not hold in some cases (Siddiqui 1972; van Huis et al. 1994), and probably does not hold in many other cases. This problem underscores a common mismatch between the temporal scales considered by models and the temporal scales required for empirical measurements (see also Schulte et al. 2011).

One way to consider the effects of environmental variation on the niche would be to decompose each environmental factor into subfactors that capture the relevant variation. For example, we can convert a unidimensional niche that considers temperature to a multidimensional niche that considers the mean, minimal, and maximal temperatures (Levins 1968). Although this approach requires tremendous work to apply experimentally, it has been adopted by researchers who combine environmental and distributional data to fit statistical models of niches (Franklin 2009). Nonetheless, even this complex version of a thermal niche ignores the temporal structure of environmental variation, which should affect the fitness of organisms with complex life cycles. Alternatively, we could abandon the concept of the niche altogether and design experiments to estimate fitness in environments with particular temporal structures. This course of action also seems impractical.

Perhaps the best way to circumvent this problem would be to model the

niche as an emergent property of a phenotype interacting with its environment. This approach has been advanced by the recent expansion of “mechanistic niche models,” which describe hypothetical relationships between environmental factors and organismal performances, such as survival, growth and reproduction (Kearney and Porter 2009, Buckley et al. 2010, Kearney et al. 2010). Behavioral and physiological ecologists can play an important role in parameterizing the relationships in these models. Transplant experiments will also help to evaluate the predictions about suitable environments (Sexton et al. 2009). Both of these empirical activities should lead to further refinement of the theory.

Conclusion

We have argued three main points in this essay. First, our inability to predict variation in niches among genotypes reflects a poor understanding of the linkages between organisms and environments. Second, our understanding of these linkages will improve if we strive to integrate models and experiments to develop a mechanistic theory. Finally, this theory will need to address the way that organisms perceive environmental variation over space and time, the way that tradeoffs constrain phenotypes, and the way that phenotypes relate to fitness in particular environments. Throughout this essay, we have intentionally adopted a provocative tone in hopes of stimulating further discourse on the subject. Whether readers find our concerns warranted or exaggerated, ecologists should periodically re-evaluate the progress of their discipline (Brown 2001), especially in light of the rapid and dramatic changes that humans continue to impose on the environment. By unraveling the proximate and ultimate mechanisms that shape niches, we might better forecast the impacts of our actions on the populations, communities and ecosystems that we value (Schwenk 2009).

Acknowledgments

We thank Arthur Woods and the Division of Ecology and Evolution for the opportunity to contribute to the

series on Grand Challenges in Organismal Biology. The perspective presented in this essay was originally prepared for a symposium supported by the Division of Ecology and Evolution and the Division of Comparative Physiology and Biochemistry. George Gilchrist, Michael Kearney, and Arthur Woods provided valuable comments on an earlier version of the article.

Funding

This work was supported by the National Center for Ecological Analysis and Synthesis, the National Evolutionary Synthesis Center, the Department of Energy (10-NICCR-1108 to M.J.A.), and the National Science Foundation (IOS 0932438 to M.W.S.).

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