Book Reviews

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VARIATIONS—HOWEVER SLIGHT AND FROM WHATEVER CAUSE

Hallgrímsson, Benedikt, and Brian K. Hall, editors. 2005. **Variation: a central concept in biology.** Elsevier, Burlington, Massachusetts. xxi + 568 p. $74.95, ISBN: 0-12-088777-0 (alk. paper)

Key words: development; evolution; morphology; phenotypic plasticity; variation.

The title, *Variation: a central concept in biology,* is sure to spark the interest of nearly all ecologists and evolutionary biologists. Variation is ubiquitous in nature, existing across scales ranging from nucleotide sequences to global climate. As such, what is ''interesting'' about variation will vary among researchers. Those anticipating chapters elucidating the role of climatic variation on species distribution, variation in disturbance on community composition, genetic variation and population response to selection, et cetera, will probably find this book lacking in its treatment of variation as a central concept. A more precise title of the book would probably include the words ''phenotypic'' and ''animal'' as modifiers for ''variation.'' However, a single volume covering all the aspects of variation of potential interest to investigators is entirely unrealistic. What this book does aim to do, however, it does well.

A universal requirement of natural selection is phenotypic variation. How does this variation arise? How do new variants evolve? What constrains variation? These are central questions of interest to ecologists and evolutionary biologists alike. Beyond a simple additive genetic framework, development, epigenetics, and phenotypic plasticity are now largely regarded as critical for our understanding of phenotypic variation. This book delves into these issues in great depth, and surely has something to offer for investigators interested in individual and population level processes.

The book begins with a chapter on the history of how variation was perceived from Darwin to the modern synthesis. Included are several philosophical advances, such as the appreciation that variation is a property of populations, rather than the deviation of individuals from an archetype, the role of development in generating variation, and the properties of variation that can be inherited. At least one historical chapter is the norm for edited volumes such as this. The historical chapter provided in this book serves a function beyond history for history's sake. Touching on the themes addressed in later chapters, it provides a useful context for our current understanding of variation.

Methods of analysis are the focus of three chapters (Chapters 3–5). Van Valen contributes a revised version of his paper on statistical methods of analyzing variation (Van Valen, L. 1978. The statistics of variation. *Evolutionary Theory* 4:33–43). This chapter is relevant for investigators interested in comparing variation at all levels of inquiry, serving as a useful guide for addressing variation. Following is a chapter on the analysis of morphological variation using landmark morphometrics. The final methodological chapter examines variation from the level of among populations to within individuals, including variation exhibited throughout ontogeny. This treatment is less about the mechanics of analyzing variation across these hierarchical levels and more about the appreciation that different levels of variation exist, and that the mechanisms underlying this variation can be different.

Chapters 6–12 largely focus on constraints on variation and the role of development. These chapters are particularly interesting and important because they address variation from the level of molecular genetics to the realized phenotype, showing that each step, or hierarchical level, has unique constraints and flexibility. Developmental pathways can be visualized as complex networks or modules. Variation arising in one step can be buffered by following steps leading to canalization of a phenotype. As pointed out by Dworkin (Chapter 8), these internal buffering systems can preserve substantial ''cryptic'' genetic variation in developmental pathways.

A recurring theme in many of these chapters is that phenotypic variation is a product of development. In and of itself, this observation doesn't sound too novel. However, it does challenge the neo-Darwinian ''genes first'' paradigm of phenotypic evolution. That variation can arise first, and later be captured genetically, was central to Waddington's ideas of genetic assimilation. This book provides a lucid description of genetic and developmental components of variation, providing the requisite material for genetic assimilation. Also included is how genetic variation in developmental pathways can arise, from the perspective of internal buffering within and between developmental modules, where variation in one module can be compensated for in another module, to the effect of stress affecting molecular variation. Finally, these chapters impose upon the reader an appreciation that canalization and variability of phenotypes, and ultimately evolvability, is the product of complex covariation among traits, be they caused by genetic, epigenetic, or environmental factors.

Although ecologists may not normally take a developmental view of phenotypic variation, they certainly appreciate the importance of phenotypic variation in populations. Chapters 13–15 address the role of the environment in generating phenotypic variation. Badyaev (Chapter 13) provides a logical bridge between the previous developmental chapters and the evolutionary consequences of environmentally imposed stress. Written in a language more familiar to ecologists, he revisits the issues of developmental buffering, constraints, and a role for genetic assimilation, and discusses non-genetic inheritance of environmentally induced plasticity. Sultan and Stearns (Chapter 14) focus on phenotypic plasticity, including a succinct description of reaction norms and genetic and developmental facets of plasticity and a discussion of the consequences of plasticity from the individual to the community.

Although the motivation of the chapter is perhaps overly ambitious, at times to its detriment, it successfully makes the case that phenotypic plasticity will retain a central place in future studies of ecology and evolution. Roff (Chapter 15) discusses the evolution of life history variation, including the role of environmental variation in maintaining and generating phenotypic variation. Although each of these chapters discusses phenotypic plasticity to a varying extent, a chapter specifically addressing the evolution of plasticity would have been a welcome addition.

Chapters 16–19 approach phenotypic variation from a macroevolutionary perspective. Included is a fascinating review by Palmer (Chapter 16) on antisymmetry, a condition where right-sided and left-sided forms are equally represented in a population (for example, the single enlarged claw of male fiddler crabs). Interestingly, the direction of symmetry is usually not inherited. Only when a bias in direction of symmetry is present is evidence of inheritance detected, suggesting that antisymmetry is an important intermediate step in the evolution of asymmetrical phenotypes.

Russell and Bauer (Chapter 17) address how variation in structure is correlated with function. They effectively address this issue from the level of individual performance to clinal and geographic variation. McShea (Chapter 18) discusses the tendency toward increased complexity through the history of lineages, arguing that complexity arises from the internal variance associated with the parts of an organism, and that complexity can be considered separately from function. Roth (Chapter 19) addresses how adaptive variants persist at macroevolutionary scales, offering three components of evolvability, (1) genetic variation, (2) phenotypic variation, and (3) natural selection. First is a discussion of mammalian teeth, focusing on the highly derived dentition of elephants, second is the macroevolutionary patterns of locomotion and body size in the Sciuridae. For traits to persist at macroevolutionary scales, they must be versatile and able to produce ecologically and functionally relevant variation.

The final three chapters serve as a conclusion and a look to the future for the study of variation. There is a call for a population-level perspective on developmental variation as a means to avoid a typological view. There is also a call to broaden the taxonomic sample of organisms under study, cautioning that generalization based on the few model systems under intensive study today is risky.

Ultimately, evolution acts on phenotypes. The link between the genotype and phenotype of an organism can be incredibly complex. The more we learn about the causes of phenotypic variation, the more we realize that the genotype alone cannot predict the phenotype, yet it is the genotype that is transmitted between generations. An understanding of the mechanisms that cause phenotypic variation is an imperative if we hope to understand phenotypic evolution. How does this variation arise? How do new variants evolve? What constrains variation? The answers are incomplete. However, the chapters of this book provide a glimpse at our current understanding of phenotypic variation.

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Turning Species Invasions to Advantage

Sax, Dov F., John J. Stachowicz, and Steven D. Gaines, editors. 2005. **Species invasions: insights into ecology, evolution, and biogeography.** Sinauer, Sunderland, Massachusetts. xiii + 495 p. $74.95 (cloth), ISBN: 0-87893-821-4; $49.95 (paper), ISBN: 0-87893-811-7.

Key words: bottleneck events; colonization; invasions; invasive species; regulation of species diversity.

Species introductions and invasions are increasingly ubiquitous—and the studies focused on them are almost as numerous, as this volume attests. The book is the product of a working group organized through the National Center for Ecological Analysis and Synthesis, focused on the concept that species invasions represent not just management challenges but scientific opportunities. The editors use the introduction to outline the general premise: invasions allow us to observe ecological and evolutionary processes in real time. Further, invasions provide a rich source of empirical evidence, with replication in space (species introduced in multiple locations) and across taxa (multiple species introduced in a single place). The volume attempts to review the varied insights that these invasion records can give into fundamental issues of ecology, evolution, and biogeography of the natural world.

There is no explicit statement about the audience or proposed use of this book as a text. It is difficult to see how one might best use the volume in teaching; there is not sufficient background presented for it to serve as a self-contained introduction to ecology or evolution, but it is unusually broad in range of topics for a graduate or advanced course. However, the volume is sure to stimulate thought and productive research across a wide range of fields. Seventeen chapters are organized into three sections, each with an introductory preface: insights into ecology, evolution, and biogeography. References cited follow each chapter, rather than being grouped at the end of the volume. The production quality of the soft-