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-

cover edition I reviewed was high, with minimal occurrences of typographical errors or other glitches.

Researchers were asked to consider the advantages to be gained from considering invasions as investigative tools for their particular area of interest, and the result is a wide-ranging review of rich detail. Some chapters are more explicit than others in addressing the limitations or remaining problems or difficulties with using exotics as experiments for insight—the book might have benefited from exerting a little more consistency in that expectation. Most chapters are very up-to-date and complete with recent literature citations, a very valuable aspect in that regard—but a few chapters were woefully lacking in recent citations. It was difficult to tell if that reflects the current state of interest and work in certain areas!

The first portion of the book comprises chapters reviewing insights into ecological processes and patterns. Most are based on the premise that the only way to truly understand those processes is to watch them in action, that is, to observe new assemblages (like those arising when non-native species arrive). Topics include frequency and specificity of biotic interactions (competition, predation, disease, facilitation), limits to local species richness, and species effects on ecosystem function—each rooted in a review of general theory and then reviewing the recent literature of invasion examples for relevant work. Taking these chapters in aggregate, an enormous range of recent literature is reviewed—with good balance between plant and animal studies. Overall the take-home message is that while biotic interactions are frequently observed to be important, the net effect of invasion is often an increase in local species richness.

Part II, ''Insights into evolution,'' takes the perspective that genetic studies of invasions represent the opportunity to watch evolutionary processes in contemporary (real) time. These chapters presented a surprising (to me) number of fascinating examples of rapid evolutionary change after invasion, many in animal populations. The most striking message from this section was that genetic bottlenecks apparently occur less frequently, or constrain the diversification of the invading population much less frequently than one would expect after a typical founder event or introduction of a small number of individuals. I found the chapters by Holt, Barfield and Gomulkiewicz (Chapter 10), and Rice and Sax (Chapter 11) to be fascinating examinations of what invasions can tell us about micro-evolutionary change in ''sink'' habitats, the interaction of novel settings with sexual selection and with reproductive (life history) strategy, and the evolution of reproductive isolation. Most provocative (but most difficult to answer) are the questions raised about the possibility that invasions are actually promoting speciation.

Part III reviews some insights gained by viewing invasion ecology as ''the experimental arm'' of biogeography (in a phrase from Lockwood's introduction to the section). Chapters here tackle some of the same broad questions as in the other sections—especially the existence or nature of upper bounds to species richness in an assemblage—but at a larger spatial scale than in the ecology chapters. The review by Vermeij reminds us that invasions following the disappearance of geographic barriers to dispersal have characterized the history of life, and draws generalizations (for example, about the relative infrequency of major extinctions in the ''receiving'' assemblage) that provide strong hypotheses for studies of current invasions. Several interesting chapters focus on patterns of genetic and evolutionary responses among invading and resident taxa (e.g., Callaway et al., Kinlan and Hastings).

The closing section by Sax, Stachowicz, and Gaines succeeds in highlighting most of the same messages that struck me as most important while reading through the chapters. First is the substantive documentation that genetic bottlenecks are not an inevitable consequence of the population bottlenecks usually accompanying invasion. There is fascinating food for thought in asking whether invasions might actually be increasing the rate of speciation, given how frequently invasions lead to events with potential evolutionary consequences (isolation of disjunct populations, hybridization, mix of diversity from multiple founder sources, novel selective regimes, etc.). There are questions of whether community assemblages are saturated with species, and whether introduced species differ consistently from residents in ecological or physiological performance. The editors ask where we should go next with the study of invasives, and suggest that researchers might focus on the interaction between evolution and ecology in determining species diversity. They call for a single integrated conceptual framework for invasion processes and consequences—which is a rather ambitious goal, given the enormous diversity of studies and questions reviewed in this volume. Overall the volume satisfies its objective, to balance the view of invasive species by looking at invasions as scientific opportunities, not just as management or economic problems.

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Sampling Rare Species

Thompson, William L., editor. 2004. **Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters.** Island Press, Washington, D.C. xv + 429 p. $70.00 (cloth), ISBN: 1-55963-450-2 (alk. paper); $35.00 (paper), ISBN: 1-55963-451-0 (alk. paper).

Key words: abundance; monitoring; population parameters; rare species; sampling.

Most species are not abundant, and many species have strategies to avoid being noticed. We are struggling with holes in our ecological understanding of systems that result from limitations on our abilities to sample species that are difficult to find. This volume collects chapters written by current researchers who are tackling problems encountered when studying rare or elusive species. The lack of adequate data on endangered species often prevents further steps being taken to protect the species. Therefore, the topics explored in this book are relevant to important decisions being made in land management and natural resource policy.

The initial chapters review the definitions and basic concepts. It is clear that problems encountered in studying rare species are widespread and highly variable. The variety of definitions and broad scope of the issues indicates that the techniques explored in the book can apply to all species. Our knowledge of rare species, and more abundant species that are either elusive or in isolated clumped distributions, is often limited by the sampling design. Even our definitions depend on the scale of sampling.

The section ''Estimating occupancy'' and the chapters in the section ''Estimating abundance, density, and other parameters'' provide excellent overviews of the relevant wildlife literature that will be useful for someone entering this field. For example, a graduate student embarking on a bat project would benefit from the review of bat sampling by O'Shea, Ellison, and Stanley. Each chapter is self-sufficient, with the references included at the end of the chapter. However, in general, the reader is assumed to have some experience with sampling. The successes and challenges of using genetic sampling was nicely reviewed by Lisette Waits. A reader already familiar with genetic techniques would benefit most from this chapter. The detailed power analyses described in the spotted owl chapter by Ganey et al. will be most appreciated by an ecologist with a sophisticated understanding of these statistical approaches. This is not an introductory text.

Only one chapter focuses on plants, although plants are often ''blamed'' as providing the means for animals to avoid detection. Outside of the chapter by Elizabeth Poon and Chris Margules, the plant ecologist will find few useful sampling techniques in this volume. However, many of the difficulties in making valid inferences from data on rare species are still relevant no matter what organism is being studied.

The focus of the book is clearly stated as pertaining to estimating population parameters. However, the same sampling issues plague ecological studies at community levels as well. Adequate sampling of rare species in a community context can provide insight into how communities function. For example, a suite of rare species may enhance the resilience of a community following disturbance. Also, a species may be rare until a critical threshold is met and then it becomes dominant in a community. A review of the pertinent theory in community ecology would be beneficial. Understanding the driving forces behind distribution and abundance of species may provide insight in how best to tackle the sampling issues. A clear framework that is explicit about the temporal and spatial scales of sampling and monitoring would also be helpful.

The final chapter indicates the need for openness to creative approaches to understand the rare and elusive species around us. The solutions to the sampling issues are often tailored to a group of species, and in some cases they need to be species-specific. This book brings to our attention the importance of improving our understanding of species that are rare or elusive.

It is clear from this volume that our traditional statistical approaches have been inadequate. There is a need to broaden our understanding of complex systems, where a large number of factors are determining the parameters of a small number of individuals of each species. This book does highlight the need to explore beyond the confines of traditional methods for of surveys and analyses. This book is not a ''how-to'' guide, and does not develop a theoretical base to understanding the distribution and abundance of rare or elusive species. However, it is a valuable addition to your library of sampling literature and can help you appreciate the problems encountered when studying many different types of species.

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