Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments

Author: Promislow, Daniel E. L.

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importance of community involvement in the development of regulations that result in limited access to land or that modify property rights. In areas with imperfect enforcement and monitoring, the implementation of conservation programs that fail to acknowledge existing areas of use or de facto property rights may be ineffective.

Indigenous knowledge about the characteristics of local flora and fauna has accrued over centuries, and this information is often of value to pharmaceutical firms in their research and development of commercial drugs. Krystyna Swiderska discusses traditional knowledge and resource use, focusing more on the impacts of conservation planning on the access afforded to indigenous peoples than on intellectual property rights and traditional knowledge. Though not explicitly mentioned in the book, this issue is of direct relevance to REDD (reduced emissions from deforestation and degradation) projects. Jane Kabubo-Mariara and Ernest L. Molua discuss in separate chapters the difficulty of adapting to climate change in ecosystems that are highly sensitive to physical conditions, such as estuaries, and in social systems in which the resources necessary for adaptation may be limited.

Although the potential development of payment programs for carbon sequestration and storage by forests is not explicitly covered, the importance of institutions and stakeholder involvement in the policymaking process, as described in the chapters in the first three sections of the book, should be acknowledged in the design of these programs. Reduced emissions from REDD projects and other successes are creating significant excitement among stakeholders. However, these programs can lead to undesirable outcomes, resulting from information asymmetry, a lack of required enforcement and monitoring infrastructure, insufficient stakeholder involvement, or an absence of institutions to ensure that national agreements provide incentives for behavioral change.

The chapters that K. N. Ninan has assembled from well-known economists serve as a solid introduction to the socioeconomic concepts fundamental to the valuation and provision of biodiversity and ecosystem services. The theoretical discussions provide nice summaries of the necessary background on many of these issues. The case studies help transform economic theory into meaningful application, allowing policymakers and readers from other disciplines to learn from the experience of others.

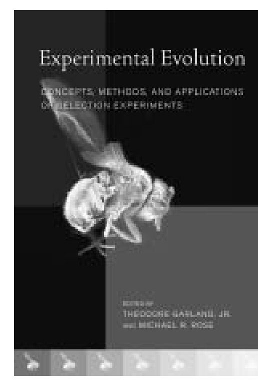
MARC N. CONTE
Marc N. Conte (mconte@stanford.edu) is an environmental economist and a postdoctoral fellow at the Woods Institute for the Environment at Stanford University, where he contributes to the Natural Capital Project.

BRINGING EVOLUTION INTO THE LAB

Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments. Theodore Garland Jr. and Michael R. Rose, eds. University of California Press, 2009. 752 pp., illus. $45.00 (ISBN 9780520261808 paper).

Evolutionary change is usually too slow for us to detect on the timescales in which we live—hours, days, even months. To illustrate selection in action, Darwin turned to domesticated species, which act as a kind of temporal microscope, magnifying patterns of phenotypic and genetic variation within a population. *On the Origin of Species* does not begin with a description of the fantastic organisms that Darwin observed on his travels through South America, but rather with a description of the humble domestic pigeon. Darwin pointed out that by applying the same principles of selection that exist in nature, humans have been able to generate incredible variety in domesticated species—fantails, frillbacks, Jacobins—and do so relatively quickly.

For millennia, humans have used artificial selection to create desirable traits: edible plants, useful animals, and aesthetic curiosities. In the edited volume *Experimental Evolution: Concepts, Methods, and Applications of Selection Experiments*, researchers review the enormous range of ways artificial selection can be used to test hypotheses that are of central interest and importance to evolutionary biologists. The book explores the methods that underlie experimental evolution and the breadth of conceptual topics that have been explored using this approach, from anatomy to altruism, sex to speciation, physiology to phages, and more.



The authors in this volume take a broad view of experimental evolution, defining it as any study that exposes a genetically variable population to some selective pressure. This selection could be deliberate (such as selection for flies with a particular wing shape) or inadvertent, as happens simply by bringing a wild species into the laboratory (discussed in detail in the chapter by Simões and colleagues). In either case, the response to these selective pressures can then be used to address evolutionary questions.

This book will surely be of interest to researchers looking for new ways to ask evolutionary questions. But the careful reader is advised to read the last chapter

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of the book first. Although experimental evolution can be a powerful tool with which to test evolutionary hypotheses, the method is not without its challenges, and there are still issues to be resolved. Many of these issues are discussed briefly throughout the book, but in the concluding chapter, Huey and Rosenzweig present an admirable summary of the pitfalls that lie in wait for the experimental evolutionist: The laboratory may be more benign or more stressful than the "real world" in which our study organisms usually live and die; the factors that we alter in the lab might not be the relevant selective forces shaping variation in the wild; and even before we deliberately impose selection in the lab, the very act of bringing an organism in to study can change its genetic and phenotypic architecture in ways that interfere with our experiments. And as others point out (e.g., Rhodes and Kawecki, Estes and Teotónio), once we begin a selection experiment, keeping control lines from evolving, especially in species that cannot be frozen and revived, may not be so simple. We can try to minimize selection (e.g., by keeping lines inbred, or by using Kondrashov's "middle class neighborhood" design), but this can increase the likelihood that novel deleterious mutations accumulate.

Even with these various caveats, this book has something for almost any evolutionary biologist. Reading through its chapters by a first-rate collection of authors, one gets a clear sense that experimental evolution has been used to study an impressive range of organisms (the book covers everything from phage [Forde and Jessup, Turner and colleagues] to fish [e.g., Irschick and Reznick]). Moreover, experimental evolution can be used to study diverse conceptual questions, from the evolution of genomes (e.g., Rosenzweig and Sherlock) to physiology (e.g., Zera and Harshman, Swallow and colleagues, Gibbs and Gefen), morphology (Frankino and colleagues), behavior (Rhodes and Kawecki), speciation (Fry), and more.

Most of the chapters provide excellent overviews of the work that has been done so far. For example, the chapter on the evolution of sex (Turner, McBride, and Zeyl) includes sections on experimental evolution in viruses, bacteria, and yeast with useful summary tables. While for the most part we do not find major new insights in this chapter (and others), it would be hard to find a clearer exposition of the problems and approaches that have been taken. On the whole, the authors of these chapters use the book as an opportunity to review the use of experimental evolution in their specific field. Broader conceptual themes and suggestions for future studies are in most cases left to the reader's imagination.

From a practical standpoint, I found the most useful chapter to be that of Roff and Fairbairn, who present a set of computer-intensive methods for modeling the outcome of selection experiments. These are particularly important for experimental design. Given what we know about a particular system, how long does an experiment need to last, how strong does selection have to be, and how many replicates are necessary to be able to detect the effect of interest? These methods can also be used to test hypotheses about the underlying genetic structure of a system. Given the strength of selection, is the observed response consistent with our understanding of the system? Even though we can't confirm that the system is as we think, we can certainly show that system behavior is inconsistent with our model of the system.

This book has appeared at a particularly exciting time in experimental evolution research. With the advent of high-throughput "omic" approaches, we can now begin to uncover the specific genetic changes that account for responses to selection. Rhodes and Kawecki note that genome sequencing and transcriptomics can help us to identify individual genes associated with traits that vary among selected lines. Rosenzweig and Sherlock's chapter offers a more detailed exploration, showing us that these tools are valuable not only for understanding the evolution of phenotypic traits under selection but also for understanding the evolution of the genome itself.

In some cases, I would have welcomed a more critical perspective on the strengths and weaknesses of previous work. That said, some criticisms are taken too far. In their review on experimental evolution and aging, Rauser and colleagues condemn those who have questioned the validity of assumptions underlying standard theoretical models in aging research. But as is clear from the targets of their criticisms (e.g., Baudisch 2005), to question the simplifying assumptions that underlie a mathematical model of theory is not the same as rejecting the theory. Also dismaying was the selective presentation of data in this chapter. A graph in the chapter claiming to show a plateau in late-age fecundity was missing the late-age increase in fecundity that appeared in the original paper (Rauser et al. 2006).

Overall, this book, almost encyclopedic in its breadth, will provide a valuable entrée for those thinking about carrying out an experimental evolution study. In his well-written chapter on speciation, James Fry suggests in his "general guidelines for experiments on speciation" that one should start by consulting earlier literature, noting that "experiments should be designed in a way that takes advantage of previous methodological advances" (p. 650). For graduate students considering an experimental evolution project for a thesis, or for the more advanced researcher considering the use of experimental evolution for the first time, one would do well to take Fry's advice to heart. For any problem under consideration, this book will lead one quickly and thoroughly into a fascinating literature, and will help one to carry out well-designed experiments.

DANIEL E. L. PROMISLOW

Daniel E. L. Promislow (promislow@uga.edu) is a professor in the Department of Genetics at the University of Georgia in Athens.

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SUBINDIVIDUAL PLANT TRAIT VARIATION MATTERS

Multiplicity in Unity: Plant Subindividual Variation and Interactions with Animals. Carlos M. Herrera. University of Chicago, 2009. 437 pp., illus. $40.00. (ISBN: 9780226327945).

Any ecologist working with plant communities will soon encounter the variability of plant organ traits at the within-individual level. Sun and shade leaves produced by the same tree often differ conspicuously in size, shape, and toughness. Foliage produced by juveniles and adults of the same plant species can differ greatly in their palatability to herbivores, as well as in the traits that cause palatability. Individual plants may produce flowers of contrasting characteristics to attract a wider spectrum of pollinating organisms. In these and numerous other cases, the occurrence and adaptive significance of within-species organ-trait variability is immediately apparent, yet many ecophysiologists and community and ecosystem ecologists largely ignore this variation, regarding it simply as unwelcome noise. For example, much work on plant-trait variation over the past 40 years, including its latest incarnation as the "leaf economics spectrum," has been preoccupied with characterizing differences among species (see Whitfield 2006). This work has often represented key functional traits of a whole species by single values, with variability of leaf trait values within species or individuals often ignored. As such, recent and rapidly growing global plant-trait databases all but ignore subindividual variability. Serious recognition in the functional plant-traits literature that even within-species (let alone within-individual) variability of traits might be important has come about only very recently (e.g., Albert et al. 2010, Hulshof and Swenson 2010).

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Multiplicity in Unity: Plant Subindividual Variation and Interactions with Animals, by Carlos N. Herrera, is the only substantial book in existence whose primary focus is the within-individual trait variability of plant organs. Herrera, a professor at Estación Biológica de Doñana in Seville, Spain, has published extensively on plant reproductive and evolutionary biology, notably in relation to pollination and frugivory. Perhaps unsurprisingly, this book draws heavily on that literature, although the scope of *Multiplicity in Unity* is considerably wider than this, and is of great relevance for a much broader range of ecologists than just those who work on plant reproduction. The message of the book is simple: Within-individual trait variability of plant organs—leaves, inflorescences, or fruits—can be considerable and of high ecological and evolutionary significance. As the author asks in the prologue, "Could there be…some interesting biology hidden behind the familiar nuisance of within-plant variance, routinely brushed under the rug of the mean?" (p. viii).

The book (excluding the introduction) consists of nine chapters that can be classified into four parts. The first part (containing chapters 2–4) characterizes the degree to which subindividual trait variation occurs in different organs with determinate growth (leaves, flowers, fruits, and seeds); other aboveground organs and all belowground structures are not considered. These three chapters collectively synthesize a vast amount of literature, alongside additional analyses, to highlight the magnitude and extent of variation across time and space (for example, across gradients within a single plant). The second part (chapters 5–7) then explores the source of this within-plant variation, including underlying ontogenic and genetic mechanisms. Here, Herrera provides compelling and recurrent evidence to show that, far from being unwanted or meaningless noise, within-plant variation is an important ecological attribute driven by plausible underlying mechanisms. At this point, any reader who has focused on the extensive array of examples presented by the author should have little doubt that within-plant variation is real, widespread, and ecologically meaningful.

The third part (chapters 8 and 9) considers the ecological consequences of within-species trait variation, both for herbivores and for the fitness of the plant itself. The chapter on herbivores synthesizes the literature linking animal behavioral responses and selectivity to within-individual variability of plant reproductive structures and leaves, as well as associated costs and benefits for herbivores. This chapter in particular is an important overview that should be of great interest to anyone who has worked in the vast field of plant-herbivore interactions. The chapter on fitness consequences makes the case that subindividual variation in plant organs may have important consequences for both plant growth and fecundity, further reinforcing Herrera's message that within-species variation is ecologically meaningful. This leads logically into the fourth section (chapter 10), which reassures us that this ecologically meaningful variation even has an evolutionary basis that can be driven and maintained by selection as well as plant-animal interactions.

Herrera's focus on plant reproductive and evolutionary biology is apparent throughout the book. There are, of course, a range of other branches of ecology in which the issue of subindividual trait variation is also highly relevant but that receive either fleeting or no attention from the author; for example, ecosystem processes, plant defenses, and the many plant community processes that drive vegetation composition.