Robustness and Evolvability in Living Systems

Author: WILKE, CLAUS O.

Source: BioScience, 56(8) : 695-696

Published By: American Institute of Biological Sciences

URL: https://doi.org/10.1641/0006-3568(2006)56[695:RAEILS]2.0.CO;2

Through the Eyes of the Invader

Species Invasions: Insights into Ecology, Evolution, and Biogeography. Dov F. Sax, John J. Stachowicz, and Steven D. Gaines, eds. Sinauer, Sunderland, MA, 2005. 495 pp. $51.95 (ISBN 0878938117 paper).

Species invasions have long provided grist for fundamental studies and insights into ecology, evolution, and biogeography. Classic marine examples are Jane Lubchenco's experimental studies on the role of the periwinkle snail *Littorina littorea* in regulating intertidal communities in New England, where this mollusk was unknown until the 1860s, and John Sutherland's experimental work in North Carolina on multiple stable points at the community level, based in large part on the phenology of the Asian sea squirt *Styela plicata.* More recently, invasions have raised increasing concerns about what to do to prevent or manage newer invasions mediated by human activity. *Species Invasions: Insights into Ecology, Evolution, and Biogeography,* edited by Dov Sax, John Stachowicz, and Steven Gaines, seeks to extend our thinking on how invasions can contribute to basic research questions.

Not long after the first cells got together on this planet, they moved, or were moved, and organisms ever since have flowed along corridors in a reasonably predictable manner. In all three main types of habitat (terrestrial, freshwater, and marine), we often interpret biological flow through physical expectation: As the winds or water flow, so do living organisms. Barriers restrict such flow: At the regional scale, these may be as simple as a river or a mountain chain; at a global scale, they may be continents or ocean basins. Over time, these barriers are created or dissolve: Land masses move and break apart, narrow bridges between them come and go, oceans become extinct or are created, or large-scale atmospheric events occur.

But humans have changed all that, and anthropogenic invasions, like many other environmental insults perpetrated by people, are *sui generis.* These are invasions that are not expected and are not historical facts of life. Human activity instantaneously dissolves all barriers of time and space across the entire planet, such that übermixing is now a fact of life. Because of human-mediated vectors, Australian insects may arrive in Britain within hours, and the estuaries of Australia are only days away from the estuaries of southern California. Such journeys are impossible without human intervention. The globalization of colonization by nonnative species is a modern-day phenomenon without precedent; the wholesale translocation of entire communities from one side of the planet to the other is quite a different story from those of the past.

The results of these anthropogenic invasions, some of which are sampled in Sax and colleagues' useful volume, are all that an ecologist or evolutionary biologist could imagine (I won't say hope for, although the results do provide an incredible array of insights into basic ecological and evolutionary processes). Thousands of species are doing quite well, thank you, in parts of the world where they did not evolve, a fact that alone provides the material for endless investigations. The editors and authors also note, summarizing earlier literature and contributing new information, that the general outcome of most invasions is to *increase* the overall pool of resident species (although losses of many species at the hands of exotic predators, pathogens, and parasites have occurred). But increased diversity often comes at the expense of fundamental alterations to community structure, and while the prior species may still be there after the invaders have become established, the former are often rendered functionally extinct. The mixing of tens of thousands of species worldwide is thus a Whitman's Sampler of competition, predation, and disturbance, with every possible positive and negative outcome (in the ecological and specifically population biological senses, not in the societal sense). Given this incredible complexity, the challenge, noted by several chapter authors and by the editors, is to construct a framework that would permit more elegant prediction in the face of the many invasions yet to come.

The editors divide the book into three parts—Ecology (5 chapters, totalling 123 pages), Evolution (6 chapters, 174 pages), and Biogeography (6 chapters, 156 pages)—bookended by a preface, an introduction, and a conclusion ("Capstone"). Each section begins with a short overview essay, for a total of 23 contributions.

This is a good book, and one worth buying. There is much to mine here, and even seasoned invasion biologists will find new juxtapositions to ponder. Invasion ecologists who typically find themselves habitat restricted will find new perspectives and numerous references throughout a rich literature that they may have overlooked. That said, and of necessity, this book offers only a sample of old and new literature: There is a vast and complex literature produced over the past 150 years of tens of thousands of papers on invasions of plants, vertebrates, and invertebrates, and this book can provide only a taste of these.

Many of the authors in *Species Invasions* attempt to provide guidance through this labyrinth. Bruno and colleagues, Stachowicz and Tilman, Huey and colleagues, Ricklefs, Kinlan and Hastings, and Sax and colleagues use invasions as a prodding or prying tool to offer synthesis, insight, and in some cases new theory on the complexities of teasing out what may regulate populations, communities, and ecosystems. Other contributors elucidate insights gained from invasions of infectious diseases, plants, birds, insects, and fish. Novak and Mack review the reality of genetic bottlenecks (and particularly the lack thereof). Wares and colleagues, Holt and colleagues, and Rice and Sax offer approaches into how invasions do or could contribute to fundamental evolutionary questions.

Vexing for the ecologist, as noted by Bruno and colleagues, is the proper weighting of studies that examine species invasions using experimentation (the preferred method) rather than correlations of abundance and diversity. The result has been an obfuscation of the impact of invasions. Perhaps 95 percent of all species invasions have not been studied experimentally. In the absence of experimental data, a common conclusion has been that the majority of species appear to insert themselves into novel communities with no impact on the invaded ecosystem. It thus remains tempting to use the large body of nonexperimental work to deduce invasion impacts: Although Bruno and colleagues note that only half of the 120 invasion studies they examined were experimental, they use all 120 studies to determine whether species have a "detectable effect." A further challenge is that the majority of studies, experimental or not, consider only one or two processes, or focus on only one of many roads within a process (such as studying the impacts on plant populations by an omnivore).

Since most species invasions in all habitats around the world have never been studied experimentally, we simply do not yet know the scale at which the impacts of invasions have been changing the face of the earth. For those invasions for which we do have data, *Species Invasions* provides a wealth of good thinking.

JAMES T. CARLTON
James T. Carlton (e-mail: jcarlton@williams.edu) is a professor of marine sciences in the Maritime Studies Program at Williams College–Mystic Seaport, Mystic, CT 06355.

BIOLOGY THROUGH THE ROBUSTNESS LENS

Robustness and Evolvability in Living Systems. Andreas Wagner. Princeton University Press, Princeton, NJ, 2005. 408 pp., illus. $49.50 (ISBN 0691122407 cloth).

If you are an active member of the biological scientific community, you cannot have escaped noticing: Everything seems to be robust these days. The genetic code is a robust encoding of amino acids into codons, RNA molecules are robust to point mutations, proteins are robust to translation errors, developmental pathways are robust to environmental or genetic disturbances, metabolic networks are robust to changes in enzyme efficiency...the list goes on and on. While not all of these ideas are new (e.g., the idea of robustness in organismal development goes back to Conrad Hal Waddington's work in the 1950s), the amount of research devoted to the robustness of various biological systems has exploded in recent years. However, there is a danger in using a concept such as robustness, in that it can be so generic and widely applicable that its use may contribute little to the understanding of specific biological systems. For example, it is not clear a priori that a robust RNA molecule that can fold correctly despite nucleotide substitutions has anything to do with a robust metabolic network that continues to function after gene deletion.

Enter Andreas Wagner's book on robustness. Wagner's book has two aims, to review the current knowledge on robustness and to identify common principles that cause biological systems to be robust. The book is divided into four parts. The first two parts, "Robustness Below the Gene Level" and "Robustness Above the Gene Level," provide a comprehensive review of all things robust. Wagner begins with nucleotides themselves; talks about the genetic code, RNA, and protein molecules; and moves to successively larger scales, including metabolic pathways, phenotypic traits, and body plans of whole organisms. Each chapter is well researched, provides a large number of useful references, and gives a concise and readable introduction to its subject area.

The third part, "Common Principles," tries to bring some order into the bewildering array of robust systems introduced in the first two parts. One of its central themes is the concept of a neutral space, defined as "a collection of equivalent solutions to the same biological problem" (p. 195). The main question raised in this section, to my mind, is whether robustness arises as a by-product of other constraints (the rules of biochemistry dictate, for example, that in metabolic pathways the overall metabolic flux is not strongly dependent on the exact enzymatic activity of each participating enzyme) or whether there is a selective pressure to increase a system's robustness to mutations (as in van Nimwegen and colleagues' model of evolution of mutational robustness, introduced in *Proceedings of the National Academy of Sciences* in June 1999). Wagner addresses this question in chapter 16, where he discusses a variety of mathematical models of evolution that lead to robust systems. I found the third part of the book somewhat less satisfying than the first two parts, not because Wagner doesn't do a good job in describing the various models he presents (he does), but because ultimately it doesn't seem possible to construct a unified theory: "These differences suggest that there may be no fundamental theory of how robustness evolves, if such a theory is required to take into account the different architectures of biological systems" (p. 268).

The book closes with a short fourth part, "Robustness Beyond the Organism." Consisting of only two chapters, it lists some more examples of robust systems beyond the main scope of the book and draws parallels to the material discussed in the previous chapters. The first of the two chapters discusses robustness that arises through self-organization. The main example in this chapter is the self-organization of ecosystem communities into assemblies that are resistant to invasion. The second chapter discusses robustness in man-made systems, such as telecommunication networks and evolved hardware.

Should you read this book? Wagner himself seems to suggest that the book is primarily for those new to the field of robustness, as he writes in the introduction: "If you are a specialist who already knows some or most of the literature in this field, much of this book will not be news to you" (p. 10). However, I would argue that this book is invaluable to everybody interested in robustness, for two reasons. First, even if you are a specialist, you will probably not be an expert in all the different areas Wagner touches on. Second, the book serves not only as an excellent introduction into a wide range of literature on robustness but also as a handy work of reference, with a bibliography totaling over 600 entries. Need some key references on the robustness of the genetic code? Just skim through chapter 3, and you have them. I predict that for many years to come, Wagner's book will be the bibliographic reference work of choice for research on robustness.

CLAUS O. WILKE
Claus O. Wilke (e-mail: cwilke@mail.utexas.edu) is an assistant professor in the Section of Integrative Biology and Center for Computational Biology and Bioinformatics at the University of Texas at Austin.

DO WE NEED HOLISM IN EVOLUTION?

Holistic Darwinism: Synergy, Cybernetics, and the Bioeconomics of Evolution. Peter A. Corning. University of Chicago Press, Chicago, 2005. 546 pp. $28.00 (ISBN 0226116166 paper).

Peter Corning is the director of the Institute for the Study of Complex Systems (though it is not clear from its Web site that this organization has any members other than Corning himself). His book is intended to convince the reader that he has developed a new perspective on biological evolution, which overcomes the perceived inadequacies of conventional neo-Darwinism as an explanation for the evolution of biological complexity. Corning's claim is that "an individualistic, gene centered theory seems insufficient to account for the evolution of more complex, multileveled biological systems" (p. 2). In his view, this should be replaced by "Holistic Darwinism," which he defines as a view of evolution "as a dynamic, multilevel process, in which there is both 'upward causation' (from the genes to the phenotype and higher levels of organization) and 'downward causation' (phenotypic influences on differential survival and reproduction), and even 'horizontal causation' (between organisms)" (p. 2).

Corning regards his "synergy hypothesis" as the core of Holistic Darwinism. He defines synergy as "combined or cooperative effects—literally, the effects produced by things that operate together (parts, elements or wholes)" (pp. 50–51). It can be observed at multiple levels of biological organization, ranging from the cooperative binding of oxygen by the monomers of hemoglobin at one end of the spectrum to the cooperative behavior of social insects at the other. Corning argues that synergy plays a key role in determining the outcome of evolutionary processes. These ideas are elaborated over several hundred pages. There are extensive discussions of human social behavior, economics, and political theory in the second half of the book, subjects on which I am not competent to comment.

Corning's key notion that components of biological systems interact with each other is not exactly novel. For example, the term "epistasis" (mentioned only once in *Holistic Darwinism*) was introduced very early into genetics to describe the fact that the phenotypic effects of an allele at one locus may be conditional on the allelic state at another locus. Epistasis plays a key role in Sewall Wright's "shifting balance" theory of evolution (not widely accepted by modern evolutionists), and in the Dobzhansky-Muller explanation of the evolution of reproductive isolation by species (which *is* widely accepted, but not mentioned by Corning). No sensible evolutionist believes that the effects of genes are necessarily independent of each other; the question is, rather, when does this matter, and what phenomena are explained by such interdependences of gene effects? This topic is not discussed by Corning, even though it has been thoroughly studied by evolutionary geneticists in connection with such important topics as the evolution of sex and recombination. Similarly, the problem of explaining altruistic and cooperative behavior was recognized early by Fisher and Haldane (and by Darwin himself), and of course has been a major focus of modern research in behavioral ecology. Corning seems to prefer group-selectionist explanations of cooperation over explanations based on kin or individual selection, but fails to provide a detailed explanation of how these are supposed to work, or to present the relevant biological data in sufficient detail for the reader to make an informed judgment. In fact, his account on page 20 is downright confusing, since he discusses group selection and game theory in the same breath, the latter being a primarily individual-based approach to selection theory. This will not convince people like me, who are unsympathetic to group selection as a significant evolutionary force.

General concepts are useful in science only if they have a precise meaning and help us to understand a wide range of phenomena, natural selection being of course the prime example in biology. Corning's idea of synergy does no more than vaguely describe what is observed in a disparate set of physical and biological systems, and lacks any genuine explanatory power. Except for its invocation of group selection, Holistic Darwinism seems little different from conventional neo-Darwinism, except that it is a lot harder to extract clear meaning from Corning's writings than from those of such lucid exponents of classical neo-Darwinism as the late John Maynard Smith.

Overall, the book reads like a treatise in social science, with a poor grasp of how problems in the natural sciences are approached and solved. Instead of tight verbal or mathematical models that are designed to explain specific phenomena, Corning presents the reader with rambling and repetitive lists of facts and ideas. Theories are backed up by reference to authority, rather than by tests against data. As the quotations suggest, the style of writing is diffuse, and there is an intrinsic vagueness to the concepts that Corning develops. This makes it hard to pin down exactly what is new or valuable in what he has to say. I have seen many new evolutionary paradigms come and go, and it would take something exceptional for me to be convinced by yet another. My impression is that there is little of value here.

BRIAN CHARLESWORTH
Brian Charlesworth (e-mail: brian.charlesworth@ed.ac.uk) is a Royal Society Research Professor at the Institute of Evolutionary Biology, School of Biological Sciences, University of Edinburgh, Edinburgh EH9 3JT, United Kingdom.

NEW TITLES

The Biology of Vibrios. Fabiano L. Thompson, Brian Austin, and Jean Swings, eds. ASM Press, Washington, DC, 2006. 454 pp., illus. $139.95 (ISBN 1555813658 cloth).

Bones: Structure and Mechanics. John D. Currey. Princeton University Press, Princeton, NJ, 2006. 456 pp., illus. $39.50 (ISBN 0691128049 paper).

Breaking Through: Essays, Journals, and Travelogues of Edward F. Ricketts. Katharine A. Rodger, ed. University of California Press, Berkeley, 2006. 369 pp., illus. $39.95 (ISBN 0520247043 cloth).

Conservation across Borders: Biodiversity in an Interdependent World. Charles C. Chester. Island Press, Washington, DC, 2006. 272 pp., illus. $29.95 (ISBN 1559636114 paper).

The Ecology of Plants. 2nd ed. Jessica Gurevitch, Samuel M. Scheiner, and Gordon A. Fox. Sinauer, Sunderland, MA, 2006. 518 pp., illus. $96.95 (ISBN 087893720X cloth).

Essentials of Conservation Biology. 4th ed. Richard B. Primack. Sinauer, Sunderland, MA, 2006. 523 pp., illus. $82.95 (ISBN 087893720X cloth).

Evolutionary Pathways in Nature: A Phylogenetic Approach. John C. Avise. Cambridge University Press, New York, 2006. 298 pp., illus. $65.00 (ISBN 0521674174 paper).

Genomes. 3rd ed. T. A. Brown. Taylor and Francis, New York, 2006. 750 pp., illus. $110.00 (ISBN 0815341385 paper).

A Machine to Make a Future: Biotech Chronicles. Paul Rabinow and Talia Dan-Cohen. Princeton University Press, Princeton, NJ, 2006. 224 pp., illus. $17.95 (ISBN 0691126143 paper).

Ocean Biogeochemical Dynamics. Jorge L. Sarmiento and Nicolas Gruber. Princeton University Press, Princeton, NJ, 2006. 526 pp., illus. $75.00 (ISBN 0691017077 cloth).

Outbreak: Cases in Real-World Microbiology. Rodney P. Anderson. ASM Press, Washington, DC, 2006. 336 pp., illus. $49.95 (ISBN 1555813666 paper).

A Problems Approach to Introductory Biology. Brian White and Michelle Mischke. ASM Press, Washington, DC, 2006. 276 pp., illus. $34.95 (ISBN 1555813720 paper).

The Structure and Dynamics of Networks. Mark Newman, Albert-László Barabási, and Duncan J. Watts, eds. Princeton University Press, Princeton, NJ, 2006. 572 pp., illus. $49.50 (ISBN 0691113572 paper).

Teaming with Microbes: A Gardener's Guide to the Soil Food Web. Jeff Lowenfels and Wayne Lewis. Timber Press, Portland, OR, 2006. 196 pp., illus. $24.95 (ISBN 0881927775 cloth).