A Grand Conversation on Evolutionary Genomics

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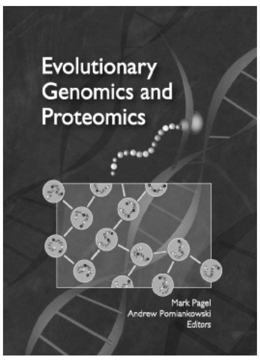
A Grand Conversation on Evolutionary Genomics

Evolutionary Genomics and Proteomics. Mark Pagel and Andrew Pomiankowski, eds. Sinauer, Sunderland, MA, 2007. 295 pp., illus. $54.95 (ISBN 9780878936540 paper).



Genomics is, by its nature, a discovery-based discipline. Like the Lewis and Clark expedition or the voyage of the *Beagle,* large-scale genome projects are exploratory journeys into the molecular wilderness, each trip yielding new and sometimes surprising findings. After each journey, data are catalogued, compared with the results of earlier explorations, and archived in large databases. Findings are often compared with broad expectations rather than used to test discrete experimental hypotheses. Nevertheless, as genomic data from different species become more plentiful and the tools more accessible and inexpensive, genomic approaches are increasingly being employed to address long-standing questions in evolutionary biology. For example, what have been the relative roles of selection and neutral processes in shaping the origins and diversification of taxa? What are the changes in gene sequences and gene expression that underlie changes in phenotype?

Enough data are at last becoming available on genome evolution to warrant book-length treatments of the field. Michael Lynch weighed in last year with a population genetics–oriented volume (*The Origins of Genome Architecture,* Sinauer, 2007). Now, Mark Pagel (University of Reading, United Kingdom) and Andrew Pomiankowski (University College London) have assembled a diverse international set of experts in both molecular and evolutionary aspects of genome science to produce *Evolutionary Genomics and Proteomics.* The 13 chapters address research on a broad spectrum of evolutionary genomics topics, including evolution of genome organization and complexity, origins of new genes and protein domains, genome robustness and redundancy, and the relationships between genomic and phenotypic diversity.

Pagel and Pomiankowski's stated rationale for an edited volume is that evolutionary genomics research draws upon a diverse array of specialized areas of expertise. It can be difficult, however, for an edited book to achieve the focus needed to capture the emergent properties of such an eclectic discipline. In my experience, volumes like this one often do more to showcase the research interests and agendas of the individual contributors than to present a cohesive treatment of their topics. *Evolutionary Genomics and Proteomics* does not present a particularly concise examination of the field, as the chapter topics overlap extensively and nearly every subject is expounded upon by multiple contributors. Nevertheless, thanks to the range of expertise and perspectives among the authors, this overlap provides useful complementary perspectives on the topics rather than repetition. The resulting tone is that of a grand conversation among the contributors, with the reader given the opportunity to view the field as a whole through the give-and-take of the various chapters. The order of the chapters seems largely haphazard, but this arrangement actually enhances this sense of conversation, whether or not it was the editors' intent. Thus, it seems to me that Pagel and Pomiankowski have succeeded in achieving the broader synthesis they desired.

A central issue throughout the book is deciphering the relative importance of selective versus neutral processes in explaining different aspects of genome and proteome evolution. Evaluating evidence of selection at the DNA sequence and network levels, respectively, are the main themes of chapters by Alan Filipski and coauthors and by Andreas Wagner, but this theme arises in some form in nearly every chapter. In their introductory chapter, Pagel and Pomiankowski put a distinctly selectionist spin on this topic and dismiss, without elaboration, Lynch's arguments that neutral mechanisms are sufficient to explain many genomic phenomena. Fortunately, the authors of the individual chapters seem much more interested in trying to understand the evolutionary processes responsible for genome evolution than in debating perspectives on their relative importance. Not surprisingly, the contributors differ in the rigor with which they discuss tests for selection and evaluate their potential shortcomings. Nearly every chapter, however, emphasizes the uncertainty that persists about evolutionary mechanisms and the amount of research that remains to be done.

A second major theme involves what might be considered the holy grail of evolutionary genomics: the mapping of genomic and other "-omic" variation onto phenotypes to explain the integrated functional basis of phenotypic diversity. The nascent field of systems biology seeks to accomplish genome-to-phenotype mapping by developing predictive models, then iteratively testing and refining these models using genomic, transcriptional, proteomic, and metabolomic data. A chapter early in the book by Eugene Koonin and Yuri Wolf introduces systems biology in the context of understanding phenotypic evolution, and sums up recent insights on the factors linking variables describing genome function (e.g., protein abundance, gene dispensability, and number of protein interactions) and genome evolution (e.g., evolutionary rate, number of paralogs, and likelihood of gene loss). Later chapters by Bernardo Lemos and coauthors, László Patthy, Laurence Hurst and Csaba Pál, and Andreas Wagner build on the systems biology theme by discussing research on the inheritance of variation in transcriptional networks, organization and scaling of protein interaction networks, genomic redundancy, and gene network evolution.

The chapters by Hurst and Pál on genomic redundancy and dispensability and by Wagner on whether a "network biology" exists were for me the twin high points of the book. Assertions that some genes are redundant or dispensable, and proposed explanations for redundancy, have long struck me as dubious, and Hurst and Pál provide a particularly insightful examination of the data on this topic. Wagner examines whether the organization of biological networks is fundamentally different from that of nonbiological networks because of natural selection, concluding that there is convincing evidence for effects of selection on local small-scale features, but not, at least so far, for global network structure.

One omission from *Evolutionary Genomics and Proteomics* that I found disappointing was the lack of discussion on how understanding genome evolution might affect society. At the end of their introductory chapter, Pagel and Pomiankowski state offhandedly that the success of the field will be measured in part by success in creating made-to-order phenotypes, a prospect I find to be at once exciting and disturbing. On the one hand, understanding the adaptive significance of genome evolution may provide important insights for controlling infectious diseases and developing more productive but less resource-demanding crop varieties. On the other, such knowledge has unprecedented potential for disastrous misuse by malicious or merely naïve practitioners. These issues deserve more than trite anticipation.

In spite of such shortcomings, Pagel and Pomiankowski have produced a volume that will benefit readers ranging from graduate students to seasoned researchers in both evolutionary and functional areas of biology who seek an understanding of this rapidly developing field. The technical language and themes, however, will put the book beyond the grasp of all but the most astute nonscientists. Much of the detail in this book will undoubtedly become dated rather quickly, given the rate at which advances are occurring. Even so, the complex questions being addressed by evolutionary genomics research will not yield quickly to definitive answers, so the broader questions addressed in the book's chapters will remain relevant for a long time to come.

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THE BIG BOOK OF ANIMAL PHYSIOLOGY

Physiological Ecology: How Animals Process Energy, Nutrients, and Toxins. William H. Karasov and Carlos Martínez del Rio. Princeton University Press, Princeton, NJ, 2007. 744 pp., illus. $65.00 (ISBN 9780691074535 cloth).

A big topic demands a big book, with some big thinkers behind it. When I agreed to review this book, I knew, given the authors, that I would see some big thinking, but the size of their effort took me by surprise. *Physiological Ecology* (all 744 pages, 2.7 liters, and 1.9 kilograms of it!) is a comprehensive yet surprisingly accessible treatment of a topic that is the linchpin for biologists of many stripes.

The authors, William H. Karasov (University of Wisconsin) and Carlos Martínez del Rio (University of Wyoming), are both physiological ecologists specializing in birds, but their book encompasses a world beyond birds that includes insects, crustaceans, fish, rats, and even giant worms and clams.

Karasov and Martínez del Rio explain difficult concepts clearly, writing in a refreshing, informal style that makes you feel you're enjoying a casual coffee with these world experts (but with high-quality diagrams on the napkins).

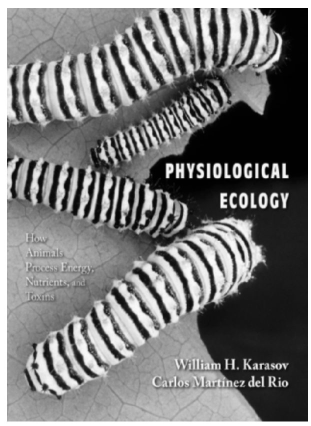
There is much of interest here for anyone concerned with key aspects of the ecological functioning of animals, with the stated target audience being advanced undergraduates, graduate students, and practicing ecologists interested in how resources are processed by animals in food webs. Here I call attention to the book's subtitle: the emphasis is on how animals process—ingest, assimilate, allocate, excrete—food. Thus, the book is a very broad treatment of animal nutritional physiology in an ecological context. So there is much missing if one imagines this tome to be a physiological ecology text, *sensu lato.* For example, there is little or no treatment of gas exchange and respiration, acid/base balance, thermal regulation and heat exchange, and other matters of importance in animal ecophysiology. I say this not as a criticism of their book, however, but only to highlight its scope; Karasov and Martínez del Rio do not promise to treat these subjects, and the book is thick enough as it is.

Essential to their approach are two philosophical underpinnings. One is the broad view that an understanding of evolution is key to insight in comparative physiological ecology. The other is a more narrow, pragmatic approach that emphasizes how all physiological insights are contingent on the methodological baggage that accompanies the measurements.

The authors have broken the book into six major sections. Section 1 consists of only one chapter (an overview introducing basic concepts of mass and energy budgets, allometry, temperature effects, and phylogenetic contrasts), but serves as an important synthesis of major strategies of analysis in animal physiological ecology. Section 2 also consists of only one chapter and provides a detailed overview of key biochemical aspects of animal food. Section 3 considers mechanisms of energy and material inputs to animals (with chapters on food intake, gut reactor theory, nutritional symbioses, and digestive symbioses). Section 4 follows the fate of absorbed materials to consider postabsorptive nutrient processing, the meaning of stable isotope signatures in animal tissues, and the physiology of toxin handling. Next is a section on the role of limiting nutrients, with treatments of ecological stoichiometry, of nitrogen and mineral nutrition, and of water limitation. The book closes with section 6, two comprehensive chapters dealing with energy and mass budgets as connected to growth and to reproductive output.

I found this book both fascinating and entertaining. It brings to the forefront some cutting-edge ideas in ecology and functional biology, such as metabolic scaling theory, ecological stoichiometry, and isotopic resource tracking. The emphasis on careful, phylogenetically controlled analyses in comparative studies is important and well presented. Karasov and Martínez del Rio explain difficult concepts clearly, writing in a refreshing, informal style that makes you feel you're enjoying a casual coffee with these world experts (but with high-quality diagrams on the napkins). This style will make the book especially effective as a text in upper-division animal physiological ecology courses.

That said, there are some problems. The authors rely heavily on information boxes, particularly to cover methodological approaches. Some readers will find these boxes invaluable, especially those readers new to physiological research who need to learn more about how things are done. Others will find some of them distracting, too long, or unnecessary (e.g., a box relating how a spectrophotometer works, hardly upper-division material). In reading groups such as the one in my lab, some members assigned to lead discussions of certain chapters may find themselves feeling victimized by the extreme variation in chapter length (from 27 to 93 pages). The editing in the text was generally thorough but less so in the figures and figure legends. For the most part, though, these are minor matters. The book is solid, engaging, and effective in presenting animal physiological ecology as the modern and vibrant field it is.



So if animals and food webs are central to your interests, you should read this book. But be sure to put it in your pack before your lunch. Otherwise you'll find that its 1.9 kilos will have done some preassimilatory processing of your sandwich.

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MULTIFUNCTIONAL AGRICULTURE: MORE THAN BREAD ALONE

Multifunctional Agriculture: A Transition Theory Perspective. G. A. Wilson. CABI, Cambridge, MA, 2007. 368 pp., illus. $130.00 (ISBN 9781845932565 cloth).

A growing number of policymakers, academics from a variety of disciplines, farmers, and consumers are expressing interest in what is called multifunctional agriculture (MFA). Under the MFA rubric, farming produces not just food, fiber, and energy but also a host of societal benefits. Research in recent years has shown that these benefits can include cleaner water, sequestered carbon, landscape amenities such as wetlands and wildlife habitat, and rural community employment. But how can we promote the development of such agricultural systems on farms and at a wider—national or even global—scale? And before we do that, how do we go about identifying MFA consistently?

Multifunctional Agriculture: A Transition Theory Perspective, a new book by Geoff Wilson, is an important step toward explaining why some narrowly focused agricultural systems are developed into those with higher levels of MFA. Wilson lays the foundation for his discussion by attempting to answer this question: How do we explain changes over time in the level of multifunctionality in agricultural systems anywhere on the globe?

At the center of MFA is the farm, Wilson says. He describes how a system's multifunctionality can be gauged using a combination of indicators such as productivity, environmental sustainability, the intensity of reliance on chemicals and other inputs, and the level of farm diversification, including the variety of crops and livestock on the land and beyond-the-farm enterprises such as agricultural tourism or processing. Also among the indicators of multifunctionality is the level of connection to the rural community that a farm attains by employing people, buying local inputs, or selling products through rural businesses. Another, according to Wilson, is agriculture's provision of food for consumption close to the farm, reducing reliance on global food chains controlled by large agribusinesses. Additionally, the attitudes of farmers, the rural population, and other decisionmakers are an MFA indicator: are they focused on high production or on producing wider societal benefits?

Wilson defines a spectrum of MFA from weak through moderate to strong. He intentionally uses these value-laden terms because he believes strong MFA is "morally best," the ideal toward which societies need to strive. Decisions pertaining to MFA are made at the farm level, but also on rural community, regional, national, and global scales.

Wilson frames the boundaries of this spectrum of MFA as "productivist" on the weak end and "nonproductivist" on the strong end. Productivist agriculture is organized for maximum production of high quantities of commodities. This level of MFA relies on global trade and high input use. It results in serious environmental impacts, and is supported at all the scales by attitudes, policies, and businesses.

The strong end of his MFA spectrum begins to merge into rural community activity beyond agriculture. Wilson characterizes this portion of the spectrum as focused on low-intensity farming, lower production, and more localized food distribution chains, with more diverse landscapes and more reliance on off-farm income. Strong MFA also tends to support rural community development and tourism based on diverse and pleasing landscapes with wetlands, animals, and other amenities. The nonproductivist concept is heavily influenced by the literature not just from the United Kingdom, the European Union, Australia, and New Zealand but also from other countries that have seen changes in some farming landscapes toward tourism and other nonfood and fiber production. As Wilson mentions, however, less food production in one area may necessitate more intense production elsewhere.

The book describes how a number of agricultural systems fit into the MFA framework, including industrial, organic, and subsistence farming; plantations in developing countries; and hobby farming. The reader should not make simple assumptions here. For example, Wilson notes that organic production may not be strong in all aspects of MFA when it produces for the global supply chain.

Strong MFA (multifunctional agriculture), I believe, must be understood as optimizing yields of high-quality food in ways that maintain highly functioning ecosystems along with socially just and economically viable human relations.

The strength of Wilson's work is that he elaborates a robust framework that can describe and explain pathways of transition in agriculture toward higher or lower levels of MFA. It applies to farming systems in developed and developing countries at the decision-making level of the farm and at other scales. His book extends the analysis to include more than simply the value of nonmarket public goods. For example, Wilson's framework accounts for the reality that a weakly multifunctional farm may have a few strongly multifunctional areas, such as wetlands tucked among the fields, that would seem monofunctional because high production of commodities is the goal to which all other ecological and social functions are subordinate. His framework also accounts for how farms and landscapes may move toward or away from strong MFA, depending on the pressures and opportunities offered by markets, policies, and attitudes.

As executive director of a nonprofit organization that works with farmers who practice sustainable agriculture here in the US Midwest, I have been involved with studies showing the benefits of MFA at the watershed scale. I've also seen firsthand how such a wider view of agriculture's potential is producing real results on working farms. Politicians in local areas are beginning to recognize the benefits of multifunctional agriculture, and consumers are showing they want to buy food with certification from the Food Alliance, Fair Trade, and other similar certification systems, denoting that some dimensions of multifunctionality have been incorporated in the food's production.

The weakness I find in Wilson's MFA spectrum is that he conceptualizes strong MFA by proximity to the nonproductivist boundary. I think this sends the wrong signal to policymakers, citizens, researchers, food companies, and farmers alike. Wilson acknowledges that goals related to food security are vital. In his framework, however, strong MFA with respect to ecological sustainability equates to low productivity.

Growing empirical evidence suggests that we can achieve relatively high food production while mimicking natural ecosystems (Jackson and Jackson 2002). A preeminent group of scientists, after studying what it called "alternative agriculture," found that "reduced use of these inputs [chemical pesticides, fertilizers, and antibiotics] lowers production costs and lessens agriculture's potential for adverse environmental and health effects without necessarily decreasing—and in some cases increasing—per acre crop yields and the productivity of livestock management systems" (Committee on the Role of Alternative Farming Methods in Modern Production Agriculture, Board on Agriculture, National Research Council 1989). Jules Pretty, whom Wilson quotes extensively, describes systems around the world that jumped from subsistence farming to highly productive MFA systems (Pretty 2002). Wilson himself acknowledges that it could be possible for "all agriculture systems" to become strongly multifunctional at the global level. In April 2008, a group of 400 experts from around the world, known as the International Assessment of Agricultural Knowledge, Science, and Technology, concluded in a report that there must be a global drive toward more sustainable farming systems, if we are to feed people and protect the very resources that will ensure food security in the future *(www.agassessment.org)*. A productive agriculture and a sustainable agriculture can be one and the same.

Strong MFA, I believe, must be understood as optimizing yields of high-quality food in ways that maintain highly functioning ecosystems along with socially just and economically viable human relations. In that sense, "strong" MFA may belong in the middle of Wilson's spectrum, with "moderate" MFA being close to the nonproductivist boundary. Quality of life and adequate food production now and in the future depend on our success at redesigning agriculture. A powerful and comprehensive analysis for understanding and directing change will speed that process.

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