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IS LESS MORE?[1]

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With the blossoming of evolutionary developmental biology and evolutionary genomics following on the heels of the recent molecular revolution in evolutionary biology, the field is arguably more expansive and integrative than ever. This growth has infused an air of excitement and anticipation into the discipline, as it appears to be on the verge of providing long-awaited answers to questions such as the structure of the tree of life, the origin of body plans, the genetic changes that underlie speciation, and the genetic basis of those traits that make us uniquely human (Avise 2003; Coyne and Orr 2004; Carroll 2005; The Chimpanzee Sequencing and Analysis Consortium 2005). At the same time, the fact that the pageantry of research in evolutionary biology is so diverse presents vexing questions for those of us faced with teaching undergraduate courses in evolutionary biology: how much of this vast discipline should we attempt to cover in a single course, and what is the best way to organize the material?

The question of how much to cover is certainly not unique to evolutionary biology. Indeed, recent examples of streamlined textbooks for other survey courses such as ecology (e.g., Molles 2005), genetics (e.g., Hartl and Jones 2006), and general biology (e.g., Cain et al. 2006), suggests a growing sense that biology students in general may be best served under a ''less is more'' model of education. It is debatable whether this trend is motivated more by the impracticalities of squeezing a rapidly expanding discipline into a single course, or by the reality of facing students who are poorly prepared for college science courses. However, one additional contributing factor is certain; most students in an upper level survey course in biology have no intention of pursuing a career in that biological subdiscipline. Thus, only a small fraction of students in such a course hunger for the subtle nuances of the field. As instructors, it is clear that these self-motivated students do not present our greatest educational challenge. Rather, our challenge in survey courses, including evolutionary biology, is in helping the uninspired majority learn both the central concepts and the ways of approaching questions in the major fields in biology. Given that challenge, it is difficult to argue against the less-is-more philosophy.

Ironically though, it is probably safe to say that the majority of those who currently teach undergraduate courses in evolutionary biology cut their eye teeth while chewing (figuratively, one hopes) on the famously dense, exhaustively integrative, and encyclopedic *Evolutionary Biology* (Futuyma 1979, and subsequent editions). But while such a textbook provided abundant inspiration for students destined to become evolutionary biologists, its very strengths made it a difficult slog for many of their classmates. Hence, Futuyma dramatically overhauled his classic text with these other biology majors explicitly in mind, and created a new rendition, renamed simply *Evolution*.

To assess whether the metamorphosis of this classic text was in keeping with the less-is-more philosophy, I focused on two key questions. First, is it less? Put another way, how streamlined is *Evolution*, compared to its progenitor? Second, is it more? In other words, to what degree have changes in organization, level of detail, and graphics rendered the book more effective for an undergraduate audience? In addition to these main questions, I also assessed whether the text would be as useful to the inspired minority of undergraduates, as well as beginning graduate students, as was the text from which *Evolution* was distilled.

Is it less? On sheer bulk alone, *Evolution* (at 22 chapters and 543 pp.) is a substantially thinner book than its predecessor (26 chapters and 751 pp.). But mere page counting does not do justice to the degree to which Futuyma streamlined this new text, as those fewer pages are also far less densely packed with text. To quantify this difference, I randomly selected 30 pages from each book to obtain estimates of the numbers of words per line and lines per page, which together could be used to estimate the mean number of words per page. The results were dramatic; compared to its predecessor, *Evolution* has approximately 30% fewer words per page ($P < 0.01$, two-tailed t-test). By combining my estimates of words per page with the respective page lengths of each text, I estimated that while the most recent edition of *Evolutionary Biology* boasts a whopping 494,000 words, *Evolution* features a mere 247,000 words—a 50% reduction!

Producing such a sleek new volume clearly involved much more than a minor edit and repackaging. Indeed, Futuyma achieved this stunning decrement in several ways. First, examples that are used to illustrate a concept are often discussed more briefly. For example, in describing how origins of higher taxa can be inferred from the fossil record, both *Evolution* and its progenitor describe the origins of Amphibia, birds, and mammals. The difference is that in *Evolution*, this discussion focuses strictly on key innovations, without burying those innovations amidst detailed descriptions of transitional forms. Second, Futuyma made a conscious effort to reduce the amount of quantitative material presented. As a result, gone are the equations describing the influence of genetic correlations on the rate of evolution, the effects of inbreeding on additive genetic variance, and the conditions favoring the evolution of iteroparity versus semelparity, to mention a few. Finally, unlike its predecessor, *Evolution* lacks chapters devoted to ecology, form and function, and human evolution (though the latter topic is integrated into chapters on classification and phylogeny, the fossil record, biogeography, and

[1] *Evolution.* Douglas J. Futuyma. 2005. Sinauer Associates, Sunderland, MA. 543 pp. HB $89.95, ISBN 0-87893-187-2.

genetic drift and the neutral theory). In short, it is clear that *Evolution* is substantially trimmer and more streamlined than the volumes that preceded it.

But is it more? Upon opening *Evolution* to any page, it is also immediately apparent that this text is designed and written far more effectively for reaching the typical biology major than is *Evolutionary Biology*. The most striking difference is in the graphics, nearly all of which are simultaneously eye-catching and informative. Indeed, the careful attention to graphics so evident in this textbook is like what one usually only encounters in introductory biology texts. Full color photographs of organisms and their anatomical features are peppered throughout most of the chapters. These vividly complement the color figures and tables, which make excellent use of explanatory bubbles to focus students' attention on important patterns. All of the graphics, which are unparalleled among evolutionary biology textbooks, are available on an instructor's CD, enabling one to easily and richly illustrate lectures.

Although the graphics alone might be enough to convince some to consider adopting *Evolution*, the text is also much more accessible and engaging, largely thanks to the aforementioned reduction in detail. Simply put, with substantially less extraneous information, it should be much easier for students to understand the major concepts and how the selected examples illustrate those concepts. At the same time, although it contains many time-tested examples, this text has a decidedly up-to-date feel. For example, the discussion of the origins of birds and whales highlights inferences made possible only through fossil discoveries over the past few years. Similarly, students are introduced to recent advances in our understanding of the genetics underlying the evolution of our species' capacity for speech and language, the use of QTLs to decipher the genetic basis of quantitative traits, and the role of ecological factors in speciation. Contributed chapters on evolutionary developmental biology and evolutionary genomics (written by J. R. True and S. V. Edwards, respectively) nicely capture the patterns emerging from these fast-growing fields. Whether by some strange quirk of convergent writing styles, or through careful editing, the tone of these two chapters matches well with the rest of the book.

In addition to providing undergraduates with a thorough, current introduction to the core concepts in evolutionary biology, *Evolution* also offers them tools for addressing arguments against evolution. Many students in survey courses in evolutionary biology will find themselves in careers in science education soon after graduation (far more, in fact, than will become practicing evolutionary biologists). Given the growing pressures to introduce nonscientific ideas such as intelligent design into the K–12 science curriculum (Alters and Alters 2001), it is important that these future biology teachers be prepared to defend both their teaching of evolution and their unwillingness to incorporate pseudoscience initiatives. In a chapter devoted to this topic, *Evolution* addresses the issues directly and pointedly, while also making a strong case for the societal benefits of knowledge gained through evolutionary thinking.

Could it be even more? Although this is an outstanding textbook for an upper division survey course in evolutionary biology, there are several aspects that could be improved further. Most of these aspects are structural, having to do with the overall organization of the chapters. In this regard, *Evolution* differs relatively little from its progenitor. It begins with an overview of the origins of modern evolutionary biology, followed by an introduction to phylogeny construction, evidence for evolution, and broad patterns of evolutionary change. Next come chapters on the fossil record and the significant evolutionary events that occurred within each of the geological periods, after which the text moves into biogeography and the causes and rates of diversification and extinction. Following this introduction to macroevolution are a series of microevolution chapters focusing on variation and its origins, evolutionary forces, the neutral theory, the evolution of quantitative traits, and an evolutionary framework for understanding intraspecific conflicts and cooperation. From here, the text shifts to a focus on speciation, life-history evolution, and coevolutionary dynamics between species, before exploring evolutionary genomics and evolutionary developmental biology. Following the evo-devo chapter, *Evolution* returns to macroevolution with a chapter focusing again on rates of evolution, as well as the origin of evolutionary novelties, and evolutionary trends, before closing with the chapter addressing creationist challenges to evolution.

One difficulty created by such an organization is that, because most of the macroevolutionary patterns are discussed before introducing microevolution and speciation, the link between patterns and processes at the two levels is not very evident. The connections between microevolution and macroevolution are often difficult for students to understand or appreciate, suggesting that an approach that emphasizes those links would be desirable in a text. For example, after motivating students with the evidence for evolution and broad evolutionary patterns, one could proceed from microevolution to speciation to macroevolution, emphasizing that phylogenetic diversification over macroevolutionary time is the result of speciation events, which are themselves molded by microevolutionary processes. While it is reasonable to use sections on earth history and the fossil record in conjunction with a unit on the evidence for evolution, it is awkward to discuss rates of diversification and the underlying factors influencing those rates prior to introducing microevolutionary processes. The tension such a structure creates is evident in *Evolution*, in that the initial chapter on rates of diversification and extinction (Ch. 7) often refers ahead to explanations of the underlying processes that are discussed in subsequent microevolution chapters.

The decision to incorporate human evolution into many different chapters, rather than having a single chapter devoted to the topic, also has negative consequences. Most students in evolutionary biology courses hunger for an understanding of what is known of the origins of modern humans. By incorporating aspects of research on human origins into a diverse array of chapters, Futuyma apparently attempts to capitalize on this interest as a means of motivating students to understand basic concepts in paleontology, biogeography, and population genetics. While well intentioned, such an organization has a significant downside, in that students cannot refer to a chapter that summarizes and integrates the work on human evolution into a single story. Thus, while their

interest in human evolution may stimulate them to learn certain basic evolutionary concepts, their hopes to gain a cohesive understanding of human origins are likely to be frustrated.

Perhaps what many will find the greatest shortcoming of *Evolution* stems from the fact that, for a number of concepts, Futuyma provides several examples, each of which is explained fairly briefly. For example, in a section describing observations of rapid evolution in natural populations, four different examples are given (critical photoperiod in introduced moth populations, migration patterns in newly formed bird populations, heavy metal tolerance in plants, and beak morphology of seed bugs on introduced plants), each represented by a single paragraph. An obvious reason for such an approach is that it underscores that evolutionary principles generally have much more support than just a single case study. However, the series of brief descriptions give those sections of the text a staccato cadence that leaves the reader feeling rushed. More importantly, a rapid series of examples does little to develop students' critical thinking skills, as they cannot be led through an unfolding logical puzzle. Using the above example, it may have been more useful to open with a question: ''Under what conditions is rapid evolution likely?'' Following this question, any one of the above examples could be explained more fully, giving students the chance first to learn of a pattern (e.g., different critical photoperiods in introduced moths, compared to the source populations), and then to walk through an explanation of the research that demonstrated that the pattern was the result of natural selection imposed by the novel environment. Thus, while *Evolution* is outstanding in presenting most of the core concepts in evolutionary biology to an audience of biology majors, it has somewhat limited potential for developing an evolutionary way of thinking in those students for whom such thinking does not come easily. In both regards, this text differs considerably from that of Freeman and Herron (2004), which is relatively light on its coverage of core concepts, but instead emphasizes the development of critical thinking in an evolutionary context.

It is important to note that any instructor who is willing to do more than just simply teach from the text can remedy nearly all of the above weaknesses of *Evolution*. For example, one could organize a course that led from microevolution to speciation to macroevolution, and assign chapter readings to reflect that sequence. Similarly, lecture would be an excellent opportunity to develop selected examples cited in *Evolution*, using them as exercises to help build critical thinking skills. To do so would of course require some effort on the part of the instructor. However, the fact that for most concepts, the text provides many examples to choose from, should give instructors many options for selecting case studies to discuss in depth. Thus, in spite of its weaknesses, *Evolution* would be a terrific complement to any undergraduate survey course in evolutionary biology.

Given that *Evolution* was produced for such a course, it is reasonable to be concerned that it may not be as useful for advanced undergraduates and graduate students. Surprisingly, though, this doesn't seem to be the case. The book is still amazingly comprehensive, so much so that it will continue to serve as an important reference for graduate students in evolutionary biology who are preparing for their comprehensive exams. The glossary and literature cited sections alone are gold mines for those needing an introduction to essentially any aspect of evolutionary biology.

Remarkably, *Evolution* enables evolutionary biology instructors to adopt a text that provides a thorough, up-to-date coverage of the field, and that should prove to be both engaging and accessible to most biology majors. The reworking of this text from its dense and encyclopedic predecessor should serve as a hallmark example of the adage that in undergraduate survey courses, less is almost always more.

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