

Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution

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An Uneven Guide to Eco-Devo

Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution. Scott F. Gilbert and David Epel. Sinauer, 2008. 459 pp., illus. \$49.95 (ISBN 9780878932993 paper).

Scott Gilbert, professor of biology at Swarthmore, has been at the forefront of efforts to distinguish eco-devo (ecological developmental biology) from evo-devo, writing a number of papers promoting it and sponsoring a symposium (with Jessica Bolker). So I was excited to hear that he had written a book on eco-devo, with David Epel, professor of biological sciences at Hopkins Marine Station, Stanford University. The resulting volume, *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution* is handsomely produced and lavishly illustrated.

The authors have two goals in mind. Their first is to introduce the excitement of the developments in this new field to advanced undergraduates and beginning graduate students. The second is to weave a new conceptual synthesis for researchers working in this and related fields; I will comment on the success of each of these. Their subtitle conveys their intention, to explicitly unite research initiatives in several emerging fields: evo-devo, environmental origins of human disease, and the epigenetic modification of gene expression patterns. The glue to bind them together is the phenomenon of phenotypic plasticity, and the scaffold on which this union will be built is the process of development.

Ecological Developmental Biology focuses on animal development; syntheses for plants and plasticity of brain development are explicitly excluded—"these fields have their own books" (strangely, citations directing the interested reader to these texts are missing). Gilbert and Epel divide their treatment into three sections. The first begins with

overviews of what we know about phenotypic and molecular responses to "normal" environmental factors, and each topic is supported by both classic and new examples, as well as cases from human biology. Two subsequent chapters present focused treatments of plasticity in relation to symbiosis and to defenses of eggs and embryos. These offer excellent examples of the authors' intentions to expand readers' perspectives on the scope of eco-devo. The symbiosis chapter makes clear that many examples of symbiosis can best be understood as not just ecological interactions, but as examples of codevelopment as well. Their unfurling of the complexity and implications of healthy microbial communities in the human gut is a superb example of the reach of eco-devo. The chapter on embryonic defenses was less successful, in my view; my qualms started when the authors suggested that robustness/canalization of development is an embryo defense mechanism. The organization seemed a bit jumbled to me: A section on strategies of defense (polyphenism, parental effects, diapause, and physiology) was followed by one on mechanisms of defense, which focused on protection against particular types of environmental insult.

The second section focuses on environmental effects leading to disease. Here, disease is intended *sensu lato*, including not just ill-health but also development gone awry. Starting such a discussion with a chapter on teratogenesis seemed to me a bold move (which is another way of saying that I would have covered the eco-devo link between normal and abnormal development later). The chapter ends with an unsatisfying section on the phenomenon of deformed frogs: too short and missing key aspects of the story. They return to frog deformities in the following chapter on endocrine disruptors (atrazine effects on immunity in frogs), but it doesn't make sense to separate elements of a first-rate eco-devo case study, nor to

leave out discussion of an extensive literature on the complexities of pesticide and herbicide effects (e.g., Relyea 2005, 2006).

The keystone chapter in section two is titled "The Epigenetic Origin of Adult Diseases." Its first half deals extensively with the relatively recent burst of research on how maternal effects can affect offspring phenotypes well into the offspring's life. The authors begin this section with a misstep when they say, "Mammals developing within the uterus can fine-tune their phenotypes to suit an expected future environment" (p. 247). Although there are those who would agree with this statement, for most biologists the idea has not risen above the level of an interesting hypothesis yet. The literature in this area is indeed intriguing, but the jury is still out on both the "thrifty phenotype" and "predictive adaptive response" models. Wells (2006, 2007), who has extensively reviewed these ideas, concludes that the evidence can be interpreted parsimoniously as supporting a view of "manipulation of offspring phenotype for the benefit of maternal fitness," a far cry from preparing the offspring for a harsh future. Nevertheless, in this chapter Gilbert and Epel offer a nice introduction to the literature in this field in this chapter. I was surprised that there was no mention of the field of evolutionary medicine, however (e.g., Trevathan 2007).

The third section of the book begins with an overview of modern evolutionary concepts, followed by a chapter on evolutionary developmental biology, focused largely on how changes in gene regulation can produce evolutionary change. Concepts and mechanisms of the evolution of development via gene regulation are generally well covered. Gilbert and Epel discuss the idea that the origins of macroevolutionary change can be seen in the changes in amount, timing, and location of gene expression. Up to this point, we have nine chapters

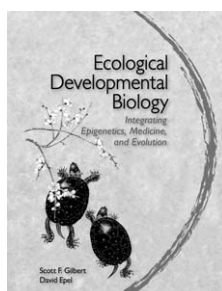
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written mainly to achieve goal one—that is, to convey enthusiasm for the new field and its way of looking at the world—and the book is fully successful at this level. Although I have some quibbles, the material is generally well presented and should capture the attention and interest of biologically savvy students. I note that although the illustrations are generally excellent, the captions accompanying them are too often inadequate. Many figures are poorly described—axes on graphs are sometimes lacking and legends are incomplete. In chapter 5, for example, several comparisons of normal and abnormal development are presented (e.g., figures 5.3 to 5.6), but insufficient detail is presented for the reader to conclude much more than that the examples look different.

This brings us to the final chapter, and to goal two of forging a new conceptual synthesis. You may have already mused, “This idea of merging development and plasticity sounds familiar,” and asked yourself, “Hasn’t this been done already (with the exception of incorporating human health)?” And you’re right—books by both Schlichting and Pigliucci (1998—way back in the 20th century, but not cited by Gilbert and Epel) and West-Eberhard (2003) undertook the melding of plasticity, development, and evolution. So it is a fair question to ask what, with the exception of incorporating human health, the authors add to the previous syntheses. Does eco-devo add significantly to our views of how evolution operates?

Gilbert and Epel suggest that eco-devo upends three supports of the modern synthesis: that only heritable variation is important, that organisms are unitary, and that the environment’s only role is as a selective agent. They argue that eco-devo, in contrast, shows that both epigenetic and environmentally induced variation are important, and that organisms are more like ecosystems. In their view, eco-devo’s key innovations are epigenetic inheritance, heterocyberny (an appalling new term for genetic accommodation), and niche construction, and each receives treatment in the final chapter. Since each of these has had a major book devoted

to it (Odling-Smee et al. 2003, West-Eberhard 2003, Jablonka and Lamb 2005), the new synthesis must be in their combination, but in the end Gilbert and Epel are not able to tie them together in new ways.



Ecological Developmental Biology also has a coda on philosophy and eco-devo, and four text appendices. Appendix B expands on topics covered less fully in the text (e.g., epigenetic mechanisms such as methylation). Appendices A, C, and D offer some historical context for the progress of evo-devo and eco-devo. I found these sections very uneven—interesting observations alternate with purple prose, and the failure of plasticity studies to gain a foothold in Western science is all Lysenko’s fault. Overall, I have to deliver one thumb up and another down. The book succeeds in its goal to provide a taste of the excitement and intrigue of viewing organismal biology through the lens of plasticity. However, for me at least, it does not deliver on its promise of a new synthesis.

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DEFINING CULTURE IN ANIMALS

The Question of Animal Culture.

Kevin N. Laland and Bennett G. Galef, eds. Harvard University Press, 2009. 351 pp., illus. \$49.95 (ISBN 9780674031265 cloth).

Ever since a troop of Japanese macaques began washing sweet potatoes in a stream, scientists have described, argued, and marveled at the degree of culture demonstrated by non-humans, and wondered what these observations had to say about human culture. *The Question of Animal Culture*, edited by Kevin N. Laland and Bennett G. Galef, is the first, most scientific, and challenging look at what culture means for animals ranging from birds to nonhuman primates.

The question of whether the traditions of animals and cultures of humans are similar is very contentious, and this book is an excellent, timely compendium of the thoughts and research of the best scientific minds as they address this issue. The approach is one of rigorous scientific inquiry and dialogue, with the recognition that this is an important, viable, and expanding field that has matured to develop paradigms, methods, and theories to describe and categorize behavioral patterns that might represent culture in animals. Also up for consideration is the question of whether

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