

BOOK REVIEW

Synthesis Version 4.1beta: a review of Scott F. Gilbert's and David Epel's *Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution*

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Ecological Developmental Biology: Integrating Epigenetics, Medicine, and Evolution by Scott F. Gilbert and David Epel. Sinauer Associates Inc., Sunderland, MA, USA. ISBN 978-0-87893-299-3.

Is evolutionary biology in the midst of a new synthesis? Historically, evolutionary biology has evolved with punctuated syntheses, such as “Darwinian evolution” and the “Modern Synthesis.” Over the last three decades Evolutionary Developmental Biology has taken up the torch and rapidly transformed itself into an integrative discipline with its own journals and funding panels. Our field has been nicknamed—whether you love it or hate it—“evodevo.” This acronym has recently started to mutate within journal articles as well as at meetings and symposia into *eco-evo-devo*, *evo-devo-eco* (*eco-*)*evodevo*, and just plain *ecodevo* (with or without the dash!). Do any of these recent variations have anything to do with a new synthesis in evolutionary biology or is this pluralism symptomatic of researchers desperate to build their own niche? The answers to these questions and much more can be found in Scott F. Gilbert's and David Epel's recent book *Ecological Developmental Biology* (2009). In their view, we are in the midst of a revolution—one that integrates evolutionary and developmental biology with epigenetics, systems biology, and the developmental origins of adult disease. Here is what we believe to be some of the most important messages of this book:

- Developmental plasticity is a universal feature of developing organisms, and can be adaptive and non-adaptive.

- The environment can be instructive and permissive during development. In some developmental interactions, the genome is instructive and the environment is permissive, while in others the environment is instructive and the genome is permissive.
- The environment is not only a filter that selects existing variation, but can also be an important source of phenotypic variation. Environmentally induced phenotypic variation can be selected upon, and through a defined set of evolutionary mechanisms (i.e., genetic assimilation and accommodation), can result in evolutionary change.
- Epigenetic variation is a source of evolutionarily significant variation, because it can be transmitted from generation to generation and can be heritable.
- Development is not a closed system. Symbioses between organisms, such as bacteria in the human gut, establish reciprocal inductive interactions between symbiotic organisms during normal development.

The book makes these and other critical points in three parts and 10 chapters. The first and last parts will be of most interest to the readers of this journal, especially chapters 1, 2, 8–10, as well as the appendix covering philosophical and historical aspects of ecological developmental biology. This is a textbook suited for seminar discussions and for researchers who are seeking connections with other related fields. For example, the whole mid-section of the book discusses the medical implications and applications of *ecodevo*. We are currently using the book as the primary reading for an advanced undergraduate/graduate seminar and the initial

student reaction is “two thumbs up.” Our students especially enjoyed that the book is well written and illustrated, and contains many bizarre examples; from the symbiosis between the Hawaiian bobtail squid’s light organ and the fluorescing bacterium *Vibio fisheri* to the altered gut bacterial communities of children born by c-section.

Gilbert and Epel refer to their book as a “Version 1.0.” We would like to predict a few challenges and ideas in ecoevodevo that next version of this book might address: first, the field has been unable, for the broader audience of biologists, to shed the “ghost of Lamark,” and the second is that there is a terminological muddle in this field. While Gilbert and Epel do a great job at dispelling the first, they don’t address the second. Integrative sciences require clear definitions that apply to the entire field rather than to special cases and ecoevodevo is no exception. In this context, Gilbert and Epel attempt to introduce a new term “heterocyberny” to describe a “change in governance.” Heterocyberny describes those mechanisms in which selection of environmentally induced phenotypes become stabilized in the genome such that the phenotypes arise even in the absence of the environmental inducer. While this term may appear useful, as it is an extension of the other “hetero-” terminology, such as heterochrony (change in the timing of gene expression) and heterotopy (change in the spatial domain of gene expression), the term is fairly restrictive in its meaning. It also overlaps with the term genetic assimilation, and does not capture the whole of environmental influence on evolution. So it is one more term we don’t need in the vexed terminology of ecoevodevo. We instead need greater clarification of existing terminologies like genetic assimilation and accommodation.

Another important idea that the next version should address is integrating community ecology with developmental biology. We need to start applying terms such as competition, stability, and resilience to understand the “ecology of development.” A good example of the “ecology of development,” is the competition that can be observed between cells within a tissue for diffusible morphogen gradients, a phenomenon known as “cell competition” (Morata and Ripoll 1975). In the wing imaginal disc in *Drosophila*, for example, those cells that do not uptake sufficient levels of the diffusible morphogen *Dpp* undergo apoptosis (Moreno et al. 2002). At a higher level of biological organization, insect imaginal discs can in turn compete for resources, a phenomenon known as “disc competition” (Nijhout and Wheeler 1996). When one of the four wing discs in a the butterfly species *Precis coenia* is excised during larval development, the other three discs grow larger (Nijhout and Emlen 1998). It is now time to view groups of cells, tissues, and organ systems as ecological communities in order to understand their emergent behavior.

The next version should also include discussion of the “measurement theory” of ecoevodevo, which is at such an early phase that most descriptions remain completely qualitative. Reaction norms and polyphenisms are described only to the extent that visually obvious traits can be measured. Polyphenisms are convenient because they are apparently discrete traits, but what about the countless other phenotypic traits that may be part of ecoevodevo interactions, such as the full 4D morphometrics of organismal shapes, their development, and gene and protein expression patterns, that are simply not measured? The physical interactions within embryos, such as the shape and size of developmental fields and regulatory dynamics (e.g., Newman and Bhat 2007; Lembong et al. 2009), have profound epigenetic affects on phenotypic development, yet have still to be included into the broader research perspective of ecoevodevo, or even pure developmental biology for that matter. These, and certainly more, issues are surely to be topics of future versions.

Finally, we think that in the context of a broader theme of the evolution of evolutionary biology, this book fits nicely into the historical stream of rapids and eddies as something like version “4.1beta,” with the four series as the union of ecology, evolution, and development (after Darwinian Evolution [v1], the Modern Synthesis [v2], and Evolutionary Developmental Biology [v3]). We think Mary-Jane West Eberhard’s (2003) book *Developmental Plasticity and Evolution* would serve as v4.0, as she has recently attempted to bring the importance of the environment and developmental plasticity back into the mainstream of evolutionary theory. Gilbert and Epel’s book will no doubt become an important part of this developing evolutionary synthesis, and should be on the bookshelf of every evolutionary and developmental biologist.

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