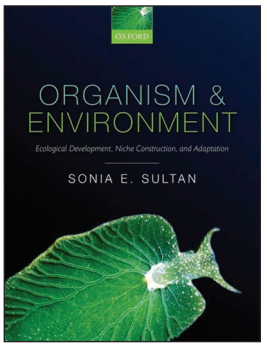
A Unified View of Development: Making Evo-Devo Operational

Organism and Environment: Ecological Development, Niche Construction, and Adaptation. Sonia E. Sultan. Oxford University Press, 2015. 224 pp., illus. $125.00 (ISBN: 9780199587070 cloth).

It is now commonly understood that genes alone do not determine phenotypes and that it is the context dependence of gene expression—interaction between the genome and the environment (biotic and abiotic)—that determines the pattern of development across the tree of life. Sonia Sultan, professor of biology and professor of environmental studies at Wesleyan University, has written a magnificent book laying out the intellectual scope for the study of the interaction between organism and environment and for using the norm of reaction as the fundamental tool to provide a unified view of development. That is, the norm of reaction provides a unified approach for the study of questions at the intersection of ecology and development (eco-devo).

Her starting point is the recognition that phenotypic expression is not determined solely by the DNA sequence but also by the regulatory processes that emerge from the interaction between genetic instructions and the environment. That is, DNA sequences are better viewed not as a blueprint for the phenotype but rather as an information-management system. Therefore, the environment becomes a source of regulatory information rather than a template on which DNA acts. The phenotype is the result of the genotypic program responding to environmental cues, and the phenotype becomes context dependent. My own group has approached salmonid life histories from this viewpoint, seeing patterns of smolt metamorphosis and maturation emerge as the result of a genetic program linked to environmental cues (e.g., Thorpe et al. 1998, Satterthwaite et al. 2009).

Sultan argues that the norm of reaction is the natural tool to use to operationalize these ideas. The *norm of reaction* is the range of phenotypes produced by a genotype across a given range of environmental conditions. In this sense, the norm of reaction replaces separate developmental categories, such as canalized (Waddington 1957) versus plastic traits. Sultan sets the tone of the book early on: "As a general rule, it may be most useful to consider norms of reaction in any particular case as the evolutionary result of natural selection on available patterns of phenotypic expression." She then goes on to illustrate this idea in depth and breadth.



She shows that using the norm of reaction allows new ways of framing questions about ecological and evolutionary diversity, as well as clarifying various common ideas. One point I would have liked emphasized more, especially for ectotherms, is that although it is more work, norms of reaction should involve studies in more than two environments. When only two environments are examined, we are forced to think in a linear manner, but biology is fundamentally nonlinear.

Using this approach, Sultan notes that the niche is really a joint property of the organism and its environment. Furthermore, organisms shape their environments (therefore the phrase "niche construction" or "environmental engineers"; Odling-Smee et al. 2003) and consequently modify their own experienced conditions.

DNA sequences alone do not provide sufficient instruction for the development of the organism. Furthermore, *epigenetic effects*—biochemical mechanisms (e.g., methylation and histone modifications) that shape gene expression in the absence of any change in DNA sequences—often change the expression of the phenotype. We now understand how environmentally induced epigenetic effects can shape the activity of genes, and Sultan gives a wide variety of examples for this phenomenon that go from the environmental change (e.g., pond drying) through the life-history event (e.g., early metamorphosis in resident tadpoles) to the mechanism.

Case studies are the way we make theoretical ideas concrete for readers. In my own books (e.g., Mangel and Clark 1988, Clark and Mangel 2000), I have done a few case studies in great detail, and Sultan has inspired me for the book that I am now writing: I will have more case studies but not in such great detail, leading the reader to a point where it is possible to begin one's own modeling of the phenomenon. In her book, we find lots of tantalizing case studies, and there is something for everyone who has a favorite species, including pond drying and amphibian metamorphosis, herbivory (and the activation of the jasmonic acid pathway), the response of plants to nutrient-poor soil, and the adaptive remodeling of fish gills in response to low oxygen conditions. As one would expect, some of these case studies include maternal effects.

Organisms live in communities that are part of the biotic, so one must consider the community-level consequences of habitat construction and eco-devo responses, which Sultan does. Parasitic systems (e.g., a plant, its herbivore, and a parasitoid of the herbivore) are wonderful tritrophic case studies for this situation.

We can therefore view the phenotype as the response of the genetic program to the maternal and offspring environment, both of which may create epigenetic cues. When norms of reaction are not parallel, we describe the phenomenon as *gene by environment* (GxE interaction), and understanding how the norm of reaction evolves is surely one of the most exciting future avenues of research; Sultan lays out the current situation, challenges, and opportunities clearly and precisely.

The book closes with a discussion of topics for future research, such as how we characterize phenotypic expression, the development of hypotheses about adaptive diversity using the norm of reaction, and incorporating niche construction into ecological and evolutionary research. There is a much-too-short section on practical applications in environmental (e.g., testing agrochemicals, with implication for the evolution of resistance; e.g., Gardner et al. 1998) and biomedical (e.g., evolutionary medicine; Gluckman et al. 2009) research. Here, I would have liked more on how the unified view of development fits squarely into Pasteur's Quadrant (Stokes 1997), in which the search for fundamental understanding is motivated by an important applied problem. Pasteur would have liked this book.

In conclusion, Sonia Sultan has written a masterful book about evolution and development, grounded in the ecology and environment of the organism, using the norm of reaction to operationalize the study of evo-devo. All of the important major topics are covered in a thoughtful and well-referenced manner, making this book ideal for graduate students getting into the subject and senior workers wanting a thorough overview.

References cited

Clark CW, Mangel M. 2000. Dynamic State Variable Models in Ecology: Methods and Applications. Oxford University Press.

Gardner S, Gressel J, Mangel M. 1998. A revolving dose strategy to delay the evolution of both quantitative vs. major monogene resistances to pesticides and drugs. International Journal of Pest Management 44: 161–180.

Gluckman P, Beedle A, Hanson M. 2009. Principles of Evolutionary Medicine. Oxford University Press.

Mangel M. 2009. Steelhead life history on California's Central Coast: Insights from a state-dependent model. Transactions of the American Fisheries Society 132: 532–548.

Mangel M, Clark CW. 1988. Dynamic Modeling in Behavioral Ecology. Princeton University Press.

Odling-Smee FJ, Laland KN, Feldman MW. 2003. Niche Construction: The Neglected Process in Evolution. Princeton University Press.

Satterthwaite WH, Beakes MP, Collins E, Swank DR, Merz JE, Titus RG, Sogard SM, Stokes D. 1997. Pasteur's Quadrant: Basic Science and Technological Innovation. Brookings Institution Press.

Thorpe JE, Mangel M, Metcalfe NB, Huntingford FA. 1997. Modelling the proximate basis of life history variation, with application to Atlantic salmon, *Salmo salar* L. Evolutionary Ecology 121: 581–600.

Waddington CH. 1957. The Strategy of Genes: A Discussion of Some Aspects of Theoretical Biology. Routledge.

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