

BOOK REVIEW

The pleasures of theory in developmental biology

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Towards a Theory of Development, edited by Alessandro Minelli and Thomas Pradeu, 2014. Oxford University Press, Oxford and New York, 304 pp. ISBN 9780199671427.

Hull (1974) lamented that “[developmental] generalizations have in the past appeared to be merely descriptive both because they were formulated largely on the basis of observation and because they were not derivable in most instances from any well-formulated body of laws... Some headway is being made in working out actual mechanisms in developmental embryology, but progress is proving to be slow and painful” (p. 76). Just 40 years later, thinking about generalities in developmental biology is anything but painful. Alessandro Minelli and Thomas Pradeu’s new edited volume, *Towards a Theory of Development*, shows that the issue is one of the conceptually and empirically juiciest in current biology, and showcases some of the most challenging and expansive visions available of our field. The book is organized in 17 contributed chapters, all of which are inspired by some aspect of the presence or absence of theory in developmental biology. The diversity of perspectives in this book paints a panorama that will be of compelling interest for a maximally broad spectrum of readers. Developmental biologists, interested in the themes overarching all of developmental biology; philosophers of science, interested in the perennially fascinating issue of what a theory is; evo-devotees, in their broadest conception; and the great mass of evolutionary biologists driven by synthetic notions where selection has primacy, will all find challenging material of fundamental interest in each chapter. Summarized in Richard Burian’s elegant Foreword, there is no consensus on whether there is a theory of development, what it would look like, or whether developmental biology even needs one. The editors and authors have done a superb job of depicting the diversity of resulting views.

Even in their diversity, some clear common themes emerge across the different chapters. Open most biological journals and you will find language of genes causing phenotypes. In Minelli and Pradeu’s volume, not a single chapter would be at home in

this traditional gene-centric world. Whether it is thought of in terms of attractors in dynamical systems, networks, or self-organization, essentially all chapters see the most profitable way of studying development as from the point of view of the interaction of multiple elements. On this view, the apparent extraordinary predictability of development is not the reflection of causally autonomous genetic directors giving instruction toward a foreseen endpoint, and it will be hard to read this volume and come through with gene-centrism unscathed. With this in mind, I will be selecting readings from the book for my graduate evolutionary biology class. The implications of viewing DNA as a vital but not sufficient participant in developmental processes is perhaps most accessibly crystallized in Gilbert and Bard’s excellent chapter, for example, “The fertilized egg inherits DNA; it does not inherit ‘genes’. Genes and gene products are constructed anew in each cell in the developing embryo by the relationships between DNA, transcription factors, and RNA-splicing factors. Only certain regions of the DNA are constructed into genes, and different regions of the genome can be genes in different cell types.” (Gilbert and Bard p. 130). This broad consensus “systems” view is contrasted by the diversity of approaches to “theory.”

As to the question of theory in developmental biology, it is here where the volume reveals the highest diversity. Philosophy of science was founded in the early 20th century on the notion that science is driven by theories consisting of sets of formal expressions from which flowed predictions to be tested. This view does not fit most real science, though, and there has been continuing controversy over what the role of theory should be or what a theory even is. In *Towards a Theory of Development*, Laplane is perhaps the one that takes on the bull/elephant-in-the-room of ‘what is a theory?’ most directly, first defining a particular view of theory and using cancer stem cell models as an example. Most authors who argue that developmental biology does have theories relax traditional notions of theory until they fit the formal elements already found in the field. Another take is that developmental biology does not have and does not need Theory in the sense of the traditional philosophical view

of good science (see Love, also Griesemer's take on traditional views of theory). In an age in which many and perhaps most scientific controversies have to do with practice and other extra theoretical considerations (treated well in Love's chapter), this book will be required reading for those philosophers who continue to focus on theory (compare the different perspectives in McMullin 1987; Winsberg 2010; Douglas 2013; Gervais 2013). Non-philosophical readers wanting a compressed introduction to the evolution of notions of theory, from the syntactic to the semantic conceptions and subsequent ideas, will find the book useful as well. Arthur sums up some of the central "theory" questions of the book: "Towards a Theory of Development implies the following: first, that a single theory of development is at least possible; second, that we do not yet have one; third, that it is desirable to seek one; fourth, that we have a consensus on what is meant by 'a theory' in the biological sciences; and finally that we likewise have a consensus on the meaning of 'development', so that we can draw a clear line between developmental and non-developmental biological processes" (p. 144). All questions that can provide a lifetime's worth of work.

The editors lament the lack of chapters on plants, though these are touched on in various chapters (e.g., Minelli, Vervoort). This gap does not seem serious, given that with its general scope this book cannot help but stimulate thinking about development across all living systems. An examination of the "theory" in developmental systems theory (DST; Oyama et al. 2001) would certainly have fit well, though Griesemer's chapter can be seen as largely cognate with this point of view. Coeditor Pradeu has argued in previous work that "DST is a theory about development" (e.g., Barberousse et al. 2010, p. 200; see also Pradeu 2010), but here dispenses with DST by citing a quote from Oyama that DST "isn't really a theory." The reader is left wanting to know more about how DST has passed from being an important theory in Pradeu's thinking to not being one. In addition to these issues, the book provides abundant food for thought in countless other aspects.

One of the most important of these aspects is that the book is rich in conceptual contributions in addition to its exploration of "theory." For example, Morange's chapter contains a very thoughtful treatment of the non-dichotomy between evolution and development (see also Kupiec and Minelli). Along these lines, Moczek paints a brilliant vision for a truly integrative evolutionary biology. With elements for just such a synthesis, Griesemer builds on his idea of "scaffolds" in development, that is, dependable environmental developmental resources (Caporael et al. 2014), to emphasize inheritance as involving material transfer between generations. Minelli builds on his foundational studies (Minelli 2003, 2011a, b, etc.) breaking down adultocentrism, traditional thinking built around the large, temporally more persistent, and visible stages as the biologically significant ones. As part of this exploration, both Minelli and Nyholm and McFall-Ngai challenge the idea of what constitutes an

"individual" in development. For example, if normal development requires the presence of a certain inherited microflora, in what sense can the development of an individual be spoken of? These are just a few examples of the vital issues that this book highlights for all of biology.

In addition to conceptual contributions, the chapters provide multiple empirical and methodological considerations that might contribute to a theory of development. The fascinating chapter by Fusco et al. provides a compact introduction to dynamical systems before exploring how the landscape metaphor (think Waddington's epigenetic ones) directs or hinders developmental research. Kupiec explains how cell differentiation involves stochastic patterns of gene expression in a striking contrast to the usual deterministic models. In his account, what gene is being expressed where and at what time is to a large degree random; selection has favored variants in which random thermodynamic processes are "harnessed" in achieving predictable outcomes. In their searches for theory, many authors concentrated on empirical universals, as in the generic properties of matter of Newman or the properties of reproducers (also Griesemer, Minelli). Vervoort and Minelli take different tacks in the search for developmental commonalities across kingdoms, but both remind us to be wary of false universals, which might be just synapomorphies of large groups, such as the Hox genes of the bilaterians (see also Moczek). Griesemer's chapter is illustrative of the universality of ontogeny because it uses unicellular organisms (malaria parasites) and even viruses as key examples. The reader is left to weigh proposals to focus on apparent instances of convergence to discover universals or throw developmental biology's weight on (taxic) homologies to understand the process of innovation. In conclusion, this book will be essential reading for readers wanting a rich introduction to current broad issues in developmental biology and evo-devo, for philosophers of science in general, and for biologists at large. Exceptional for an edited volume, each chapter in *Towards a Theory of Development* is deeply thoughtful, provoking reflection on some of the most important ideas in current biology. I can think of no higher recommendation.

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