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BOOK REVIEW

Russell Bonduriansky & Troy Day, *Extended heredity*: *a new understanding of inheritance and evolution*, Princeton University Press, 2018, 288 pp, ISBN 9780691157672

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Extended Heredity (EH) has posed a challenge for twentieth and early twenty-first century 'normal' evolutionary biology, but the accumulation of models and experimental evidence for it obliges us to acknowledge its importance. This book, written by Russell Bonduriansky and Troy Day, aims at making space for EH by systematizing its potential for explanation and prediction, given that it "changes the rules governing what can and cannot be transmitted from parents to offspring and how stable the inherited phenotypes are likely to be across generations" (p. 22). Appearing as the first encyclopedic essay on EH and evolution since Jablonka and Lamb's *Evolution in Four Dimensions* (2005, Cambridge: MIT Press), this volume offers a particularly valuable state of the art of the literature on this important topic.

Its main claims can be grouped into two principal objectives. The first one is to make a plea for the notion of EH itself, justified by the fact that "there is more to heredity than DNA sequences (genes)" (p. ix). In this book, heredity is presented as a dual system of genetic and a non-genetic inheritance, described as two complementary channels of information transmission. The former concerns "the transmission of DNA sequences" and the latter encompasses "the transmission of other factors (epigenetic, cytoplasmic, structural, somatic, symbiotic, environmental, behavioral) from parents to offspring at conception or during subsequent development" (pp. 17–18). The second main objective of the book is to integrate non-genetic

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inheritance into evolutionary biology and to develop an inclusive approach that "can provide us with new insights into how evolution works" (p. ix). The volume is structured in ten chapters, half of which is dedicated to each of the two main objectives pursued by the authors.

Chapters 1 and 2 show the theoretical limits of an exclusively genetic model of biological heredity, based on the need of two kinds of principles to (re)construct living systems. Going back to the reproduction of a single cell, which comprises both DNA and cytoplasm perpetuation, they argue that the basic elements of the reproductive process imply an "inherent duality in the nature of heredity" (p. 8). These chapters examine the example of Craig Venter's artificial cells to establish that DNA continuity is not sufficient to create an organism that resembles its parents. Chapter 3 elaborates a historical rationalization of how heredity, starting with Galton, came to be conceived as relying on a single channel. Chapters 4 and 5 discuss various examples of diverse forms of non-genetic inheritance, including different kinds of epigenetic maintenance, the transmission of cytoplasm structures, seminal vesicles, diet, parental care, traditions, microorganisms, organelles, structural templates, and protein conformation. Of special interest among those examples are parental effects, which are described as changes in parental bodies that are induced by environment, age or experiences such as stress, and that can affect offspring development.

Chapters 6 and 7 argue that the Price equation provides a theoretical framework that allows studying general selection processes in terms of adaptive changes of frequencies of any kind of genetic and/or non-genetic inherited traits, according to their fitness values and variable fidelities in transmission. After didactically introducing this equation and explaining how it can integrate non-genetic inheritance in evolutionary studies, the authors show that inclusion of EH leads to predictions that deviate from "those of conventional population-genetics analyses" (p. 128). Chapter 8 analyses and responds to criticisms frequently addressed to EH, notably the claim that non-genetic inheritance cannot have any effect on evolutionary processes because it is limited and unstable, and the claim that it cannot drive adaptive evolution. Chapter 9 shows how EH can provide new insights into a series of evolutionary problems ranging from the micro to the macro evolutionary scale, such as the coevolution of host and symbionts, and the evolution of aging. Finally, Chapter 10 raises awareness about how non-genetic inheritance impacts health and society, drawing attention to the effects of parental exposures and behaviours on offspring (alcohol, drug, and food intake). It shows how the Developmental Origins of Health and Disease (DOHaD) research program highlights that "many aspects of our physical and mental health as adults are shaped by the environment that we experienced inside the womb or in early childhood" (p. 201).

The book presents an argument that is systematic and well sustained, readable for lay people and informative for scientists and philosophers. Some of its original contributions deserve to be specifically emphasized. Of note is the fact that it sheds light on the distinct roles of genetic and non-genetic inheritance in evolutionary processes, and that it consequently characterizes different paces of evolutionary change. This theoretical distinction, which can be found in earlier studies (Mesoudi A., Blanchet S., Charmantier A., Danchin E., Fogarty L., Jabolonka E., Laland K. N., Morgan T. J. H., Müller G. B., Odling-Smee J., Pujol B., 2013, Is Non-Genetic

Inheritance Just a Proximate Mechanism? A Corroboration of the Extended Evolutionary Synthesis. *Biological Theory* 7: 189–195), is clearly articulated by Bonduriansky and Day. The authors underline common points and differences between genetic and non-genetic variation: both kinds can be random, but non-genetic variation can be environmentally induced, as well as both environmentally induced and directed (advantageous) (p. 148). Another illuminating contribution of this book is the analysis of non-genetic inheritance as neither 'Lamarckian inheritance' nor 'genetic encoding'. The authors develop a helpful analysis of different meanings of 'soft inheritance' and specify how this controversial concept developed through time. Bonduriansky and Day's endeavour to include medical and social concerns related to EH in a book primarily focused on evolutionary biology should also be hailed. Their hints about the importance of understanding EH—and not only epigenetics—for crucial health and ecological issues (antibiotic resistance, genetic engineering via CRISPR-Cas technologies, recurrent diseases, global warming, etc.) is particularly appreciated. Finally, the book states that the integration of non-genetic inheritance in evolutionary biology does not dehorn the 'Modern Synthesis' theoretical framework (p. xii, p. 128). In doing so, it advocates a view that departs from the one announcing a revolutionary change in biological thinking (Jablonka and Lamb 2005), or from those arguing, more cautiously, that as EH modifies some tenets of Neo-Darwinism (e.g. gradualism), it therefore motivates the elaboration of an Extended Evolutionary Synthesis (Laland K. N., Uller T., Feldman M. W., Sterelny K., Müller G. B., Moczek M., Jablonka E., Odling-Smee J., 2015, The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B* 282: 1019).

Many aspects of the volume will require further elaboration as they rely on very recent findings that have not yet been fully internalized by the broader scientific community. First, we need to raise some conceptual concerns about the very notion of heredity summoned by the authors, given that to Bonduriansky and Day it "makes sense to treat all instances of parental influence on the features of descendants under the rubric of heredity" (p. 18). While this broad view leaves room to include more than genes in heredity, it is so wide that it does not allow distinguishing heredity from other kinds of transmission and may even invite to admit, in a quite counter-intuitive way, that flu transmission could count as heredity. One important philosophical question is therefore whether such a broad concept is useful for biological theory. A second concern is that Bonduriansky and Day regard both genetic and non-genetic factors as information carriers. This theoretical choice is in line with a tradition that associates hereditary determinants to informational messages. However, this informational framework is never explicitly justified (although the links between Price and Shannon, the father of information theory, are mentioned at some point, p. 103). More precisely, the authors do not clearly specify the concept of information upon which they rely. This omission contrasts with other contributions that have analyzed heredity as the transmission of a well-defined genetic and non-genetic biological information (Jablonka, E., 2002, Information: Its interpretation, its inheritance and its sharing. *Philosophy of Science* 69: 578–605; Shea, N., 2007, Representation in the genome, and in other developmental systems. *Biology & Philosophy* 22: 313–331).

Moreover, while Jablonka and Lamb (2005) conceptualized four systems of inheritance related to four identified mechanisms of transmission, here the authors propose to think about heredity as a dual—genetic and non-genetic—system. This choice is justified by the fact that, according to them, all non-genetic inheritance systems have common features that make them distinct from genetic inheritance (p. 103). In the wake of their work, future studies will need to better characterize the different roles of these two sub-systems in evolution, the dynamics with which they are associated, and their interplays. However—and this is a crucial point—the success of the authors' proposal will depend on how a plurality of non-genetic factors and mechanisms (epigenetic, behavioural, etc.) can be theoretically treated as a uniform kind, i.e. as 'non-genetic inheritance'.

Finally, while Bonduriansky and Day agree that extended heredity expands the scope of the Modern Synthesis, as "it seems disingenuous to claim that the Modern Synthesis already accounts for it" (p. 128), they also argue that it is not challenging for the received framework. Innovative as this work is, it is actually tied to orthodox views of natural selection as a provider of design and adaptation, and it surprisingly pays little attention to organizational and material principles operating among living entities. In other words, it remains committed to a statistical and selectionist view of evolution. In contrast to the authors' stance, accepting EH often seems to lead to considerations about a 'paradigm shift' in evolutionary biology; or, at least, it encourages the adoption of a more developmental view of evolution.

To conclude, this noteworthy book vindicates the important role of EH in evolution, but it also—rather unexpectedly—argues that this role is fully compatible with the existing theoretical framework of mainstream evolutionary biology. Such a position will certainly trigger vivid and passionate discussions among biologists and philosophers of biology in the years to come.