

Book review of Bonduriansky; R. & Day, T. 2018. *Extending heredity to better understand evolution*, Princeton University Press, 288 pages, ISBN: 9780691157672, \$29.95

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According to the Oxford Dictionary, heredity is ‘the passing on of physical or mental characteristics genetically from one generation to another’ (<https://oxforddictionaries.com>). My biological dictionary agrees (Lawrence 2008). In this fascinating book, evolutionary biologists Russell Bonduriansky and Troy Day (B&D from here on) argue that we should abandon this genetic definition of heredity, and instead embrace a heredity concept that includes all the mechanisms by which parents influence the development of their offspring.

Does this not sound immensely sensible? After all, parents do not just dump genomes on the ground and hope that something will happen—they always produce a highly organized egg, may sometimes build a nest, or interact behaviorally with their offspring to enable them to acquire the skills they need in life. Yet, evolutionary biology is built on transmission genetics, assuming that everything else that parents do to their offspring can be considered ‘fully encoded in the genome’ (p.12). B&D reveal that this gene-centric perspective on heredity was never particularly well grounded or supported, and they draw on the contemporary literature to show that extra-genetic inheritance is not just an empirical fact, but that it also is predicted theoretically to affect what happens in evolution.

B&D’s perspective is a generalization of what is known as ‘dual-inheritance theory’, which is familiar from models of gene-culture co-evolution (Boyd and Richerson 1985). Genetic and extra-genetic inheritances are considered separate, but potentially interacting, channels that transmit ‘distinct types of information’ (p.18). While this is a sensible way to handle heredity, the rationale for the distinction is largely left to the

reader’s intuition. In particular, one may wonder what it actually means to ‘transmit information’, and if all mechanisms by which parents influence their offspring also are ‘channels of transmission of information’ (Shea et al. 2011)?

Be that as it may, B&D demonstrate the power of dual inheritance modeling by establishing that extra-genetic inheritance influences evolution in both the short- and long-term. Their starting point is the Price Equation, a general mathematical formulation of change in the average trait value within any population of entities (Gardner 2008). While this may sound bold for a book aimed at a general biology readership, the treatment is light-hearted, explanations are intuitive rather than technical, and there is ample use of simple graphics instead of formulas. The result is an excellent introduction to how and why extra-genetic inheritance influences phenotypic and genetic evolution. Here, as well as throughout the book, the extensive use of informative footnotes makes it easy for the curious reader to figure out where to go for more.

One refreshing aspect of the book is the no-nonsense, down to earth, perspective on the relationship between science and society. B&D point out that, similarly to how politics fueled Lysenkoism in the Soviet Union, racist views in Western Europe and North America promoted the view that inheritance is synonymous with genetic transmission. Another extraordinary story is how the widely known effects of maternal alcoholism on fetal development were purged from the collective memory, because it did not fit the genetic view of heredity, and later had to be rediscovered. These are reminders that science is a social enterprise, and that there is scientific value in reflecting on the core concepts of our disciplines.

B&D are exemplary in their efforts to give due attention to different views. The result is a balanced account of the controversy surrounding extra-genetic inheritance. B&D are sensitive to how deeply entrenched—and useful—the gene-centric view is, while not shying away from taking stands that, at least until recently, would have made many of their colleagues uncomfortable. One contentious issue is how extra-genetic inheritance contributes to evolutionary innovation. Some authors (e.g., Gerhart and Kirschner 2007) have emphasized that organisms can maintain ‘better-than-random’ function in the face of genetic and environmental perturbation because developmental processes make use of, for example, exploration and positive feedback. B&D ask how such ‘facilitated’ or ‘directed’ variation squares with extra-genetic inheritance. Whereas behavioral innovation and social learning may allow adaptive features to arise and spread in the absence of fitness differences between individuals, B&D rightfully point out that this hardly seems like a sensible standpoint for organic evolution more generally. They further make the point that if organisms are to respond appropriately, novel environments cannot be truly novel—a history of evolution by natural selection is necessary to put the appropriate mechanisms of plasticity and extra-genetic inheritance in place. In other words, B&D suggest that instances of adaptation through facilitated variation are explained by more, not less, natural selection. In this skepticism over the explanatory role of development in adaptive evolution, B&D appear to part ways with some fellow advocates of an extended view of heredity (e.g., Jablonka and Lamb 2014; Laland et al. 2015). However, one suspects that this is, at least in part, because B&D interpret facilitated variation to be the claim that most variants are beneficial, and that they take a very strict view on what it means for an environment to be ‘evolutionarily novel’ (pp. 147–154). A different reading of the literature is that evolution by natural selection can produce developmental systems that will tend to vary along dimensions that maintain functional correlations between traits, even if there has been no direct selection for the capacity to vary (Uller et al. 2018). Such developmental biases are in fact found in purely genetic models (e.g., Watson et al. 2014), which implies that their evolution do not rely on extra-genetic inheritance (although, as with within-generation plasticity, it may make them more important).

While this may mean that B&D agree with more people than it seems (making them even more radical in the eyes of others), some readers will undoubtedly take issue with their quite optimistic reading of the empirical evidence for, for example, adaptive divergence mediated by epigenetic inheritance. The appropriate caveats are there if you look for them, however, and it is difficult to not become smitten by B&D’s enthusiasm when they share their wealth of ideas ready to be tested. If you are looking for inspiration and topics for your graduate studies, this is a great place to start.

The existing literature on extra-genetic inheritance and evolution is both extensive and insightful (recent books include (Muller-Wille and Rheinberger 2011; Griffiths and Stotz 2013; Jablonka and Lamb 2014). What sets B&D apart from the existing literature is that their account is so exceptionally well-tuned toward practicing biologists. While B&D do not shy away from conceptual issues, and devote substantial attention to science history, their explanation for why extra-genetic inheritance matters to evolution follow from basic principles that should be familiar to all biologists. There really is no need to panic about extended heredity. The result is a book that should be highly entertaining, illuminating, and inspiring to undergraduate or postgraduate students, as well as to researchers active in any field of biology where heredity matters.

Students can find it surprising to learn that there were once heated debates about the reality of natural selection or neutral genetic variation, or that the evolutionary significance of regulatory evolution was ever in doubt. Such changes in attitudes are good arguments for reflecting on the history of our field and its core concepts. I suspect that future biology students will find some of the controversy surrounding extra-genetic inheritance equally puzzling. B&D have done evolutionary biologists a great service by writing this book, and it deserves to be widely read. May we predict that the dictionary entry for “heredity” will change in the near future?

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