The practice of theorizing: Homage to Richard C. Lewontin (1929-2021)

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I met Richard C. Lewontin in 2004. I had been invited to teach at the Dibner Summer School in Woods Hole, Mass., organized by Mike Dietrich, Jim Griesemer, and Jane Meieschein. Some of today's most recognized scholars in our field, like Matt Haber, Roberta Millstein, and Vivette García were still graduate students attending the workshop. The most challenging session to me was a roundtable on the neutral theory of molecular evolution (NTME). I took the stage nervously, as Mike and I shared the stage with two of our most admired writers on the subject: Lewontin and William Provine. I reiterated my critique to the interpretation that the NTME was but a theoretical extension of the classical school of population genetics, a claim defended both by Dick and Will—as they liked to be called. This idea, indeed, had been baptized by Mike as "Lewontin's historical thesis" (Dietrich 1994), and formally introduced in Dick's iconic textbook, *The Genetic Basis of Evolutionary Chang*e (1974).

Enthusiastically received and reviewed at the time of its publication, this book soon became a landmark revolutionary text. In what probably is the most critically praising, and bright book review of the time, Joe Felsenstein wrote:

> In its breadth, accuracy, and profundity the book will be illuminating to population biologists and geneticists. No graduate student in these areas should be allowed to receive a degree before reading it […]. Lewontin has in the past expressed disappointment in texts which did not integrate theory with observation and experiment. He has not done so in this book, but has taken the opposite tack. He concentrates on the biological issues and the evidence, citing mathematical theory only when necessary.

Felsenstein compliments targeted the book's clarity and "raising the [most important] issues", as well on Lewontin's framing of those issues in the philosophy of science, rather than mathematical theory. Even so, Felsen-

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stein did no save his observations on the shortcomings of the book and the weaknesses of some of the author's positions, to which I will return.

The book's crucial contribution, by all means, was the author's tackle of the *paradox of variation*. The electrophoretic revolution, started a decade before by Lewontin and many others, had revealed the enormous amount of genetic variation at the molecular level (Hubby and Lewontin 1966, Dietrich 1994). Thanks to a crucial collaboration with biochemist Jack L. Hubby, his colleague at the University of Chicago, Lewontin's team was among the first to provide fresh data that promised to "revolutionize evolutionary biology [1]." Until then, he claimed, there had been "not enough empirical data to feed the theoretical machine." As we know, however, the amount of genetic variation he and Hubby found in *Drosophila pseudoobscura* populations blew out the theoretical models: electrophoresis experiments had provided too much variation to account for, in terms of natural selection models, and thus the paradox. First, there was not much empirical evidence; then, there was too much.

By then, the neutral theory of molecular evolution had been published, the dual result of molecular evolutionists and population geneticists Jack King and Thomas Jukes (1969), and Motoo Kimura (1968) and Tomoko Ohta (1969, 1973). Bringing back the debate between the classical and balance schools of population genetics, Lewontin famously described the NTME as a "neoclassical" theory, the heir of a connoted lineage of biologists including Hermann Muller, J.B. S. Haldane, and James F. Crow. This was Dietrich's "Lewontin's historical thesis" (1994). To Lewontin—closer to the balance view—the solution offered by the neutralists was not satisfactory enough. He proceeded—in the book and in his later research—to revise all the available evidence, including total heterozygosity, geographic variation, rated of protein evolution, selection observed in natural populations, and many others.

Though Felsenstein's review found the results of Lewontin's analysis *discouraging*, and "his molecular evolution arguments unconvincing," he did not fail to notice the difficulty of the endeavor and the fact that the 1974 textbook raised the crucial issues for future debates—not the least, of political and philosophical character [2].

I also found Lewontin's account unconvincing—and almost disappointing—but for very different reasons. In a nutshell, he had come with an oversimplistic take on the rise of the NTME, giving primacy to theoretical over experimental considerations and practices. In framing the neutral theory as the result of a mathematical theoretical debate, Lewontin had failed himself and missed the revolutionary impact of the new molecular techniques, problems, and approaches, in the understanding of evolutionary mechanisms and patterns; a revolution that had started at the end of the 1950s, before his famous experiments (Suárez-Díaz 1996; Suárez-Díaz and Barahona 1996). In the context within the *practical turn* in the history and philosophy of science of the 1980s and 1990s, along with the rising interest of professional historians on post-WWII life sciences, Lewontin's interpretation provided ample grounds to critique. A couple of historiographical comments will help me to illustrate the relevance of the debate, and to illuminate Lewontin's personality and intellectual temperament.

The controversy between the classical and balance schools of population genetics (dubbed as such by Theodosius Dobzhansky in 1955) concerned the amount of heterocigocity in natural populations. In the 1950s, this issue had serious policy and political implications, amid widespread interest about the atomic fallout and radiation induced mutations in human populations around the world [3]. The discovery of (unexpected) huge amounts of genetic variation by Lewontin and Hubby in *Drosophila*, and by Harry Harris in human populations, made possible by the use of zone gel electrophoresis, was highly problematic for contemporary prevalent theories which had established limits for variation, in the concept of mutation—or genetic load [4].

In writing their histories, scientists not only provide an interested interpretation of their own role in history, but a legitimation (either conscious or unconscious) of what they consider to be the relevant factors and aspects to stick for future comprehensions of their practice (Abir-Am 1985), Lewontin, inadvertently as it happened, provided a history of the NTME as centered on mathematical population genetics, with experimental practices and techniques subordinated to their once traditional role of providers of evidence for theories to be tested. Indeed, "Lewontin's *Genetic Basis of Evolutionary Change* has been jokingly called '101 Ways to Save the Classical and Balance Positions'. In many ways, Lewontin [was] trying to save this controversy, the question of the nature of genetic variation is the problem that has driven his career" (Dietrich 1994, p. 57).

Moreover, in the 1990s, in tune with the contemporary developments in the history of science, and influenced by sociological and philosophical developments, theories no longer concentrated research interests within students of science. Their place was taken by middle-range theories and models, the diversity of experimental practices and the material culture of the laboratory, as well as the collection and classificatory practices more fit with expeditions, cabinets and museums. The diversity of the *sciences* had been recently captured in the radical idea of its *heterogeneity*, that is, the recognition that science was made up of incommensurable non-reducible practices. Dietrich's critical account of Lewontin´s work was followed by my own account, which put a heavier weight on the heterogeinity of experimental, comparative, and theoretical sources that gave way to the NTME (Suárez-Díaz 1996; Suárez-Díaz 2009).

It is telling of Lewontin's intellectual stature that this vision of empirical and experimental findings as autonomous to theoretical debates was promptly recognized by him as closer to his philosophical sympathies, along with his embracement to the complexity of biological explanations. Moreover, these visions move along with his personal trajectory in developing some of evolutionary biology's most transformative experiments. (See Grodwohl 2017, on Lewontin's experimental contributions after 1966, which are traditional ignored by philosophers of science.)

In May 2004, after the vivid debate at the Woods Hole Marine Laboratory's roundtable, Dick approached me. He generously accepted the interpretation that both Mike and I had developed a decade before, in which experimentally oriented fields and traditions played a major role in explaining the origins of the NTME [5]. It is, to this date, one of the most precious memories in my academic career.

NOTES

1 https://authors.library.caltech.edu/5456/1/hrst.mit.edu/hrs/evolution/public/techniques/hubbylewontin.html
2 Felsenstein critique included a thorough review of Lewontin's mixed "interactionist" and bean-bag view of genetics and the ambiguity resulting from this mix, but most important for this article, Felsenstein rebelled against the over-simplistic identification of the classical school as "conservative" (in political terms) and the balance school as "progressive" or liberal. Felsenstein's pointed arguments deserve careful attention in order to provide a more balanced view of Lewontin's personal and political preferences shaping his biological theories.
3 The growing secondary literature on atomic fallout and mutation includes the work of John Beatty (1987, 1993), Diane Paul (1987), Susan Lindee (1992), Soraya De Chadarevian (2006), Karen Rader (2006), Jacob D. Hamblin (2007), Angela Creager (2013), Mateos and Suárez-Díaz (2015) to name a few. On the Neutral Theory of Molecular Evolution, see also Provine (1990) and Crow (2008).
4 This was originally developed by Muller and Haldane; see Paul (1987). There is also a contested story about a third team contributing with relevant data at the University of Texas, who published on the same subject; see Suárez and Barahona (1996) for diverging accounts.
5 Jim Crow also acknowledged our interpretation (November 16th 1996, personal communication).

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