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The evolution of phenotypic plasticity: Genealogy of a debate in genetics

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ABSTRACT

The paper describes the context and the origin of a particular debate that concerns the evolution of phenotypic plasticity. In 1965, British biologist A. D. Bradshaw proposed a widely cited model intended to explain the evolution of norms of reaction, based on his studies of plant populations. Bradshaw's model went beyond the notion of the "adaptive norm of reaction" discussed before him by Dobzhansky and Schmalhausen by suggesting that "plasticity"—the ability of a phenotype to be modified by the environment—should be genetically determined. To prove Bradshaw's hypothesis, it became necessary for some authors to identify the pressures exerted by natural selection on phenotypic plasticity in particular traits, and thus to model its evolution. In this paper, I contrast two different views, based on quantitative genetic models, proposed in the mid-1980s: Russell Lande and Sara Via's conception of phenotypic plasticity, which assumes that the evolution of plasticity is linked to the evolution of the plastic trait itself, and Samuel Scheiner and Richard Lyman's view, which assumes that the evolution of plasticity is independent from the evolution of the trait. I show how the origin of this specific debate, and different assumptions about the evolution of phenotypic plasticity, depended on Bradshaw's definition of plasticity and the context of quantitative genetics.

1. Introduction

Since the end of 1970s, some biologists (e.g., Coleman, 1980; Gould, 1977; Hamburger, 1980; Lauder, 1982; Wallace, 1986) have started to question the adequacy of the genocentric conception of the Modern Synthesis—which brought together Mendelian genetics, and evolution through population genetics (Huxley, Pigliucci, & Müller, 1942)—in explaining the evolution of phenotypic traits, suggesting that developmental issues should also be included in the synthesis (Gilbert, Opitz, & Raff, 1996). More recently, some authors have stressed that phenotypic plasticity should be seen as one important element in an extended synthesis of evolution including these developmental issues (see, Pigliucci & Müller, 2010). The present paper comes back on a precise controversy in the history of phenotypic plasticity in biology, which is a debate in the 1980s between two representative views (among others)—these of Via & Lande and Scheiner & Lyman—concerning the evolution of phenotypic plasticity. The aim of the paper is to lay the groundwork for a genealogy of phenotypic plasticity and to show that the notion was defined and discussed since a long time before the 2010s, and that it adopted a specific meaning in the emerging field of quantitative genetics. Through a clarification of the origins and the basis of a specific debate concerning the evolution of phenotypic plasticity that occurred in the 1980s, the purpose here is to enlighten some of the implicit ideas, which used to be associated with the notion of plasticity at that time, and to show the reasons why it remains difficult to associate the notion with something different from the Modern Synthesis.

In 1965, Anthony D. Bradshaw (1926–2008) published an article entitled *The Evolutionary Significance of Phenotypic Plasticity in Plants*. In the article, he proposed for the first time a model intended to explain the evolution of norms of reaction mainly based on his

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studies of plant populations, realized during his sabbatical year in California[1] (e.g., Allard & Bradshaw, 1964; Bradshaw, 1959; Jain & Bradshaw, 1966). Bradshaw's article has been widely cited and discussed thereafter. It is considered, by most of the commentators, as one of the founding articles defining the notion of phenotypic plasticity: the ability of a genetically determined phenotype to be modified by the environment (see Pigliucci, 2001; Sarkar, 1999).

Almost twenty years later, in the 1980s, a heated debate erupted between biologists over the possible ways to understand the evolution of phenotypic plasticity, which was precisely the topic of Bradshaw's seminal article. While Bradshaw's purpose was to demonstrate that phenotypic plasticity evolved using a kind of optimality approach before the heyday of optimality studies, Via & Lande and Scheiner & Lyman tried to explicitly model how plasticity evolves using quantitative genetics theory. In the 1980s, quantitative genetics[2]—the branch of population genetics dealing with phenotypes which vary continuously, and that employs the frequencies of trait variation in breeding populations, combined with principles from Mendelian inheritance, in order to analyze inheritance patterns across generations and descendant lines (i.e., their evolution)—was a central discipline in biology, and most of the scientists were looking for models to explain the evolution of phenotypic traits. Consequently, since the protagonists of the debate were active research members in the field, they tried to offer precise models to explain the evolution of phenotypic plasticity. However, their approaches differed. On the one side, biologists Russell Lande and Sara Via wanted to analyze trait evolution in environments with discrete states given a specific genetic architecture. That is essentially expanding existing quantitative genetics models of multiple traits into single trait in multiple environments. And in such a perspective, they concluded that the evolution of plasticity should be seen as a by-product of evolution, assuming that selection would not act directly upon plasticity, which Via did not consider to be a distinct trait with its own genetic etiology. On the other side, Samuel Scheiner and Richard Lyman wanted a tool by which they could model adaptive evolution of reaction norms. And in their perspective, they considered that plasticity had its own genetic basis, independent from the one of the plastic trait, and, therefore, that it had its own model of evolution (Scheiner & Lyman, 1991; Via & Lande, 1985, 1987).

Since both authors refer to Bradshaw's seminal article of 1965, one purpose of the present paper is to analyze in what way Bradshaw's understanding of phenotypic plasticity might have influenced the works of the main protagonists of the debate and so how it might have perpetuated in the current literature. In other words, the purpose is both to understand whether those divergent approaches concerning the evolution of plasticity might have a common ground and whether the differences between them could help to enlighten the current understanding biologists have of phenotypic plasticity. There are two interrelated problems here. The first one concerns their common reference to Bradshaw and the relationship of their models with Bradshaw's view on plasticity. The second one concerns the disagreement, our precise understanding of it, and the potential consequences for the current understanding of phenotypic plasticity in biology. However, in order to answer the second problem—that is to say: what was the disagreement about?—, it seems necessary to provide some main clues concerning the first one—that is to say: what was Bradshaw's influence on the protagonists of the debate? With this being said, I shall then come back to my main goal here and conclude on the reasons why the disagreement seems to have disappeared in the current understanding biologists have of the evolution of phenotypic plasticity. But let us first start with Bradshaw's view on phenotypic plasticity.

2. Bradshaw and the notion of "phenotypic plasticity"

In the article of 1965, British ecologist and geneticist Anthony Bradshaw proposed a model to explain the evolution of what was previously considered as the "shape of reaction norms" and that he will call "plasticity." In the article, Bradshaw pointed out the importance of the environmental effects on organisms: "We are becoming increasingly aware that the individual cannot be considered out of the context of its environment" (Bradshaw, 1965, p. 115). Before him, the "instability" produced by the environment was mostly conceived as a source of perturbation for geneticists (Falconer, 1952). And as Bradshaw claimed: "Any modifications induced by the environment during the course of an experiment are usually considered only an embarrassment" (Bradshaw, 1965, p. 148). Therefore, they mostly tried to eliminate it in their studies.

Another example, which is somehow less expected, is that of Conrad Hall Waddington (1905–1975), who was interested in the issue of "stability" through the process of canalization. His most quoted book *The Strategy of the Genes* (Waddington, 1957) has been often, and justifiably, used by biologists and theorists to argue that he was one of the first evolutionary biologists to make an effort to bring genetics and development together, and, therefore, to pay a specific attention to environment. However, in most other books where he dealt with the question of "stability" (or "canalization"), he did not refer explicitly to the environment. In *Principles of Embryology* (Waddington, 1956), in which he developed and explained the process of "canalization," the term "environment" and its derivatives (e.g., "environmental") appeared only 16 times in a book of 528 pages. In the book *How Animals Develop*, (Waddington, 1962 [1935])[3] the term "environment" and its derivatives appeared only 6 times in a book of 148 pages. Waddington considered the process of canalization as the expression of some robustness to genetic variability and not to *environmental variability*. It appears that Waddington, like many geneticists of his time, mostly depicted—with the notable exception of *The Strategy of the Genes*—the environment, even if influent, as a source of perturbation that should be removed from the analysis of phenogenesis for experimental purposes. He also explicitly considered that environmental effects were minimal during early development of organisms (Waddington, 1962, p. 122). Despite this major rejection of the "unstable" factor, the problem remained, nevertheless, to understand how the individual could maintain some stability in an unstable environment. After World War II, the question became one of the main issues among geneticists (e.g., Dobzhansky & Wallace, 1953; Jinks & Mather, 1955; Kimura, 1955; Lerner, 1954; Levins, 1963; Lewontin, 1957; Mather, 1953; Waddington, 1959).

Unlike most of his colleagues and even though he was a geneticist, Bradshaw did not see the environment as a disruptive force. Far from it, he explicitly incorporated the environment in his genetic analysis (see Fitter, 2010). Therefore, in the article of 1965, Bradshaw was striving to demonstrate: "first, that environmental effects on the phenotype were as important as genetic effects (rather than simply inconvenient error), and second, that these effects were themselves under genetic control and could therefore

[1] For further details on Bradshaw's works, see E. Peirson, this issue.

[2] The field was founded by some of the proponents of the Modern Synthesis, R. A. Fisher, S. Wright and J. B. S. Haldane, and aimed to predict the response to selection given data on the phenotype and relationships of individuals.

[3] When the book was republished in 1962, a new section entitled "gene activity during development" is added.