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The Modern Synthesis and Soft Inheritance

Thomas Dickins and Benjamin Dickins

Thomas E. Dickins

School of Science and Technology

Middlesex University

London, U.K. NW4 4BT

*[t.dickins@mdx.ac.uk](mailto:t.dickins@mdx.ac.uk)*

Benjamin J.A. Dickins

School of Science and Technology

Nottingham Trent University

Nottingham, U.K. NG1 4BU

[*benjamin.dickins@ntu.ac.uk*](mailto:benjamin.dickins@ntu.ac.uk)

**Abstract:**

Evolution is a kind of change. Any system that permits variation, competition and inheritance will be capable of evolving [1]. This is one version of a common abstraction [2] and might be said to capture a General Theory of Evolution. By contrast the Modern Synthesis, from its inception [3,4], has been a Special Theory of Evolution, applying to biological change. It was a marriage of Darwinian and Mendelian views on the origins of phenotypic variation in populations, and the dynamics of change [5,6]. The synthesis was achieved through the development of population level thinking in genetics. The Modern Synthesis conforms to the General Theory, but specifically introduces variation through migration and mutation, and sorts variation through genetic drift and selection. The principal focus of most evolutionary biologists is upon mutation and selection.

In recent years a number of researchers have advocated extending the Modern Synthesis in evolutionary biology [7]. One of the core arguments made in favour of an extension comes from work on soft inheritance systems including transgenerational epigenetic effects, cultural transmission, and niche construction [8]. In this chapter we first detail the Modern Synthesis and its conceptual framework, and then critically evaluate the arguments in favour of an Extended Evolutionary Synthesis.

We will argue that a key aspect of evolutionary thinking is to infer process from outcome and that arguments incorporating soft inheritance into general explanations should be scrutinised carefully. Whilst it is true that the details of inheritance matter and influence evolutionary outcomes, a rigorous approach to a system of inheritance demands that we consider the full range of variation produced and alternative processes responsible for these outcomes. Here the Modern Synthetic emphasis upon natural selection and genetic drift is apt. Selection explains adaptation and not the reverse because, by definition, selection is the only source of discrimination between beneficial and deleterious outcomes. Drift leads to divergence and, by weakening negative selection, to complexity.

We will also explore the role of selection in shaping variation-generating mechanisms [9–11]. One critical means by which this can be achieved is by changing the rate at which variants emerge and we examine the evolution of elevated mutation rates by mutator allele hitchhiking and via bet hedging in response to variable environments. Our chapter will also examine the roles that selection and drift play in the evolution of inheritance systems of varying complexity in different organisms. We attempt to disentangle the origin and maintenance of these systems.

The fundamental claim we make throughout is that the focus upon soft inheritance has led to a conflation of proximate and ultimate causation [12], which has in turn obscured key questions about biological organization and calibration across the lifespan to maximize average lifetime inclusive fitness. More strongly we claim that some theorists have included chance and historical processes within ultimate causation [13,14]. The important thing about chance and history as causes is that they do not explain the particular.

**Keywords:** Soft inheritance; Extended Evolutionary Synthesis; Epigenetic inheritance; Proximate and Ultimate causation

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