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Extending and expanding the Darwinian synthesis: the role of complex systems dynamics

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ABSTRACT

Darwinism is defined here as an evolving research tradition based upon the concepts of natural selection acting upon heritable variation articulated via background assumptions about systems dynamics. Darwin's theory of evolution was developed within a context of the background assumptions of Newtonian systems dynamics. The Modern Evolutionary Synthesis, or *neo*-Darwinism, successfully joined Darwinian selection and Mendelian genetics by developing population genetics informed by background assumptions of Boltzmannian systems dynamics. Currently the Darwinian Research Tradition is changing as it incorporates new information and ideas from molecular biology, paleontology, developmental biology, and systems ecology. This putative expanded and extended synthesis is most perspicuously deployed using background assumptions from complex systems dynamics. Such attempts seek to not only broaden the range of phenomena encompassed by the Darwinian Research Tradition, such as neutral molecular evolution, punctuated equilibrium, as well as developmental biology, and systems ecology more generally, but to also address issues of the emergence of evolutionary novelties as well as of life itself.

1. Darwinian anniversaries

It is a behavioral characteristic of our species to commemorate anniversaries, especially those at fifty-year intervals. As 1909 approached, representing the hundredth anniversary of the birth of Charles Darwin and the fiftieth anniversary of the publication of his *On the Origin of Species* there were assessments of the impact of Darwin's thought. For example, Vernon Kellogg addressed the problem of reconciling the gradualism of Darwinian selection with the discontinuous nature of the newly rediscovered Mendelian mutations (Kellogg, 1907; see Bowler, 1988, 1989). Edward Poulton, in an address to the American Association for the Advancement of Science commemorating fifty years of Darwinism undertook a defense of Darwinism from the apparent challenge of Mendelianism using the concept of adaptation resulting from natural selection (Poulton, 1909).

It was during the 1920s and 1930s that a synthesis of Darwinian natural selection and Mendelian genetics was forged by J.B.S. Haldane, Sewell Wright and Ronald Fisher by making the move to population genetics informed by background assumptions that David Depew and I have characterized as Boltzmannian (Depew & Weber, 1995; Weber & Depew, 1996). This constituted what we have called the first phase of the synthesis. The second phase population genetics, with natural selection reconceptualized as acting to change gene frequencies in populations, was deployed to bring a number of research areas, such as biogeography, paleontology, systematics, taxonomy, and population ecology into a more broadly construed Modern Evolutionary Synthesis (also known as the Modern Synthesis, or *neo*-Darwinism) through the efforts of biologists such as Theodosius Dobzhansky, Ernst Mayr, George Gaylord Simpson, and George Ledyard Stebbins (Depew & Weber, 1995; Delisle, 2009; Gayon, 1998, 2003).

In 1959 the triumph of the Modern Synthesis, based upon population genetics, was celebrated by the University of Chicago's symposia resulting in a three-volume set (Tax, 1960a, 1960b, 1960c). It was assumed by the contributors to these volumes that the rise of

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molecular biology would just fill in the details of the overarching synthesis. By then the Modern Synthesis had "hardened" in Stephen Gould's phrase, to a pan-adaptationist position, although he did not very carefully distinguish between different brands or kinds of adaptationism (Gould, 1983; see Depew, this volume).

The commemorations leading up to and including 2009 have expressed a range of reactions from triumphalism of Richard Dawkins to calls for an extended synthesis by Massimo Pigliucci, in a slightly different way by Sean Carroll, and by others in even more diverse ways (Carroll, 2008; Dawkins, 2009; Pigliucci, 2008a, 2008b). All these proposals for extending the Modern Synthesis are based upon the incorporation of developmental biology with evolutionary theory, i.e. Evo-Devo. Also, there has been the suggestion of extending Evo-Devo to include ecology as suggested by Gilbert and Epel (2009). Alternatively, Robert Ulanowicz has proposed the need for a new synthesis or "Third Window" based upon systems ecology (Ulanowicz, 2009).

My purpose in this paper is to work through these various proposals by a review of the literature, clarifying what these calls actually mean and commending some more than others.

2. Darwin's unique contribution

There is an uncomfortably contingent element in the development of evolutionary theory. In his analysis of the impact of Darwin's thought, the historian of biology Peter Bowler claims that Darwin was unique. Without him natural selection would not have been central to evolutionary theory (Bowler, 2008). Bowler further asserts that we can imagine a plausible trajectory of non-Darwinian biology. Bowler contends that no one else was in Darwin's unique position to put together natural variation over populations compared to resources, struggle for existence, and hard heredity to deduce such a compelling argument for natural selection. Further, much of late 19th century evolution was non-Darwinian in any case, tending toward orthogenesis and Lamarckianism (Bowler, 1988, 1996). Without natural selection it is likely that there would have been a 20th century synthesis of heredity and development, rather than of heredity and natural selection, and Bowler speculates that the genetic code might have been deduced through developmental studies. Bowler concludes:

> The struggle to emancipate genetics from its over-simplified origins, which has taken up so much time and attention through the later twentieth century, and which still drives the debate about evo-devo today would have been sidestepped. The resulting synthesis might have the same components as those we now recognize as essential for understanding of development, but we would have very different ideas about their implications. (Bowler, 2008, 566).

Whereas Bowler expects that the end result will be an extended synthesis that will encompass Darwinian selection and evo-devo (see 6 below), Patricia Princehouse has argued that there was a rival synthesis in the 1920s and 1930s, which she denotes as the 'German Synthesis'. This synthesis by Richard Goldschmidt and O.H. Schinderwolf, *inter alia*—encompassed paleontology, genetics, biogeography, taxonomy, and embryology (Princehouse, 2009). It was characterized by causal plurality at multiple levels in which micro-mutations as well as macro-mutations could lead to adaptation and speciation, with higher taxa arising because of genome rearrangements and/or changes in the regulation and timing of developmental processes. It is just these phenomena and mechanisms that have been getting a second hearing in contemporary calls for expanding or extending the Modern Synthesis.

The German Synthesis explained stasis over changing environments, parallelism, macro-extinctions, and radiation of novel morphotypes. It was attacked by Mayr and Simpson and it receded with the triumph of the Modern Synthesis; however, Julian Huxley (who was concerned that embryology was not integrated in the Modern Synthesis) was less unfriendly toward it even though he considered many of Goldschmidt's mechanisms to be erroneous (Huxley, 1942). It was Stephen Jay Gould who subsequently revived interest in this German Synthesis (Gould, 1977, 2002).

3. The Darwinian research tradition

How do calls for a new, expanded, or extended synthesis relate to the continuity of Darwinism? In *Darwinism Evolving*, David Depew and I argued that there is not, never was, and never will be a single Darwinism synonymous with evolutionary theory. Rather we defined Darwinism as a research tradition rather than as a single theory or even a research programme (Depew & Weber, 1995). We see a research tradition, following Larry Laudan, as a more encompassing historical entity that includes specific theories and programmes within it and which is characterized by specific causal and explanatory commitments even as these are conceptualized and connected to phenomena differently over time due to changes in the background and auxiliary assumptions that connect its core concepts to the phenomena in the natural world it seeks to explain (Depew & Weber, 1995; Laudan, 1977).

If common descent is a phenomenon inferred from a number of lines of factual evidence, it does not constitute a theory, once accepted, even though it can correlate a number of factual observations from many lines of evidence (Weber, 2007). For example, it does not explain why a particular fossil has a particular shape or is found in a particular stratum of rock. A theory is needed to explain the phenomenon of common descent. This is what Darwin provided in his theory of natural selection, if appropriate background and auxiliary assumptions and observations are included to connect the theory to the specifics in question. These assumptions are characteristic of a particular programme in the research tradition, such as the Modern Synthesis, but do not define or demarcate the tradition itself. It is natural selection, acting as the major source of biological order, adaptation, information and novelty through its action on heritable variation, which defines the Darwinian Research Tradition. But how natural selection is conceptualized and deployed can differ depending upon the particular set of assumptions that are characteristic of a particular programme within the Darwinian Research Tradition.

Seen in this light, the conceptual shifts required to produce the Modern Synthesis involved changing one of the background assumptions of systems dynamics of the original Darwinism from deterministic to probabilistic or statistical behavior. Other of the "Newtonian" assumptions: equilibrium, closure, decomposability or atomistic construction, and reversibility were retained, although equilibrium became redefined in the Hardy-Weinberg Equilibrium as an absence of change of gene frequencies rather than a balance of "forces" (Depew & Weber, 1995). Although the Modern Synthesis did bring a number of disparate fields together in terms of population genetics, there were important areas of biological research that were marginalized, such as developmental biology, which was viewed as just the "read out" of the genes, and ecology, which was included only as it could be described by population genetics. Indeed, as noted above Huxley in 1942 worried that embryology was not truly a part of the synthesis. Mayr in particular was uncomfortable with over emphasis on population genetics. He also argued for the autonomy of biology (Mayr, 1982). As will be seen below (see 4–6), Niles Eldredge, Stephen Gould, and Richard Lewontin, among others, have argued for an expanded synthesis in which not only selection can act at different hierarchical levels but also an extended synthesis in which there is