

The So-Called Extended Synthesis and Population Genetics

Lindsay R. Craig

Department of Philosophy, University of Oklahoma

Lindsay.R.Craig-1@ou.edu

Abstract: In recent years, several prominent biologists have pointed to the relatively new field of evolutionary developmental biology (evo-devo) as evidence of an Extended Synthesis in evolutionary biology. More particularly, these biologists claim that theoretical and empirical evo-devo research is extending the Modern Synthesis framework of evolutionary theory through investigation of evolutionarily important concepts that are not part of the framework developed during the 20th century. To describe the current changes in evolutionary biology as an Extended Synthesis, however, is incorrect. Through review of Extended Synthesis arguments and analysis of the same biological concepts used to support these arguments, I argue that the foundation of the Modern Synthesis framework, theoretical population genetics, faces significant, perhaps insurmountable challenges from the concepts highlighted by evo-devo research. Because the foundation of the Modern Synthesis framework will require considerable remodeling—if possible—in light of the concepts emphasized by evo-devo, it is incorrect to describe the ongoing changes in evolutionary biology as an Extended Synthesis.

Keywords: evolutionary developmental biology (evo-devo); evolutionary theory; Extended Synthesis; population genetics

Introduction

Several prominent biologists have recently argued that the framework of evolutionary theory developed during the Modern Synthesis of the 1920s through the 1950s is undergoing an extension (e.g., Müller 2007; Pigliucci 2007; Carroll 2008; Pigliucci 2009; Pigliucci and Müller 2010). These authors support the claim that a so-called Extended Synthesis is underway with discussions of various areas of research within the field of evolutionary developmental biology (evo-devo) and the biological concepts that are the empirical and theoretical focuses of evo-devo research. The general argument offered by these biologists is that biological concepts such as organization (see Burian 2005; Laubichler 2007), evolvability (see G.P. Wagner and Altenberg 1996; A. Wagner 2005), and phenotypic plasticity (see Pigliucci 2001; West-Eberhard 2003) are important conceptual aspects of evolutionary theory that are not part of the Modern Synthesis framework. So, evo-devo research is extending the predominant framework through investigation of evolutionarily important concepts not included in the Modern Synthesis framework.

I argue that it is incorrect to describe the changes currently taking place in evolutionary biology as an extension of the framework of the Modern Synthesis. The ongoing episode of change in the study of evolution is not an Extended Synthesis, at least in part, because the concepts highlighted by evo-devo research pose substantial conceptual obstacles for the models of population genetics, the foundation of the framework developed during the Modern Synthesis. Differently put, the population genetics foundation of the Modern Synthesis framework faces serious, potentially devastating challenges from the biological concepts emphasized by evo-devo research. If the foundation of the Modern Synthesis framework must be discarded or drastically modified in light of these concepts, something different than extension of the existing framework is taking place.

I begin with a discussion of the framework of evolutionary theory developed during the Modern Synthesis. I then discuss work by biologists Gerd Müller (2007) and Massimo Pigliucci (2007), as well as their recent collaboration (2010), in an effort to flesh out the intended interpretation of the claim that ongoing change in evolutionary biology is a so-called Extended Synthesis. Next, through consideration of

the same biological concepts appealed to in arguments supporting a so-called Extended Synthesis, I argue that the foundation of the framework developed during the Modern Synthesis, theoretical population genetics, faces what may well be unsolvable conceptual problems. As a result, it is incorrect to describe the current episode of change as an Extended Synthesis.

The Modern Synthesis of the 1920s-1950s

In the years following the publication of Charles Darwin's *On the Origin of Species* (1859), the biological sciences experienced a divergence of fields during which fields such as cytology, genetics, embryology, and ecology developed their own conceptual frameworks, experimental techniques, and phenomena of interest (Mayr and Provine 1980). In addition, the birth of Mendelian genetics following the "rediscovery" of Mendel's work in 1900 exacerbated the conflict between Mendelian geneticists and Darwinian naturalists (Provine 1971). The Mendelians quickly associated Mendelian inheritance with the mutation theory of evolution, which claimed mutation was the primary directive force of evolution and, hence, directly conflicted with Darwin's theory of gradual evolution by natural selection.

The Darwinians, on the other hand, adopted the populational species concept and believed that gradual evolution took place through natural selection acting upon continuous variation (Provine 1971). Because the Mendelians' views were not supported by observations of natural populations, the Darwinians were increasingly reluctant to incorporate Mendelian findings into their own work. Mendelians and Darwinians continued to work in relative isolation, and by 1918, the study of evolution was not only divided among several specialized fields but suffered from a growing rift between Mendelian geneticists and Darwinian naturalists as well (Huxley 1942; Amundson 2005).

It was during the third decade of the 20th century that the stark conceptual differences between the Mendelians and the Darwinians were reconciled. The principle architects of population genetics, Ronald Fisher (1930), J.B.S. Haldane (1932), and Sewall Wright (1931, 1932), developed statistical models that addressed the controversies surrounding the nature of variation in populations and evolutionary change

** In Press for 2010 in *Biological Theory: Integrating Development, Evolution, and Cognition*, 5(2)

(Millstein and Skipper 2007). Fisher, Haldane, and Wright demonstrated mathematically that mutation, migration, drift, and natural selection are responsible for evolution in natural, sexually reproducing populations. The mathematical models of theoretical population genetics established the complementary nature of Mendelian inheritance and Darwinian natural selection. That is, these statistical models reconciled the conceptual differences between the Mendelians and the Darwinians by elucidating the compatibility of their conceptual commitments. In this way, theoretical population geneticists attempted to account for the dynamics of genetic variation at the population level (Millstein and Skipper 2007).

But theoretical population genetics did more than bridge the conceptual divide that separated the Mendelians and the Darwinians. While the population geneticists successfully demonstrated that the distribution of gene frequencies in a population are the result of particular evolutionary causes, their theoretical models had nothing to say about the values of these parameters describing those causes in actual natural populations (Beatty 1986: 128). The investigation of mutation, migration, selection, and drift carried out with population genetics models explains possible modes of evolution, but population genetics itself does not explain how actual traits evolve in actual taxa. For explanations of evolutionary change in actual populations, fields such as botany, paleontology, ecology, and systematics investigated the role of these parameters in particular cases and attempted to extrapolate from these investigations to “the overall relative importances of the various possible modes of evolutionary change” (Beatty 1986).

The statistical models of population genetics were adopted and applied by biologists working in various fields in order to explain how evolution proceeds in actual populations. Important contributions include Huxley’s *Evolution: The Modern Synthesis* (1942), Ernst Mayr’s *Systematics and the Origin of Species* (1942), George Gaylord Simpson’s *Tempo and Mode in Evolution* (1944), Bernhard Rensch’s *Evolution Above the Species Level* (1947), and George Ledyard Stebbins’s *Variation and Evolution in Plants* (1950). These pivotal publications took the first steps toward integrating the fields of taxonomy and zoology, systematics, paleontology, and botany during development of the Modern Synthesis framework of evolutionary theory.

Theoretical population genetics models of evolutionary change are collectively a pivotal component of the framework of evolutionary theory developed during the Modern Synthesis. Indeed, population genetics is foundational to the framework of the Modern Synthesis. In addition to mathematically reconciling the conceptual differences between the Mendelians and the Darwinians, these models played a foundational role in studies of both laboratory and natural populations. Population geneticists provided the statistical tools needed to investigate the actual causes of evolutionary change in different kinds of populations at different levels of biological organization. In fact, just as the Modern Synthesis framework has come to define evolutionary theory, population genetics models have become a staple in the study of evolutionary phenomena.

In the next section, I discuss Müller (2007), Pigliucci (2007), and Pigliucci and Müller (2010) in order to clarify the claim that an Extended Synthesis is taking place. I focus on these biologists because they have both defended this claim many times in recent years. Plus, their 2010 volume on the Extended Synthesis is one of the most recent high-profile investigations of the topic.

The So-Called Extended Synthesis

Müller (2007), Pigliucci (2007), and most recently Pigliucci and Müller (2010) consider major theoretical concepts emphasized by current evo-devo research and argue that these concepts are extending the framework of the Modern Synthesis. Their discussions of extension are unclear, however, primarily because neither provides a straightforward articulation of the notion of an Extended Synthesis. Without such a description, the claim that an Extended Synthesis is underway is at best premature. My goal here, then, is to clarify what these biologists mean when they claim the ongoing episode of change in evolutionary biology is an Extended Synthesis.

For Pigliucci, the major conceptual contributions of evo-devo that will alter the “conceptual edifice” of evolutionary theory are evolvability, phenotypic plasticity, epigenetics, biological systems, and reconsideration of evolutionary adaptive landscapes (2007: 2747). Pigliucci states that it is safe to

argue that these concepts and associated empirical work do not contradict the framework of the Modern Synthesis but “may eventually force a shift of emphasis away from the population genetic-centered view of evolution that characterizes the [Modern Synthesis]” (2007: 2748). Moreover, he claims that the empirical and theoretical exploration of these five concepts may lead to a “series of complex developments that build on...Darwinism, neo-Darwinism, and the [Modern Synthesis] itself” (2007: 2748).

Pigliucci’s discussion of an Extended Synthesis is unclear, however. First, he claims the five recurring concepts found in evo-devo research may eventually lead to a shift of emphasis away from population genetics, which he describes as the “backbone” of the framework developed during the Modern Synthesis in his 2009 work. Here, confusion arises regarding the nature of the shift away from population genetics. Taken in the strong sense, this “shift” entails that population genetics will be discarded in the wake of scientific change. Indeed, the reader may interpret this claim as stating that the shift away from population genetics will leave population genetics out of evolutionary theory altogether¹. Taken in the weak sense, though, Pigliucci’s claim that the foundational emphasis will shift away from population genetics entails that population genetics will still play an explanatory role in evolutionary theory but will no longer be the whole of the explanatory foundation.

There is no obvious reason to assume Pigliucci intended the reader to interpret this claim in the strong sense. In fact, because Pigliucci is a biologist trained in the tradition of population biology, it is likely that Pigliucci had in mind something akin to the weaker interpretation, and this is supported by one of his more recent publications. In his 2009 paper on the Extended Synthesis, which gives the same general argument for the Extended Synthesis claim, Pigliucci maintains that the evolution of genes and the evolution of form should both be explained by evolutionary theory. For him, population genetics

¹ Such a strong position on the possibly bleak future of population genetics was mentioned by Gilbert et al. (1996). “Population genetics is destined to change if it is not to become as irrelevant to evolution as Newtonian mechanics is to contemporary physics” (368).

“does a good job” of explaining the former while explanations of the latter are being developed within the field of evo-devo (2009: 220). Pigliucci (2009) suggests that population genetics will still play an explanatory role in evolutionary theory despite extension of the explanatory framework.

In addition to his claim that evo-devo will shift emphasis away from population genetics, Pigliucci (2007) claims the future of evo-devo research is likely to build upon the foundations of evolutionary theory, at least partly because the frameworks of established sciences tend to expand rather than be replaced (2748). Confusion arises when the reader attempts to interpret the shifting claim together with the building claim because Pigliucci does not clearly bridge the two. While these claims are not necessarily mutually exclusive, the claim that the foundational emphasis will shift is indeed distinct from the claim that evo-devo research will build upon an existing theoretical framework. However, I believe the most charitable reading, and the likely intended interpretation, is as follows: the current Extended Synthesis in evolutionary biology includes both a foundational shift away from population genetics, understood in the weak sense, *and* continued building of evolutionary theory upon the augmented foundation.

Müller (2007) provides a clearer account of Extended Synthesis. For him, the explanatory aims of evo-devo differ from those of the Modern Synthesis framework, and this is surely true. While evo-devo is concerned with explaining phenotypic change with a causal mechanistic account of changes in developmental networks, the central explanatory goal of the Modern Synthesis was to explain adaptive change via changes in gene frequencies in populations (945-946). Evo-devo research also aims to explain the effects of genetic, epigenetic, and environmental factors on the evolution and control of developmental processes (946). Evo-devo explanations of these phenomena include the concepts of evolvability, emergence, and organization, none of which play a role in the framework constructed during the Modern Synthesis.

Like Pigliucci, Müller is clear that the concepts highlighted by evo-devo research that are not part of the Modern Synthesis framework do not contradict or invalidate what was developed during the Modern Synthesis. Instead, evo-devo “adds another level of explanation” (947). He continues, “The reach

of evolutionary theory is expanded in that evo-devo accounts not for what kinds of variation are going to be maintained through natural selection, but also what kinds of variation can possibly arise from specific developmental systems” (947). From this, it is clear that part of what Müller means by an Extended Synthesis is that evo-devo research provides explanations for evolutionary phenomena that have until now remained unexplained, thereby expanding the framework of the Modern Synthesis. The theory developing within the field of evo-devo attempts to explain, in part, how developmental systems give rise to novel variations. An explanation of this phenomenon, the origin of novel phenotypes, extends the explanatory scope of current evolutionary theory as represented by the framework of the Modern Synthesis. As is the case with Pigliucci, Müller claims that the Extended Synthesis involves a shift in emphasis away from population genetics toward developmental systems.

Pigliucci and Müller seem to have similar understandings of Extended Synthesis. If the reader understands Pigliucci’s shift and build claim to entail that the explanatory scope of evolutionary theory is expanded through building upon a shifted explanatory foundation, then both Pigliucci and Müller are talking about explanatory extensions that involve foundational shifts in emphasis away from population genetics. This is the most plausible reading of both Pigliucci and Müller since there is no apparent reason to view their accounts of Extended Synthesis as in opposition to one another. Indeed, Pigliucci and Müller seem to agree.

That Pigliucci and Müller share a similar understanding of the nature of the so-called Extended Synthesis as an expansion of explanatory scope is evidenced by their recent collaborative effort. In the co-authored introductory chapter to their jointly edited volume *Evolution—The Extended Synthesis* (2010), Pigliucci and Müller claim that novel concepts have expanded the explanatory scope of the Modern Synthesis framework. Additionally, they point to fields that did not significantly contribute to the Modern Synthesis, such as embryology, developmental biology, and ecology, and claim that the recent integration of these fields into the study of evolutionary phenomena is evidence that the scope of the Modern Synthesis framework is being expanded (2010: 8). Again, Pigliucci and Müller claim that evo-devo research and its conceptual focuses demonstrate a foundational shift away from the quantitative

models of population genetics, and this shift “brings with it a significantly expanded explanatory capacity of evolutionary theory” (2010: 12).

In the next section, I briefly discuss the most prominent theoretical concepts highlighted by evo-devo research that are most commonly used as evidence for an Extended Synthesis. I argue that these concepts pose serious problems for population genetics models, and these conceptual difficulties, in my view, render the Extended Synthesis claim incorrect.

Conceptual Difficulties

Research indicates that the organization of developmental systems and other aspects of biological organization play an important causal role in phenotypic evolution. Under the general umbrella of organization fall the concepts of homology and modularity. Studies suggest 1) distinct processes may result in homologous segments or structures; 2) distinct products may be the results of homologous processes; and 3) homologous processes may result in non-homologous structures that perform similar functions (Burian 2005; Müller 2007).

Evo-devo research emphasizes the concept of homology by focusing on homologous aspects of developmental pathways, their evolutionary conservation, and the role of homology in integrating genetic and epigenetic developmental systems (Müller 2007: 947). The integration of developmental systems results in increasingly complex regulatory systems that retain developmentally important homologies. So, the organizational concept of homology is important because it is an evolutionary outcome that profoundly affects future evolution of developmental systems. Also, the historical homology concept is often used in phylogenetic analyses to explain evolutionary relatedness by way of the distribution of homologues (Laubichler 2007: 352).

Modularity is another important organizational concept found in evo-devo research programs. Biological modules, defined as functional units that can act independently of other functional units, exist at all levels of biological organization (Hoekstra and Coyne 2007). This relative independence means

gene expression can be affected at different times and in different locations such that the same gene or gene complex, in different circumstances or against different genetic backgrounds, can have a staggering variety of phenotypic outcomes. Modular *cis*-regulatory elements act in a multitude of combinations, which leads to different patterns of gene expression and morphological differences. Of particular importance for evo-devoers are explanations of how modular organization aids evolutionary change and how modularity itself evolved.

Also emphasized by evo-devo research is phenotypic plasticity. This is the capacity of a genotype, in conjunction with different external and internal environmental conditions, to produce a range of phenotypes. Causally relevant environmental factors include but are not limited to diet, pH, temperature, population density, social interactions, and humidity (Müller 2007: 945). Explaining plasticity requires functions that relate genotypic responses to specific environmental differences; that is, developmental reaction norms are adopted to explain the role of plasticity in evolution (West-Eberhard 2003; Müller 2007; Pigliucci 2007, 2009).

Phenotypic plasticity has been found in nearly every species in which biologists have looked for it (Pigliucci 2007: 2746). As is the case with modularity, phenotypic plasticity can be both a result of evolutionary factors and an influence on the way evolution proceeds. Indeed, it may be the case that under certain circumstances, plasticity within developmental systems catalyzes evolutionary change before genetic change occurs (West-Eberhard 2003). If plasticity acts in this way, focus on gene-centric explanations of evolution will certainly shift toward explanations that integrate aspects of genetics, development, and the environment.

Evolvability is another concept important to evo-devo research. Like the gene, evolvability is defined in a number of different ways (Pigliucci 2007: 2746). Fortunately, the biologists I focus on in this section employ similar definitions. Evolvability is the ability of a lineage to further its own evolution through the production of heritable phenotypic variation (Müller 2007: 946; Pigliucci 2009: 223). It remains to be seen to what extent evolvability is the result of neutral evolution versus natural selection, but either way, evolvability is the result of evolution. A living system's inherent ability to evolve via

heritable variation is an evolving trait. Evo-devoers investigate the relationship between developmental systems and the capacity to produce phenotypic variation. Many evo-devoers, according to Müller (2007), agree that variational capacity is the result of the modularity and mechanistic dynamics of developmental systems (946). Pigliucci makes a similar claim. He states, “[E]volvability depends on biological phenomena that the [Modern Synthesis] simply did not consider, such as the degree of modularity of developmental systems,” as well as the system’s susceptibility to perturbations (2007, 2746).

Epigenetic inheritance, yet another concept important to evo-devo research that is not included in the Modern Synthesis framework, is the inheritance of alternative traits that occurs with no difference in nucleotide sequence in the causal chain that yields the alternative traits. While there is considerable empirical evidence that some epigenetic change is heritable, there are serious unanswered questions regarding epigenetic inheritance. For example, it is unclear how exactly heritable epigenetic variation interacts with genetic variation or how long epigenetic effects can last (Pigliucci 2007: 2747). We do know, however, that epigenetic effects can modify gene regulation, and gene regulation can affect methylation patterns, an epigenetic effect. So, we know that epigenetically inherited variations can and do affect developmental systems and that developmental systems can and do affect heritable epigenetic variation (Müller 2007). This suggests inheritance is much more complex than had been assumed by population genetics and requires much more empirical and theoretical attention.

At present, it is unclear how population genetics models can be modified to account for these concepts (Laubichler 2007; Müller 2007; Pigliucci 2007; Carroll 2008; Pigliucci 2009). To determine whether (and how) such modifications are possible, continued study of each of these concepts is necessary, as is continued exploration of the ways in which population genetics models can be modified or rebuilt to account for these concepts in the evolution of populations.

Importantly, the explanatory aim of population genetics must be kept in mind—the statistical models of population genetics attempt to measure the influence of mutation, migration, natural selection, and genetic drift on gene frequencies of populations (Millstein and Skipper 2007: 22). The explanatory purpose of these mathematical models is to describe and predict the dynamical effects of the causes of

evolution on the maintenance and refinement of gene frequencies in populations. Making the relevant changes to population genetics suggests at least that the central explanatory entity will no longer be the gene (as a Mendelian unit). Whatever scientists call the new explanatory unit or units, they will have to include non-nuclear modes of inheritance, such as epigenetic inheritance, that are themselves evolutionary causes that constrain the effects of selection, mutation, drift, and migration. Certainly this sort of change will integrate population genetics and development. However, practical reasons suggest this is not the sort of integration that is likely to happen.

Notice that the concepts of organization, phenotypic plasticity, and evolvability are each importantly linked to the causal relationship between genotypes and phenotypes. That is, each of these concepts addresses some aspect of the complex causal pathways that start with a genotype and produce a particular phenotypic outcome. As biologists Johnson and Porter (2001) point out, population genetics models do not address the construction of phenotypes from genotypes (45). Rather, population genetics assumes the simplest possible biologically reasonable situation: single alleles at a single locus using the Mendelian rules of inheritance generalized for populations. To be sure, theoreticians have shown how to expand the models to account for genetic interaction (e.g., models including linkage disequilibrium). But this is but a small step toward the sort of complications required of these models.

Richard Lewontin (1974) famously claimed that population genetics is just not able to address the complex relationship between genotypes and phenotypes. Essentially, the reason is that the dimensionality of the models that would be required to do so would simply not be tractable even with virtually limitless computational power. Sewall Wright knew this in 1931-1932; he used a two dimensional adaptive landscape metaphor to graphically depict his shifting balance process because there was simply no way to do so considering that a biologically realistic model would require, among other things, representing the 10^{800} gene combinations possible in a given population (Wright 1932).

The simplest mathematical case of evolution in Mendelian populations has been the rule since Fisher, Haldane, and Wright invented population genetics. Wright knew that the real biological situation was substantially more complicated than the models of the times because of his interest in physiological

genetics. This is reflected in the difference between his quantitative and qualitative theories (Skipper 2009). Lewontin (1974) pressed a similar point. And if these biologists are correct, population genetics will be of no use in elucidating the complexity of evolution and development using statistical, population level models.

How do these difficulties relate to the claim that evolutionary biology is in the midst of an Extended Synthesis? Given that population genetics is the foundation of the Modern Synthesis framework, and given the serious, potentially overwhelming difficulties faced by population genetics models in light of the concepts emphasized by evo-devo research, it cannot be the case that the framework of the Modern Synthesis is being extended in any clear way. The framework of the Modern Synthesis was built upon population genetics, but this foundation faces something different from a shift in emphasis in the weak sense. More accurately, the population genetics foundation of the Modern Synthesis framework faces substantial, extreme rebuilding if these models are in any way explanatorily relevant to evolutionary developmental phenomena. From the current vantage point, a weak shift in emphasis away from the population genetics foundation of the Modern Synthesis framework is an extraordinarily unlikely possibility. The claim that evo-devo, in its pursuit of explanations for evolutionary developmental phenomena, is currently shifting emphasis away from population genetics is, at best, an understatement.

In my view, an Extended Synthesis expands the explanatory scope of the prevailing framework without drastic modifications to the structure of that framework, including the framework's foundation. To say that an Extended Synthesis is underway is to say that the original framework, including the foundation, will be sufficiently similar to the final extended framework. By way of analogy, consider the framework and foundation of a building. A building's square footage is extended when a room or wing is added to the original structure. The original framework is reshaped, and the original foundation may have to be extended depending on type and location of the addition. In extending the square footage, the foundation of the original framework is not significantly modified or rebuilt, and, so, the original building and the resulting extended building have the original foundation in common. In cases where the foundation of a building requires serious reconstruction, this is much more than the mere addition of

square footage. In short, when foundations, be they theoretical or concrete, require substantial modification, it is too simplistic, indeed incorrect, to describe what is taking place as an extension of an existing framework.

To be sure, empirical and theoretical evo-devo research has expanded the explanatory scope of evolutionary theory and is likely to continue to do so. However, developments that extend the explanatory scope of a theory should not be confused with the shifting of a framework's foundation and continued building upon that framework. The two are not the same.

Conclusion

I have argued that the explanatory foundation of the Modern Synthesis framework, population genetics, is likely to require profound remodeling—if possible—if it is to take into account the theoretical concepts emphasized by the field of evo-devo. More accurately, I believe what is currently taking place within evo-devo is the development of a long-needed explanatory framework for evolutionary developmental phenomena such as the origin of novel morphologies and the evolution of developmental systems. The framework under construction complements the framework developed during the Modern Synthesis but is not accurately described as an extension of it because these frameworks have different foundations. Instead of an explanatory foundation that emphasizes genes in populations, the explanatory foundation of the framework emerging from evo-devo emphasizes, among other things, the complexity of the components and interactions of developmental systems at multiple levels of biological organization. Rather than an Extended Synthesis, what we have here is the development of a compatible evolutionary framework that addresses phenomena not accounted for by the framework developed during the Modern Synthesis.

What lies ahead is further empirical and theoretical examination of the causal roles of organization, phenotypic plasticity, evolvability, epigenetic inheritance, and other aspects of evolutionary developmental phenomena. Through its various areas of research, evo-devo will continue to contribute

** In Press for 2010 in *Biological Theory: Integrating Development, Evolution, and Cognition*, 5(2)

significantly to our understanding of evolution. We are indeed on our way toward a more comprehensive theory of evolution.

Acknowledgements

Special thanks to Rob Skipper, Dick Burian, Koffi Maglo, and Bob Richardson for their comments on this piece. Also, thanks to the philosophy departments at the University of Cincinnati and the University of Oklahoma for funding my work.

References

- Amundson R (2005) *The Changing Role of the Embryo in Evolutionary Biology: Structure and Synthesis*. New York: Cambridge University Press.
- Beatty J (1986) The synthesis and the synthetic theory. In: *Integrating Scientific Disciplines* (Bechtel W, ed), 125-135. Dordrecht, The Netherlands: Martinus Nijhoff Publishers.
- Burian RM (2005) Reconceiving animals and their evolution: On some consequences of new research on the modularity of development and evolution. In: *The Epistemology of Development, Evolution, and Genetics: Selected Essays* (Burian RM, ed), 234-262. New York: Cambridge University Press.
- Carroll SB (2008) Evo-devo and an expanding evolutionary synthesis: A genetic theory of morphological evolution. *Cell* 134 (1): 25-36.
- Darwin C (2000) *On the Origin of Species: A Facsimile of the First Edition*. Cambridge, MA: Harvard University Press.
- Fisher RA (1930) *The Genetical Theory of Natural Selection*. Oxford: Oxford University Press.
- Gilbert SF, Opitz JM, Raff RA (1996) Resynthesizing evolutionary and developmental biology. *Developmental Biology* 173 (2): 357-372.
- Haldane JBS (1990) *The Causes of Evolution*. Princeton, NJ: Princeton University Press.
- Hoekstra HE, Coyne JA (2007) The locus of evolution: Evo devo and the genetics of adaptation. *Evolution* 61 (5): 995–1016.
- Huxley J (1942) *Evolution: The Modern Synthesis*. London: Allen and Unwin.
- Johnson NA, Porter AH (2001) Toward a new synthesis: Population genetics and evolutionary developmental biology. *Genetica* 112-113 (1): 45-58.
- Laubichler MD (2007) Evolutionary developmental biology. In: *The Cambridge Companion to the Philosophy of Biology* (Hull DL, Ruse M, eds), 342-360. New York: Cambridge University Press.
- Lewontin RC (1974) *The Genetic Basis of Evolutionary Change*. New York: Columbia University Press.
- Mayr E (1942) *Systematics and the Origin of Species*. New York: Columbia University Press.
- Mayr E, Provine W (1980) *The Evolutionary Synthesis: Perspectives on the Unification of Biology*. Cambridge, MA: Harvard University Press.
- Millstein RL, Skipper RA Jr (2007) Population genetics. In: *The Cambridge Companion to the Philosophy of Biology* (Hull DL, Ruse M, eds), 22-43. New York: Cambridge University Press.
- Müller GB (2007) Evo-devo: Extending the evolutionary synthesis. *Nature Reviews: Genetics* 8 (12): 943-949.
- Pigliucci M (2001) *Phenotypic Plasticity: Beyond Nature and Nurture*. Baltimore, MD: The Johns Hopkins University Press.

** In Press for 2010 in *Biological Theory: Integrating Development, Evolution, and Cognition*, 5(2)

Pigliucci M (2007) Do we need an extended evolutionary synthesis? *Evolution* 61 (12): 2743-2749.

Pigliucci M (2009) An extended synthesis for evolutionary biology. *The Year in Evolutionary Biology 2009: Annals of the New York Academy of Sciences* 1168: 218-228.

Pigliucci M, Müller GB (2010) Elements of an extended evolutionary synthesis. In: *Evolution—The Extended Synthesis* (Pigliucci M, Müller GB, eds), 3-17. Cambridge, MA: The MIT Press.

Provine W (2001) *The Origins of Theoretical Population Genetics*. Chicago: University of Chicago Press.

Rensch B (1947) *Evolution Above the Species Level*. New York: Columbia University Press.

Simpson GG (1944) *Tempo and Mode in Evolution*. New York: Columbia University Press.

Skipper RA Jr (2009) Revisiting the Fisher-Wright controversy. In: *Descended from Darwin: Insights into the History of Evolutionary Studies, 1900-1970* (Cain JA, Ruse M, eds), 299-322. Philadelphia: American Philosophical Society.

Stebbins GL (1950) *Variation and Evolution in Plants*. New York: Columbia University Press.

Wagner A (2005) *Robustness and Evolvability in Living Systems*. Princeton, NJ: Princeton University Press.

Wagner GP, Altenberg L (1996) Perspective: Complex adaptations and the evolution of evolvability. *Evolution* 50 (3): 967-976.

West-Eberhard MJ (2003) *Developmental Plasticity and Evolution*. New York: Oxford University Press.

Wright S (1931) Evolution in Mendelian populations. In: *Sewall Wright, Evolution, Selected Papers*. (Provine W, ed), 98-160. Chicago: University of Chicago Press.

Wright S (1932) The roles of mutation, inbreeding, crossbreeding and selection in evolution. In: *Sewall Wright, Evolution, Selected Papers* (Provine W, ed), 161-171. Chicago: University of Chicago Press.