Neo-Darwinism and Evo-Devo: An Argument for Theoretical Pluralism in Evolutionary Biology

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There is an ongoing debate over the relationship between so-called neo-Darwinism and evolutionary developmental biology (evo-devo) that is motivated in part by the possibility of a theoretical synthesis of the two (e.g., Amundson 2005; Brigandt and Love 2010; Laubichler 2010; Minelli 2010; Pigliucci and Müller 2010). Through analysis of the terms and arguments employed in this debate, I argue that an alternative line of argument has been missed. Specifically, I use the terms of this debate to argue that a relative significance issue (Beatty 1995, 1997) exists and reflects a theoretical pluralism that is likely to remain.

1. Introduction

The relatively new field of evolutionary developmental biology (evo-devo) continues to attract considerable attention from biologists, philosophers, and historians, in part, because work in this field demonstrates that important changes are underway within biology (e.g., Gilbert, Opitz and Raff 1996; Love 2003; Amundson 2005; Burian 2005a; Müller and Newman 2005; Laubichler 2007, 2010; Müller 2007; Pigliucci 2007, 2009; Minelli 2010). Though studies of development and evolution were closely connected during the 19th century, continued work in genetics fostered a general split between the two during the first decades of the twentieth century (e.g., Allen 1978; Gilbert 1978; Mayr and Provine 1980; Gilbert, Opitz and Raff 1996). Consequently, embryology and developmental biology did not play a significant role in the development of so-called neo-Darwinism[1] during the

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1. The term *neo-Darwinism* is problematic; its contemporary usage is prone to ambiguity and confusion. Here, I use the term and its derivatives in order to remain consistent with the language of the debate that is my current focus. I attempt to specify the usage of the term in this debate in section 2.1 below.

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Modern Synthesis of the mid-twentieth century (e.g., Allen 1978; Mayr and Provine 1980; Hamburger 1988; Maienschein 1991; Gottlieb 1992; Gilbert 1994; Gilbert, Opitz and Raff 1996). Evo-devo, which emerged as a field of study in the 1980s and continues to grow well into the current millennium, focuses on the intersection of individual development and evolutionary change to explain evolutionary phenomena such as the origin of novel morphological structures, the evolution of developmental systems and their components, and morphological diversity within and between taxonomic groups. By investigating evolutionary phenomena that are causally related to developmental processes, evo-devo casts development in a staring role in the study of evolution.

Indeed, the relationship between neo-Darwinism and evo-devo has fostered much debate in recent years (e.g., Amundson 2005; Müller 2007; Pigliucci 2009; Brigandt and Love 2010; Craig 2010; Laubichler 2010; Minelli 2010). A strong motivation, though not the only motivation, for discussing the relationship is the possibility of a theoretical synthesis of neo-Darwinism and evo-devo that results in, or at least does much to pave the way toward, a synthetic theory of evolution applicable to all evolutionary phenomena (e.g., Amundson 2005; Müller 2007; Pigliucci 2009; Brigandt and Love 2010; Laubichler 2010; Minelli 2010). Whether such a synthesis is possible depends on the relation between the two frameworks. That is, if the two fundamentally conflict or contradict, a theoretical synthesis of them is less likely, or at least will take more theoretical, conceptual, and empirical work, than if the two are compatible or complementary. So, to answer whether a synthesis of neo-Darwinism and evo-devo is possible, many have taken a necessary step back to address the relationship between the frameworks.

In *The Changing Role of the Embryo in Evolutionary Thought* (2005), Ron Amundson provides a comprehensive narrative of the relationship between development and evolution from pre-Darwinian thought through the start of the twenty-first century. He ends his account with discussion of recent debates related to neo-Darwinism and evo-devo, including the debate regarding a synthesis of the two. At the start of his final section titled "A Newer Synthesis?," he insists that "[t]he field of evo-devo is changing so fast that predictions about its future relations with neo-Darwinism are foolhardy" (p. 250). For him, the two currently conflict in serious ways, but despite his skepticism, Amundson very cautiously concludes that with the continued success of both, they may be shown to be consistent and a synthetic theory may be possible (2005, p. 257). Similarly, Alessandro Minelli (2010) argues that though a synthesis of neo-Darwinism and evo-devo has proved difficult, they are complementary nonetheless and a "natural integration" is possible (p. 224). Massimo Pigliucci and Gerd Müller (2010) argue that evo-devo is part of the extension of neo-Darwinism (p. 12). On the other side of the debate are those who believe that there are serious insurmountable conflicts between neo-Darwinism and evo-devo. For example, Manfred Laubichler (2010) claims that evo-devo conflicts with neo-Darwinism to the extent that evo-devo represents a Kuhnian paradigm shift within evolutionary biology (p. 200).

My view is that this debate misses an important line of argument in favor of theoretical pluralism—the accommodation and pursuit of more than one explanatory framework—in evolutionary biology. The terms and existing arguments of this debate stipulate that neo-Darwinism and evo-devo explain different evolutionary phenomena by way of different explanatory frameworks that are well supported by the available evidence. In what follows, I use the terms and arguments set forth by these authors to argue that a relative significance issue (Beatty 1995, 1997), which concerns the extent of applicability of two different explanatory frameworks, currently exists between neo-Darwinism and evo-devo. That is, at present, both neo-Darwinism and evo-devo explain or account for some evolutionary phenomena, which raises the question of the significance of these explanatory frameworks relative to one another. Like Amundson, I believe that there is an element of foolishness in making too strong claims about the future relations between neo-Darwinism and evo-devo precisely because continued experimental and explanatory successes will drive those relations in directions with unforeseeable details. But a look at the current state of things allows for mediated claims about what may come to be the case. Rather than argue that a synthesis is or is not possible, claims that may indeed be too strong at this point, I use the current relative significance issue to argue further that to continue to account for different evolutionary phenomena, more than one explanatory framework may obtain instead. Theoretical pluralism may prevail in evolutionary biology. That neo-Darwinism and evo-devo, two very conceptually different explanatory frameworks, explain different kinds of evolutionary phenomena suggests that a relative significance issue currently exists between the two, and this issue of relative significance suggests that both will continue to develop as relatively independent and distinct frameworks.

To be clear, I am not concerned with resolving the relative significance issue between neo-Darwinism and evo-devo. In fact, I am not convinced that it is possible to answer which of these frameworks correctly accounts for the largest proportion of evolutionary phenomena, the underlying question of all relative significance disputes. At the very least, there are a large number of experimental, epistemological, and metaphysical tangles to be combed out before such an answer could be confidently proposed. My concern here is to contribute to the debate over the relation between and synthesis of neo-Darwinism and evo-devo. I plan to do this by making clear and expanding upon what has been previously missed by the debate's participants, namely, the relative significance issue that suggests that neo-Darwinism and evo-devo will remain unsynthesized, individual explanatory frameworks. Moreover, I take this to be a more moderate claim than those espoused in the debate up to this point. In particular, the following argument does not address whether a synthesis is possible because, as Amundson points out, such a possibility is at least partially dependent upon more immediate developments. Instead of staking a claim on the possibility question, I contend that the current debate has missed something important, the relative significance issue between neo-Darwinism and evo-devo, and this issue is important to this debate because it presently indicates that the two will continue to develop as individuals rather than participate in a theoretical synthesis.

To support my view, and to avoid confusion, the following section is devoted to clarification of the two major terms of this debate, neo-Darwinism (section 2.1) and evo-devo (section 2.2), and review of the arguments provided by Amundson (2005), Minelli (2010), Pigliucci and Müller (2010), and Laubichler (2010) (section 2.3). In section three, I use the terms and arguments of the current debate to illustrate that neo-Darwinism (section 3.1) and evo-devo (section 3.2) explain different evolutionary phenomena, a considerable aspect of all relative significance issues. Sections two and three lay the groundwork for my argument in section four that the relative significance controversy between neo-Darwinism and evo-devo indicates that the two will survive as individual frameworks. Finally, section five includes concluding remarks.

2. Neo-Darwinism and Evo-Devo: The Current Debate

Those engaged in the ongoing debate over the relationship between neo-Darwinism and evo-devo define *neo-Darwinism* and *evo-devo* in importantly similar ways. Analysis of this debate and my argument that there is a relative significance issue in the midst require a close look at how these terms are used by these authors. Once these terms are generally defined within the context of the debate, the different arguments concerning the relationship between the two offered by Amundson, Minelli, Pigliucci and Müller, and Laubichler will be examined as well.

2.1 Neo-Darwinism Defined

Amundson, a philosopher and "self-styled" historian of biology (2005, p. 2), devotes four out of eleven chapters of his book to the Evolutionary Synthesis[2], an episode in twentieth century history of biology during which pivotal theoretical, conceptual, and experimental strides were made in evolutionary biology. In these chapters, which follow Amundson's detailed account of the relationship between development and evolution prior to

2. The Evolutionary Synthesis is also known as the Modern Synthesis.

the Synthesis, he describes the nature of the Synthesis, reactions to it, and ongoing debates that have sprung from it. The section immediately preceding his characterization of the Synthesis acknowledges that there are a number of difficulties associated with a definitive description of this complicated period, and despite numerous attempts to develop such a description, "the Synthesis as a scientific and historical entity remains elusive" (p. 162). Of particular interest to Amundson, and what he describes as the inspiration for his book, is the somewhat contentious claim that developmental biology played no role in the Synthesis (p. 162). Analysis of this claim requires a description of the Synthesis, and it is from this description that the reader receives a more detailed understanding of Amundson's take on neo-Darwinism.

For Amundson, the Evolutionary Synthesis, which he places between the 1930s and 1940s, led to the "mainstream of evolutionary biology" (p. 1), or neo-Darwinism. Interestingly, on the second page of his introductory chapter, Amundson states that his interest is not in the theoretical and methodological debates between scientific theories but is instead in those debates between "scientific views" (p. 2). What, exactly, Amundson takes to be the differences between scientific theories, on the one hand, and scientific views, on the other, is somewhat unclear, but his account of the Synthesis and neo-Darwinism sheds some light on the matter. In contrast to a description of neo-Darwinism as a concrete and identifiable theory of evolution that epitomizes a contemporary research program, Amundson characterizes[3] neo-Darwinism more generally as a way of thinking about and explaining evolution, an "approach" (e.g., p. 236), "perspective" (e.g., p. 237), or "viewpoint" (e.g., p. 237) for understanding the components and processes of evolutionary change. Indeed, part of what typifies neo-Darwinism on his account is what he refers to as "population thinking," or thinking of evolutionary change in terms of organismal populations with particular genetic makeups that are maintained and refined over time. This way of thinking about evolution is fostered by population genetics, which, he argues, is genuinely inconsistent with developmental or "typological thinking"—thinking of evolutionary change in terms of developmental processes and components, morphological traits, and how they change over time—contemporarily demonstrated by evo-devo practitioners (p. 225). I believe that Amundson takes neo-Darwinism to be more general than a specific, discrete theory of evolution. For him, contemporary neo-Darwinism is best

3. Amundson also refers to neo-Darwinian *theory* throughout the book. Given his characterization of both neo-Darwinism and evo-devo, however, I suspect that his use of *theory* is the result of convention, of how we speak about certain scientific entities, and does not indicate a particular commitment to neo-Darwinism as such. I say more about this in the following pages.

characterized as a pervasive view of evolution with a particular—though muddy—history, conceptual commitments, and related implications rather than as an axiomatization, or semantic, hierarchical, or structural model of the principles, laws, and relations relevant to evolutionary processes, components, and outcomes. Amundson's introductory statement that he is interested in scientific views rather than scientific theories is indicative of what neo-Darwinism represents in the larger debate; as I argue in the rest of this section, each of the authors involved provide descriptions of neo-Darwinism that are similarly general.

Contemporary neo-Darwinian commitments, according to Amundson, can be traced back, in part, to population genetics, which demonstrates the compatibility of Mendelian inheritance and Darwinian natural selection. He describes population genetics as part of the "early core" of the Evolutionary Synthesis from which neo-Darwinism resulted. Another part of the "early core" of the Synthesis is the Mendelian-chromosomal theory of heredity (p. 163), which claims that chromosomes are the basis for genetic inheritance since chromosomes are sequences of Mendelian "factors" or "particles," later referred to as "genes," at particular loci associated with adult characters or traits. A third component of this core is the demonstrated consistence of population genetics with variation in wild populations by way of field studies (p. 163). More generally, Amundson says that the "core of the Synthesis was the formal description of populations that was enabled by population genetics" (p. 163). His discussion of the core of the Synthesis illustrates that Amundson's take on "neo-Darwinian thinking", a phrase he uses throughout, is partially characterized by a population approach, or population thinking, to understanding and explaining evolution.

Also at the foundation of neo-Darwinian thinking are the views that natural selection is the primary mechanism of evolution (p. 131) and that macroevolutionary change is the result of microevolutionary processes. Amundson points out that other areas of study within biology reexamined their specialized theories "in ways that were consistent with this core" (p. 163). Amundson is somewhat vague about which specializations were involved in this reinterpretation, though he does argue that "ontogenetic development of individual organisms had no place in this framework" (p. 1). So, developmental insights, on Amundson's account, did not significantly impact neo-Darwinian thinking. This is largely because neo-Darwinism, with its population genetics foundation, identifies genes by tracking associated phenotypes through generations, which allows for explanations of generational gene sorting (p. 7) and renders ontogenetic causal processes irrelevant (p. 161). The ontogenetic relationship between genes and phenotypes is black-boxed within neo-Darwinism (p. 212); that is, the ontogenetic causal processes that are the causal bridges between genes and phenotypes are taken as unimportant to patterns of gene transmission over generational time according to Amundson's account.

In his characterization of the Synthesis and neo-Darwinism, Amundson appeals to Wolf-Ernst Reif, Thomas Junker, and Uwe Hoßfeld's analysis of the so-called Synthetic Theory of Evolution (2000). Here, too, is evidence that Amundson's description of neo-Darwinism is of a mainstream way of thinking or a predominant approach to understanding evolution rather than a more concrete scientific theory. Reif and his colleagues take aim at traditional analyses of the Evolutionary Synthesis and its result, the Synthetic Theory (Reif et al., p. 42), which they argue is different from neo-Darwinism (Reif et al., p. 43). They claim that while neo-Darwinism refers to the view that evolutionary change is caused exclusively by natural selection, the Synthetic Theory "includes modern genetics, population genetics, systematics, and theories of speciation and macroevolution (based on paleontology, comparative morphology, and developmental biology)", as well as factors other than selection, including isolation, drift, and population size (Reif et al., pp. 43–44). On their account, both the Synthetic Theory and neo-Darwinism are stages in the historical development of evolutionary theory, and the Synthesis is different from its result, the Synthetic Theory. Neo-Darwinism, coined in 1895 by George Romanes, predates the Synthetic Theory, which originated in the early 1930s (Reif et al., p. 43).

Amundson's portrayal of neo-Darwinism does not coincide with the Romanesian description from Reif et al., though Amundson does emphasize the role of adaptationism and natural selection in neo-Darwinian thinking (for example, p. 164). But perhaps more important for the present purpose of fleshing out Amundson's take on neo-Darwinism as a general way of thinking about evolution instead of as a more concrete theory, Amundson does not mention Reif et al.'s discussions of potential identifying criteria of a contemporary synthetic evolutionary theory, difficulties associated with these criteria, or their proposal of a structuralistic concept of the Synthetic Theory and its advantages (Reif et al., pp. 56–58). Reif et al. provide an argument for a way to understand the result of the Synthesis as a kind of scientific theory, and Amundson does not mention it. This is important because Amundson does rely upon the authors' discussion of what they refer to as "the essential five components *of the Synthetic Theory*" (Reif et al. p. 58, emphasis added), the "relevant components [that] follow naturally from this basic structure" (Reif et al., p. 59), and what "the *Synthetic Theory* rejects" (p. 59, emphasis added). However, Amundson uses this part of Reif et al.'s argument to elucidate what he believes are aspects and commitments of the Synthesis itself. Reif et al. are clear that they believe there is a difference between the Synthesis, the resulting Synthetic Theory, and neo-Darwinism, but Amundson describes Synthesis commitments, and ultimately neo-Darwinian thinking, by co-opting their discussion of the Synthetic Theory. So, not only do Amundson and Reif et al. define neo-Darwinism differently, but Amundson avoids all talk of Reif et al.'s conception of the Synthetic Theory of Evolution in favor of a less restricted, broader-ranging account of neo-Darwinian thinking that is, nonetheless, based on Reif et al.'s description of a particular way of understanding what they take to be the Synthetic Theory.

Amundson's use and discussion of Reif et al., I believe, serves as further evidence that his description of neo-Darwinism is of a way of thinking about or an approach to understanding evolution, not a particular kind of scientific theory. I do not mean to suggest that Amundson unfairly uses Reif et al. or that he mischaracterizes their claims; I do not think that is the case. More accurately, Amundson characterizes neo-Darwinism, in part, by way of Reif et al.'s discussion of what they refer to as the Synthetic Theory of Evolution while at the same time avoiding reference to an evolutionary theory himself. More simply, Amundson agrees with Reif et al.'s description of the results of the Synthesis but does not describe these results as comprising a specific evolutionary theory. Instead, Amundson depicts the concepts, implications, and rejections that were, according to Reif et al., the results of the Evolutionary Synthesis as comprising a general neo-Darwinian view of evolution.

Using Reif et al., Amundson claims that five central concepts of the Synthesis and the neo-Darwinian view are: 1) "mutations (random with respect to adaptation); 2) "selection as the primary directional force (and largely restricted to the individual level)"; 3) "recombination in sexually reproducing populations"; 4) "isolation (various mechanisms preventing gene flow)"; and 5) "drift (the importance of which depends on effective population size)" (p. 165). Again following Reif et al., Amundson states that the implications that follow from these concepts and are important for understanding the Synthesis are: 1) "Speciation is predominantly allopatric or parapatric"; 2) "Evolution is gradual but can have a wide range of velocities"; and 3) "'Developmental, historical and constructional constraints limit the opportunism of evolution to a certain degree, but do not lead to non-adaptive evolution'" (165). The Synthesis forbids, according to Amundson via Reif et. al., that "genetic factors are macromutations (see, e.g., Goldschmidt 1940) and Lamarckian inheritance" and "'Baupläne' or types as actors in evolution" (Amundson p. 166).

Preceding this characterization of the Synthesis, Amundson devotes a chapter to various responses to the Synthesis from more developmentally inclined biologists. Amundson is careful, and correct, to point out that there was some interest in developmental studies around and during the time of the Synthesis. Here, Amundson cites T. H. Morgan's eventually abandoned symbolism that was developed in order to keep track of those genes that were thought to "developmentally influence a trait" (p. 189). Sewall Wright, recognized as a member of the inaugural generation of population geneticists and as a pivotal contributor to the Synthesis, was also considerably interested in development. Amundson discusses Wright's interest in the influence of cytological factors on heredity (Wright 1941), but Wright's focus on pleiotropy, which stemmed from his work in both population genetics and physiological genetics, is also noteworthy. For example, in *Evolution and the Genetics of Populations* (1968), Wright follows a section titled "The Developmental Process" with the claim that the "netlike relationship between genome and complex characters" leads to the generalizations that most character variations are affected by multiple loci and that a gene replacement can affect multiple characters (pp. 59–60). Wright refers to these generalizations as the multiple factor hypothesis and the principle of universal pleiotropy, respectively. Nonetheless, Amundson argues that the developmental interests of those active during this time did not affect the insignificant role of development during the Synthesis (p. 191).

Minelli (2010), an active evo-devo researcher, characterizes neo-Darwinism in much the same way as Amundson. Minelli notes that the term originally referred to the view that natural selection was the sole cause of evolutionary change, but because of the changes and advances that took place during the Modern Synthesis, *neo-Darwinism* no longer refers to this view. His 2010 paper begins with the statement that "There are brands of scientists who should find it intrinsically difficult to identify their views, or those of their colleagues, with a frozen set of tenets. These scientists specialize in the study of change [...]" (p. 213). Before his more detailed description of neo-Darwinism, Minelli states

> In the context of the debate about the challenge evolutionary developmental biology may offer to the neo-Darwinian view of evolution, the problem cannot be seriously attacked by limiting the comparison to sets of specific statements expressed by individual scientists, in either camp at some specified time, along the evolution of their personal thought. Indeed, it would be dangerously restrictive even to extract definitive sets of principles from mainstream textbooks or current research practice to be aseptically compared. Specifically, it can be seriously doubted whether the history of the disciplines relevant to our discussion can really offer evidence for neatly defined alternative paradigms and neatly defined revolutions. (2010, p. 214)

Like Amundson, Minelli does not explain neo-Darwinism as a kind of scientific theory with an identifiable theoretic structure. Indeed, Minelli goes so far as to say that attempting such an explanation would be "dangerously restrictive". The language that he uses to define neo-Darwinism is much the same as Amundson's; Minelli describes neo-Darwinism as a kind of "view of evolution", a "framework" (e.g., p. 220), "tradition" (e.g., p. 221), and "approach" (e.g., p. 222) to explaining and understanding evolutionary phenomena.

Minelli claims that neo-Darwinism is a view that grew increasingly focused on the adaptive results of natural selection acting on heritable variations, a reductionist view further entrenched by geneticist Theodosius Dobzhansky's widely influential 1937 claim that evolution is change in the genetic compositions of populations (p. 216). Neo-Darwinian thinking, for Minelli, explains adaptive change by way of the statistical models of population genetics, which became the explanatory foundation of neo-Darwinism. Despite the "broad absence" of development from neo-Darwinism, Minelli correctly argues that some neo-Darwinists, particularly J. B. S. Haldane, Julian Huxley, and Gavin R. de Beer, were very much interested in the intersection of development and evolution (pp. 214–215). Others, including Amundson as discussed above, have argued similarly that development was not completely absent from neo-Darwinist thinking (e.g., Burian, Gayon, and Zallen 1991; Allen 2007; Dietrich 2011).

Pigliucci and Müller (2010), however, present a different take on neo-Darwinism. Pigliucci, who has Ph.D.s in both biology and philosophy, and Müller, an evo-devo practitioner, make it clear that, on their view, neo-Darwinism helped set the intellectual stage for the Modern Synthesis of the twentieth century (p. 6). For these authors, neo-Darwinism refers to the resurgence of the Darwinian view that natural selection is the primary cause of evolutionary change and is "not to be confused, as it so often is, with the Modern Synthesis" (p. 5). They explain that Romanes coined the term *neo-Darwinism* to mock Alfred Russel Wallace's and August Weismann's pan-selectionist responses to various evolutionary alternatives to Darwinian natural selection promoted after the publication of *On the Origin of Species* in 1859. They explain further that into the twentieth century, this brand of neo-Darwinism was thought to conflict with Mendelism, the view that Mendel's recently rediscovered transmission work ruled out gradual selection of small variations, and it was this perceived conflict between neo-Darwinism and Mendelism that led to the Modern Synthesis (pp. 5–6).

The Modern Synthesis, according to Pigliucci and Müller, is "the conceptual framework that has defined evolutionary theory since the 1940s" (p. 3) that resulted from the dismantling of the Mendelian/neo-Darwinian conflict by population genetics and the "understanding and acceptance of population genetics by the majority of practicing evolutionary biologists" that followed

(p. 6). They flesh out what they refer to as the Modern Synthesis "conceptual framework" with Douglas Futuyma's (1986) summary.

> The major tenets of the evolutionary synthesis, then, were that populations contain genetic variation that arises by random (i.e., not adaptively directed) mutation and recombination; that populations evolve by changes in gene frequencies brought about by random genetic drift, gene flow, and especially natural selection; that most adaptive genetic variants have individually slight phenotypic effects so that phenotypic changes are gradual (although some alleles with discrete effects may be advantageous, as in certain color polymorphisms); that diversification comes about by speciation, which normally entails the gradual evolution of reproductive isolation among populations; and that these processes, continued for sufficiently long, give rise to changes of such great magnitude as to warrant the designation of higher taxonomic levels (genera, families, and so forth). (From Pigliucci and Müller 2010, p. 9)

Pigliucci and Müller claim that the Modern Synthesis framework is restricted by the assumption of population genetics models that genetic variation is continuous and small (gradualism) (p. 13). The framework is further restricted by its commitment to externalism, or the view that the external process of natural selection is primary (p. 13), and gene centrism, the view that the gene is the only source of heritable variation (p. 14).

How does Pigliucci and Müller's view compare to those of Amundson and Minelli? Amundson and Minelli agree that the neo-Darwinian framework 1) is founded on population genetic models of the maintenance and refinement of gene frequencies in populations through generations; 2) recognizes natural selection as the primary cause of evolutionary change; and 3) does not include developmental input. And though Piglucci and Müller's description of neo-Darwinism differs from those of Amundson and Minelli, Pigliucci and Müller's account of the framework developed during the Modern Synthesis is very much like Amundson's and Minelli's accounts of neo-Darwinism. So, for present purposes, I replace Pigliucci and Müller's take on neo-Darwinism with their account of the Modern Synthesis framework; nonetheless, it should be noted that Pigliucci and Müller adopt Romanes' original concept of neo-Darwinism and are clear that it ought not be confused with the Modern Synthesis.

Laubichler's description of neo-Darwinism is a departure from each of the accounts discussed so far. Unlike other participants in the debate of interest here, Laubichler claims that as a conceptual framework, neo-Darwinism is a gene-centered Kuhnian paradigm (pp. 199–200). He does not expand on the nature of a Kuhnian paradigm, a notoriously problematic concept (e.g., Lakatos and Musgrave 1970; Masterman 1970; Laudan 1984), but he does argue that evo-devo represents what he refers to as a counter-revolutionary paradigm shift away from the neo-Darwinian paradigm that is roughly Kuhnian in nature (p. 200). What makes this so-called counter-revolution different from a Kuhnian revolution is the return to a more Darwinian broad understanding of phenotypic evolution.

On Laubichler's view, neo-Darwinism treats phenotypes more narrowly, as epiphenomenal results of interactions between genes and populations, which are fundamental within the neo-Darwinian framework. The statistical models of population genetics are fundamental to neo-Darwinism as well since they model the dynamic effects of various conditions and population structures on genes. According to Laubichler, neo-Darwinism does not include a mechanistic account of the relations between genotypes and phenotypes because such an account requires developmental input; neo-Darwinism considers development as something that is irrelevant to the dynamic interactions that affect genetic maintenance and refinement in populations and, so, is unable to mechanistically explain phenotypic evolution (p. 201). Like the others, though, Laubichler acknowledges that some neo-Darwinists included development in their studies of evolution (p. 202). Likewise, Laubichler acknowledges the successes of neo-Darwinism. In particular for him, the mathematical models of population genetics boosted evolutionary biology to the ranks of an exact science, and neo-Darwinism has provided fruitful insights into genetic variation, speciation, and population dynamics (p. 200).

There are good reasons to ignore Laubichler's appeal to Kuhnian paradigms. First, he does not elaborate on the concept despite the many well-known criticisms of Kuhn's discussion of paradigms in *The Structure of Scientific Revolutions* ([1962] 2012). Indeed, Margaret Masterman identified twenty-one different uses of *paradigm* by Kuhn in *Structure* (Masterman 1970). Kuhn subsequently acknowledged his ambiguous use of the term and continued to rework the concept of a scientific paradigm late into his career. For the claim that neo-Darwinism is a Kuhnian paradigm to be taken seriously in light of well-known and arguably devastating criticisms, the concept of a Kuhnian paradigm must be clarified. That Laubichler did not do this indicates, most charitably, that the claim can be ignored for the present purpose of fleshing out neo-Darwinism.

A second reason to ignore Laubichler's appeal to Kuhnian paradigms is that he weakens his thesis that evo-devo represents a Kuhnian-like "counter-revolution" in relation to neo-Darwinism by pointing to the successes of neo-Darwinism. He claims that neo-Darwinism, with its abstraction of phenotypes and genes, led to conceptual innovations that "were a major theoretical breakthrough" (p. 200). He goes on to say that the combination of mathematical population genetics models with empirical studies "was no small accomplishment" because it allowed for both the theoretical and empirical study of parts of the evolutionary process. This "firmly established evolutionary biology as an exact science" (p. 200) and was supported further by the insights of molecular biology regarding the population genetics concepts of gene, allele, and mutation (p. 201). Laubichler's own description of the successes of neo-Darwinism indicates that evo-devo does not represent anything like a Kuhnian revolution since a Kuhnian revolution is the wholesale replacement of one paradigm by another. Since Laubichler acknowledges that evo-devo does not replace neo-Darwinism, neo-Darwinism need not be described as a Kuhnian paradigm, not even for argumentative purposes.

Based on the accounts of the participants of the current debate, then, neo-Darwinism is, roughly, as follows:

> Neo-Darwinism: An explanatory framework, way of thinking about, or approach to understanding and explaining evolution that is founded on the mathematical models of population genetics that model the dynamic effects of mutation, migration, drift, and natural selection on gene frequencies in populations over generational time and include abstract and limited concepts of genes and phenotypes; natural selection is understood to be the primary cause of adaptive evolutionary change narrowly defined as change in gene frequencies in populations; changes above the species level are the results of the processes modeled by population genetics over a sufficiently long time span; ontogenetic processes that bridge genotypes and phenotypes are set aside as irrelevant to explanations of evolutionary change.

Part of the difficulty of assessing whether neo-Darwinian thinking and evo-devo are compatible and, further, whether the two can be successfully merged into a synthetic theory of evolution is defining neo-Darwinism. The term has its own historical lineage that dates back to the late 19th century, to the days of Romanes, Wallace, and Weismann, and what, exactly, the term refers to has been muddied by more than 100 years of intellectual efforts in evolutionary biology. Neo-Darwinism has become closely associated with the Modern Synthesis, but the Modern Synthesis is itself a fuzzy target that many different authors have described in many different ways. My goal, however, is to investigate and strengthen the current debate, not to provide a definitive account of neo-Darwinism. Toward this end, I have provided analysis of the term as it is used by Amundson, Minelli, Pigliucci and Müller, and Laubichler, and I believe that I have provided a definition of *neo-Darwinism* that generally fits the ways in which the term is used in this debate. The question of whether neo-Darwinism so-defined accurately reflects current evolutionary biology is a different, albeit important and interesting, question.

2.2 Evo-Devo Defined

Fortunately, less work is required to find consensus among these authors on the nature of evo-devo. Amundson is clear that while the dramatic growth of molecular biology, specifically molecular developmental genetics during the 1990s, transformed interest in the connection between ontogeny and phylogeny, the interest itself is not new (p. 1). In fact, interest in the relationship between development and evolution precedes Darwin. But, discoveries of highly evolutionarily-conserved *Hox* genes and other genetic homologies in very distantly related species renewed this interest with an unprecedented molecular perspective. *Hox* genes, which contain a 180 base pair sequence called a homeobox, play important causal roles during development. The homeobox codes for a 60 amino acid protein sequence, the homeodomain, that binds with specific DNA sequences to regulate gene expression during the course of embryogenesis and are causally efficacious in the production of identifiable phenotypic units (Burian 2005b, p. 215). Differently put, *Hox* genes encode proteins that help regulate when and where specific morphologically important proteins are synthesized during development of the embryo. Through protein sequencing and molecular comparisons, it was confirmed that incredibly morphologically diverse organisms, such as *Drosophila*, or fruit flies, and humans, have *Hox* genes with stunningly similar homeoboxes. Despite our dramatic morphological differences, *Hox* genes serve as evidence of our evolutionary relatedness with *Drosophila* (p. 5). Evo-devo explains away the initial paradox by way of a complex gene regulatory network. Phenotypic evolution proceeds, in part, by way of changes in the regulation of gene expression during development.

With the insights from molecular developmental genetics, Amundson claims that the contemporary field of evo-devo aims to explain "evolution as the modification of developmental processes" (p. 247) that involve interactions between genes that work as a kind of network within a developmental system; evolutionary change takes place when the network is modified, resulting in changes in form (p. 7). In contrast with neo-Darwinism, "[e]vo-devo advocates merely believe that additional mechanisms, mechanisms involved with ontogeny rather than population genetics, must contribute to a full understanding of evolution" (p. 3). For Amundson, among the explanatory themes of evo-devo that are not part of neo-Darwinism are innovation (p. 245), homology (p. 241), modularity (p. 244), and evolvability (p. 244). The emphasis on these concepts illustrates that evo-devo breathes new life into the long-standing problems tied to the crossroads of development and evolution.

Similarly, Minelli claims that a defining feature of evo-devo is its focus on the ability (or inability) of a system to generate alternative heritable phenotypes, or the evolvability of a trait. He states, "In fact, evo-devo provides its unique contribution to understanding the evolutionary process by a description and analysis of developmental constraint and its elements" (p. 218). For Minelli, evo-devo is a research field separate from developmental biology and evolutionary biology, but it remains related to those fields through investigation of questions, like evolvability, that are of interest to both and through use of investigative tools from both (p. 220).

Pigliucci and Müller largely agree with Amundson and Minelli. They claim that evo-devo has developed as a field in its own right since the 1980s because of questions concerning phenotypic evolution that remained unanswered by the Modern Synthesis framework (p. 4). They argue that evolutionary theory needs this growing field because embryology and developmental biology did not play a role in the Modern Synthesis, and, so, the resulting explanatory framework cannot explain some evolutionary phenomena. More specifically, evo-devo eases the restriction of the framework's commitment to externalism by providing insights into the role of developmental processes and systems on phenotype specificity (p. 13). That evo-devo needs to be included in evolutionary theory because of evolutionary theory's explanatory restriction is, for them, "obvious and largely undisputed" (p. 8).

If we overlook Laubichler's Kuhnian language once again, his account of evo-devo is consistent with those of Amundson, Minelli, and Pigliucci and Müller. On Laubichler's account, evo-devo is comprised of multiple research programs and explanatory structures united in their pursuit of a mechanistic theory of phenotypic evolution (p. 201). Again, Laubichler argues that the phenotype concept of evo-devo is importantly different from the narrow concept of the phenotype emphasized by neo-Darwinism. He contends that phenotypic evolution and innovation, the core of evo-devo, rest upon an understanding of the phenotype that incorporates a broad range of causal mechanisms, including gene regulation, from various levels of biological organization and temporal scales (p. 203). That is, the phenotype of evo-devo is the dynamic result of a host of molecular, developmental, physiological, and environmental causal mechanisms across developmental, generational, and geologic time. A mechanistic theory of phenotypic evolution, then, requires much more than what is offered by the statistical models of population genetics, and, according to Laubichler, it is likely that evo-devo has the tools to provide such a theory.

Indeed, within the current debate, there is little disagreement over the nature of evo-devo. All agree that evo-devo provides unique explanations of evolutionary phenomena that are left unaddressed by the neo-Darwinian approach. The consensus is that the phenotype concept foundational to evo-devo is broader and less abstract than that of neo-Darwinism. Instead of thinking of phenotypes merely as gene products and black-boxing the rest, evo-devo conceives of phenotypes as the results of complex arrays of developmental processes that involve very specific entities and interactions at multiple levels of biological organization. Evo-devo aims to explain the evolution of phenotypes so defined, unlike neo-Darwinism, which, according to these authors, generally aims to explain changes in the genetic compositions of populations. These authors also agree that evo-devo is partially defined by the emphasis placed on the explanatory role of concepts such as evolvability, innovation, modularity, and regulation. Arguably, these concepts have little or no role in the neo-Darwinian approach because of the insignificant role of embryology and developmental biology during the Modern Synthesis.

So, evo-devo, as a term in the current debate, is generally understood in the following way:

> Evo-devo: A scientific field of study that emerged during the last decades of the twentieth century to explain evolutionary phenomena not explained by neo-Darwinism because of the lack of embryological and developmental input during the Modern Synthesis; evo-devo aims to explain phenotypic evolution, where phenotypes are understood to be the effects of complex, multi-level causal processes, and these explanations incorporate the biological concepts of evolvability, innovation, modularity, regulation, and others.

2.3 The Arguments

There are two prominent, if general, camps in the current debate. On one side are those who claim that neo-Darwinism and evo-devo are compatible and, so, some kind of synthesis is possible. Minelli and Pigliucci and Müller most clearly fall into this camp. Minelli argues that evo-devo's unique focus on evolvability does not conflict with the neo-Darwinian framework since evolvability is "amenable to" or at least partially defined by neo-Darwinian concepts (p. 218). Evolvability understood as "the ability of a genetic system to produce and maintain potentially adaptive genetic variants" (p. 219) importantly involves heritable genetic variation and selection, the two major components of neo-Darwinian thought. Evo-devo expands the neo-Darwinian framework by including the developmental processes that lie between genotypes and phenotypes as objects of investigation relevant to evolvability (p. 220). He explains that the "evo-devo perspective" constitutes a "conceptual advance" in that it examines phenotypes and genes from the joint perspective of development and evolution. Minelli states, "By focusing on evolvability, evo-devo does not disrupt the neo-Darwinian view of evolution, as a process of change based on variation and selection (plus drift). Rather, it shows what can be gained by avoiding the myopic identification of variation with allelic differences only" (p. 220). Indeed, for Minelli, the unique perspectives and explanations offered by evo-devo "may well be described as extending or complementing" the neo-Darwinian view.

Both Pigliucci (2007, 2009) and Müller (2007) have argued independently that the concepts emphasized by evo-devo research (e.g., evolvability, phenotypic plasticity, emergence, epigenetic traits, and organization) in pursuit of a mechanistic explanation of phenotypic evolution do not contradict or challenge traditional evolutionary theory. Instead, these concepts and related research work to explain previously unexplained evolutionary phenomena, thereby extending the explanatory framework developed during the Modern Synthesis.[4] Their collaboration, *Evolution: The Extended Synthesis* (2010), is devoted to what they refer to as the ongoing Extended Synthesis of evolutionary biology, the offspring of the Modern Synthesis. Here, they claim that insights from molecular genetics and genomics, as well as the concepts of epigenetics, plasticity, environmental factors, and innovation, were not part of the Modern Synthesis (p. 12). As these findings and concepts continue to gain more attention, what is currently taking place, according to them, is a shift away from statistical population dynamics toward a causal-mechanistic account of evolution that takes organismal phenotypic change out of the black box in which it was previously placed. This shift, Pigliucci and Müller claim, "brings with it a significantly expanded explanatory capacity of evolutionary theory" (p. 12).

Amundson straddles the two camps in the contemporary debate. He claims that evo-devo, which is fundamentally concerned with evolutionary changes in morphologies or developmental types, and neo-Darwinism, which is fundamentally concerned with evolutionary changes in genes in populations, are "deeply inconsistent" (p. 225). For him, the ontologies and explanatory aims of evo-devo and neo-Darwinism are severely at odds

4. In direct response to Pigliucci and Müller, I have argued elsewhere (2010, 2011) that it is incorrect to describe the ongoing changes as an extension of the Modern Synthesis framework. The Extended Synthesis view offered by Pigliucci and Müller and endorsed, perhaps weakly, by Minelli is incorrect in large part because the concepts highlighted by evo-devo research pose serious conceptual challenges to the foundation of the Modern Synthesis framework, population genetics. While it is certainly true that previously unanswered questions about the origination of novel phenotypes and the evolution of morphological diversity can now be addressed, Pigliucci and Müller fail to adequately describe the current episode of change as an extension of the Modern Synthesis framework given that framework's population genetics foundation.

with one another. Amundson argues that if a synthesis of the two is possible, either the population thinking of neo-Darwinism must weaken in order to allow room for developmental types, or the developmental types of evo-devo must be redefined in a way that makes them applicable to population thinking (pp. 256–7). Despite this, Amundson is (very) cautiously optimistic in his conclusion. He admits that it is probably the case that there is a more moderate path between these two options, though he does not see a clear way to dismantle the dichotomous conflicts between evo-devo and neo-Darwinism. Still, Amundson is hopeful that the continued success of both will illuminate their compatibility and the path toward a new synthesis (p. 257).

Laubichler represents the opposing camp by arguing that evo-devo significantly challenges neo-Darwinian thinking on conceptual grounds. This conceptual challenge is two-fold: 1) at the core of evo-devo is a more inclusive concept of the phenotype than that of neo-Darwinism; and 2) alongside the broader phenotype concept are concepts that are either original to or crucially transformed by evo-devo's organism-based approach. The latter include regulatory networks and their evolution, modularity, plasticity, and innovation (p. 204). Evo-devo's conceptual challenge to neo-Darwinism, then, takes the form of a causally complex mechanistic approach to phenotypic evolution grounded in concepts that are integral to organismal developmental processes rather than the "conceptual abstractions of 'gene' and 'population'" (p. 209) of gene-centric neo-Darwinism.

In terms of this debate, there is at least one thing upon which all of the participants agree: both neo-Darwinism and evo-devo, two different, evidentially supported explanatory apparatuses, explain or account for different evolutionary phenomena. That is, both explanatory frameworks, with their different concepts and focuses, are applicable to the study and explanation of evolutionary changes. In what remains, I argue that this indicates that there is a relative significance issue between neo-Darwinism and evo-devo. Differently put, I contend that the applicability of these two different explanatory frameworks to different evolutionary phenomena demonstrates that there is a relative significance issue here, which suggests further that both neo-Darwinism and evo-devo will continue to develop as different frameworks rather than participate in a theoretical synthesis. Though it has been overlooked until now, this line of argument is supported by the terms and arguments of this debate as they have been developed by these authors. First, in section three, I expand upon the claim that neo-Darwinism and evo-devo explain different evolutionary phenomena.

3. Different Phenomena Explained

A closer look at what is uncontroversially agreed upon, at least by those involved in the current debate, to be the foundation of the neo-Darwinian framework, the models of population genetics, and evo-devo helps to show that they explain different things. In section four below, I use this and the work of John Beatty (1995, 1997) to argue that a relative significance issue exists between neo-Darwinism and evo-devo.

3.1 The Population Genetics Foundation of Neo-Darwinism

Between 1918 and 1932, population geneticists Ronald Fisher, Sewell Wright, and J. B. S. Haldane developed the statistical models needed to explain the dynamic effects of mutation, migration, drift, and natural selection on gene frequencies of actual populations over generational time, thereby demonstrating the compatibility of Mendelian inheritance and Darwinian natural selection (e.g., Provine 1971; Lewontin 1980; Beatty 1986; Ridley 2004; Millstein and Skipper 2007). Simply put, these statistical models, according to William Provine, demonstrated how mutation, migration, drift, and natural selection could account for evolution (1980, p. 55). Indeed, Provine (1971) claims that Fisher, Wright, and Haldane did more than develop theoretical population genetics—they were the architects of the Modern Synthesis, during which they succeeded in quantitatively synthesizing Mendelian heredity, Darwinian selection, and statistical methods through the development of population genetics models (139–140). However, Provine later admitted that his initial description of the Modern Synthesis was inaccurate, and, in response, he argues that the Modern Synthesis is more accurately described as an "evolutionary constriction" (1989, p. 165). Provine (1989) claims that the Modern Synthesis was a time during which biologists from various fields winnowed down non-Darwinian alternatives (p. 176) because the mathematical and theoretical works of Fisher, Wright, and Haldane clearly showed that evolution could be explained with relatively few variables, far fewer variables than biologists had ever anticipated. It was during the Modern Synthesis that constriction based on the tools of population genetics spread throughout the study of evolution, and population genetics resulted in "a new way of seeing evolutionary biology" (p. 177).

Fisher's most detailed explication of his general theory of evolution, which I refer to as his Genetical Theory of Natural Selection (GTNS)[5], is found in his book of the same name, *The Genetical Theory of Natural Selection* ([1930b] 1958a). Here, Fisher relies on an analogy with statistical mechanics to demonstrate the relationship between Darwinian natural selection and Mendelian inheritance. Fisher's particular aim was to explain how natural selection affects evolutionary change in populations given the principles of Mendelian inheritance (Fisher 1930; Skipper 2002, p. 343). The details of Fisher's GTNS remain a topic of debate over 80 years after the publication

5. This abbreviation comes from Skipper (2002, p. 342).

of the first edition of his treatise. For example, papers by George Price (1972), Warren Ewens (1989), Anthony Edwards (1994), Anya Plutynski (2006), and Robert Skipper (2007) each argue for a particular interpretation of Fisher's "Fundamental Theorem of Natural Selection," which Fisher discusses in chapter two of *The Genetical Theory of Natural Selection*.

Generally, Fisher's GTNS is understood as follows:

> GTNS: Evolution occurs in large, randomly mating or panmictic populations and is driven primarily by natural selection, or mass selection, at low levels acting on the average effects of single allele changes (of weak effect) at single loci independent of all other loci (Skipper 2002, p. 343).[6]

As the GTNS illustrates, Fisher believed evolutionary phenomena take place in large populations where mating is random. All evolutionary change is primarily the result of natural selection, which acts upon allelic variation supplied by mutation.

Wright's earliest presentations of what he referred to as the Shifting Balance Theory (SBT) are his highly mathematical long paper of 1931 and its non-technical 1932 complement (Wright 1931, 1932; Skipper and Dietrich 2012, p. 16). In his four-volume *Evolution and the Genetics of Populations* (1968, 1969, 1977, 1978), Wright further develops his SBT. Throughout the course of his work, Wright describes the goal of his SBT in various ways. In 1931 and 1932, Wright claimed the goal of the SBT was to explain the ideal conditions needed for evolutionary change. By 1978, however, Wright strengthened this claim, stating that the SBT explained the "principal process by which cumulative evolutionary change occurred in nature" (Skipper 2002, 344). Wright readopted his statement from the 1931 and 1932 papers, once again claiming the goal of his SBT was to explain the ideal conditions required for evolution to take place (Skipper 2002; Skipper and Dietrich 2012).

To illustrate the three phase shifting balance process through which Wright believed evolution proceeded, he graphically depicted a two-dimensional metaphorical adaptive landscape that has become one of the most influential diagrams in evolutionary biology (Dietrich and Skipper 2012; Skipper and Dietrich 2012; for Wright's adaptive landscape figures, see Figure 1 at the end of this article). The diagram represents possible gene combinations along with their adaptive values. The contour lines of the diagram depict the "hilly"

6. As Skipper (2002) points out, this summary of the GTNS "has remained essentially unchanged for the last 70 years" (p. 344). While some of the details of Fisher's GTNS, such as the Fundamental Theorem, still foster debate over the correct interpretation, this summary of the GTNS is fairly uncontroversial.

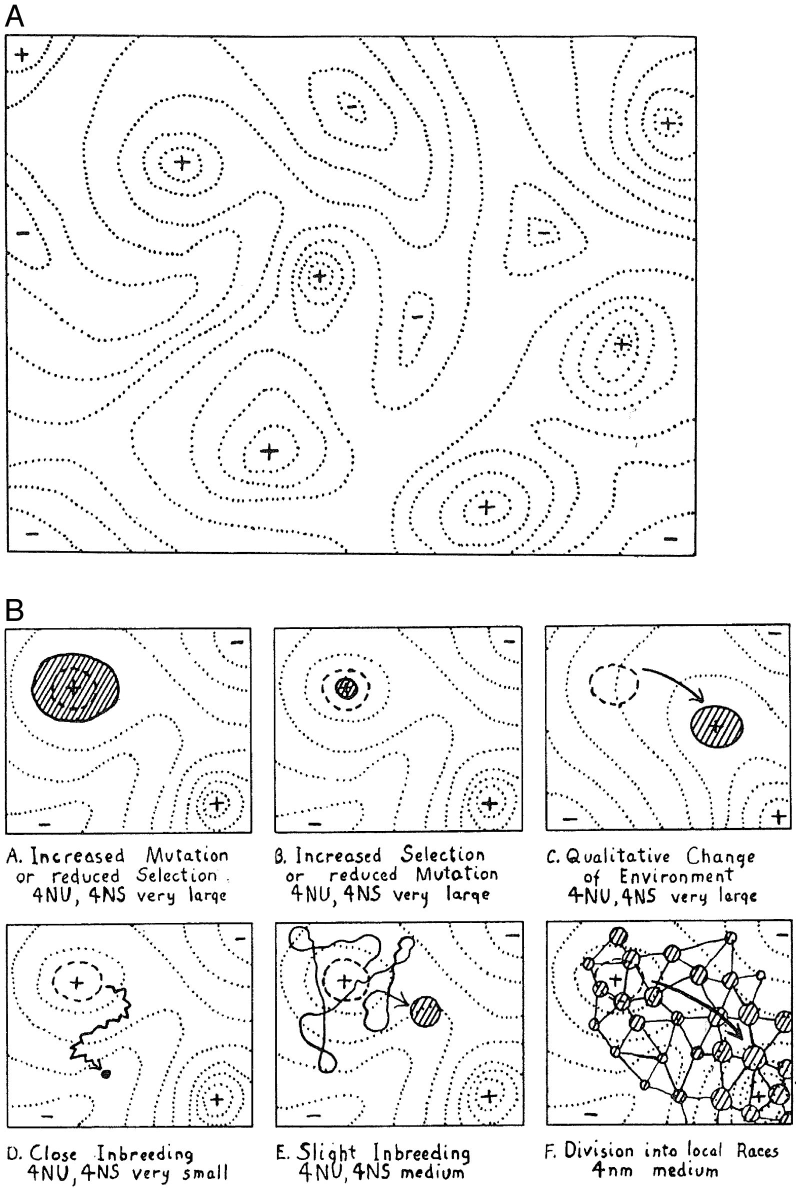

Figure 1. Wright's adaptive landscape figures (Wright 1932: 358, 361). 1A represents possible gene combinations and their respective adaptive values. 1B represents evolution on the landscape of 1A under different conditions. In A–E, the intensity of selection (s) and rate of mutation (u) vary, as does population size (N, nm). The view that Wright explains in the SBT is represented by F.

surface of the landscape due to the epistatic relations between genes. The adaptive "peaks" of the landscape, designated by "+", represent possible gene combinations with high adaptive value. The adaptive "valleys", designated by "−", represent possible gene combinations with low adaptive value. Wright was clear that due to the number of possible gene combinations, the actual population genetics of how evolution proceeds would require a diagram depicting several thousand dimensions (Wright 1932; Skipper 2002, p. 344; Dietrich and Skipper 2012).

Wright used his adaptive landscape to describe what he believed were the ideal conditions for a population to reach the optimal adaptive peak. Ideally, peak shifts take place in three stages or phases, according to Wright. First, genetic drift, typically maladaptive, moves semi-isolated subpopulations into adaptive valleys. In this first phase, drift changes the gene frequency distribution of subpopulations in such a way that subpopulations lose fitness, thus landing them in adaptive valleys. Second, within the subpopulations, mass selection acts to move subpopulations to adaptive peaks and out of adaptive valleys. In this second phase, mass selection changes the gene frequency distributions of subpopulations in such a way that the fitnesses of those subpopulations is raised, thus pushing them from adaptive valleys to adaptive peaks. Third, differential dispersion, or the migration of some members of more fit subpopulations to less fit subpopulations, drives interdemic selection, or selection between subpopulations, which pulls the global population up its optimal peak. In this third phase, interdemic selection changes the gene frequency distribution of the global population in such a way that the fitness of the entire population is raised.

As the foundation of neo-Darwinism, Fisher's GTNS and Wright's SBT illustrate the kinds of evolutionary phenomena explained by the framework. Fisher and Wright both provided mathematical models that attempt to explain how dynamic microevolutionary processes and population size and structure cause evolutionary change where evolutionary change is defined as change in the genetic compositions of populations. The models of population genetics provided the theoretical and statistical tools needed to investigate the possible causes of evolutionary change in different kinds of actual populations.

3.2 Evo-Devo Research

Evo-devo is partially comprised of several areas of research, many of which overlap. Müller (2007) provides an introduction to predominant areas of research within the field. A quick look at these research areas sheds light on the phenomena explained by evo-devo.

One predominant area of research within the field of evo-devo integrates comparative embryology, morphology, and genetics to focus on similarities and differences at multiple levels of biological organization, from the genetic, molecular, and cellular levels up, in order to understand how the ontogenies and morphologies of species have changed over time. Fossilized embryos and other evidence from paleontology allows for comparison of the morphogenetic and embryological differences between primitive and extant species (Müller 2007, p. 943). Comparative genomics compares sequences, expression patterns, and gene products and interactions, which allows for comparison of developmental sequences (Laubichler 2007, p. 349). The comparative approach provides evidence of significant changes in developmental pathways and morphologies in species over geologic time and provides evidence of phylogenetic relationships. This particular area of research utilizes comparative techniques to determine how aspects of development changed over time. Concepts and methodologies from paleontology, comparative embryology, comparative morphology, comparative genomics, and systematics are integrated to better understand the evolution of developmental processes and outcomes.

A second area of research within evo-devo focuses on the components and interactions of both genetically determined and non-genetically determined properties of developmental systems. What is of interest here are the properties of development that are not controlled directly by genes, such as self-organization, cell-cell signaling, and developmental timing, and how these epigenetic factors influence evolutionary changes. Changes in cell number or developmental timing can produce phenotypes found in ancestral organisms (Alberch and Gale 1985). The aim of this research is twofold. One goal is to better understand and explain the complex dynamics of development, as well as the effects of environmental influences on developmental systems and resulting morphologies. A second goal of this research is to understand and explain how particular changes to developmental systems can affect evolutionary change. Such research is closely related to experimental embryology (Laubichler 2007, p. 349), and thus borrows methodologies and concepts from its predecessor. Also integrated in this research are aspects of developmental genetics, systems biology, epigenetics, and ecology.[7]

7. Laubichler (2007, p. 349) and Müller (2007, p. 943) distinguish this area of research from what they both refer to as the evolutionary developmental genetics program. Both programs focus on components and interactions that comprise developmental processes; the only difference I see is that Laubichler and Müller's evolutionary developmental genetics program does not include epigenetic or environmental factors. Fundamentally, however, I see no reason to describe these as two different areas of research because the general focus of both is developmental systems. The researcher who focuses on developmental genes and the researcher who focuses on epigenetic and environmental factors still share a common object of interest—developmental systems. At any rate, nothing much hangs on Laubichler and Müller's separation of these research areas.

Another evo-devo area of research uses computational modeling and simulation to relate changes at the genetic level to changes at the cellular and tissue levels (Müller 2007, 943). Exciting results of this research include the computational ability to reconstruct gene expression during embryonic development in three-dimensions and the development of a quantitative approach to model the trajectories of ontogenetic shapes (Müller 2007, p. 943). Müller claims that the theoretical tools utilized in this research "help to localize the ontogenetic components of phenotypic change, assist in the organization of data and link evo-devo with quantitative genetics and with the study of morphological integration" (pp. 943–4).

3.3 Explanatory Differences

The areas of research within evo-devo explain morphological, or phenotypic, change within and across taxonomic levels over a range of time spans. Explanations of this kind include the origin of novel morphologies and changes in gene regulation, ontogenetic processes, and the diverse causally-relevant components of those processes, e.g., genes, molecular and environmental signals, transcription factors. Each of the aforementioned areas of research involve investigations of entities, activities, and the organization of those entities and activities at multiple levels of biological organization, including, at least, the genetic, molecular, cellular, tissue, and organismal levels. No particular level is privileged in evo-devo's multi-level approach to mechanistically explaining phenotypic change.

As characterized by the current debate, neo-Darwinism, on the other hand, explains the effects of microevolutionary processes, most particularly natural selection, and population structures on the genetic makeup of organismal populations where phenotypes are narrowly thought of as a means of tracking genes. Such explanations pay no significant attention to the entities and processes involved in individual development, and the general explanatory focuses are the genetic and populational levels. Perhaps most indicative of the explanatory differences between neo-Darwinism and evo-devo are the different ways in which the two treat the relations between genes and phenotypes. According to the debate of interest here, neo-Darwinism places the causally complex processes of development that are the physiological links between genes and phenotypes into a black box and sets that box aside as explanatorily irrelevant while evo-devo takes the contents of the black box and attempts a multifaceted explanation of its origin and subsequent evolution. More simply, evo-devo explains phenomena that are seemingly explanatorily irrelevant within the neo-Darwinian framework as that framework is depicted by the current debate. The neo-Darwinian framework, absent significant embryological and developmental influence, explains populational changes using a phenotype concept that allows for gene tracking through generations.

Nonetheless, the phenomena explained by each are evolutionary phenomena. Changes in and maintenance of the genetic compositions of populations and heritable changes in morphologies and developmental processes are ways in which biological entities, understood to include super-organismic entities such as populations and species, are modified in relation to their ancestors over time. Natural selection, mutation, migration, drift, environmental factors, and heritability all play some role in both kinds of changes. That neo-Darwinism and evo-devo explain different evolutionary phenomena shows that evolutionary change is indeed heterogeneous. That is, not all evolutionary phenomena are the same; evolution encompasses different phenomena that are explained by different explanatory frameworks. This heterogeneity is apparent within the current controversy—all engaged in it acknowledge, if only implicitly, that neo-Darwinism explains some evolutionary phenomena and evo-devo explains others.

As I see it, this heterogeneity and the different explanatory frameworks that explain different parts of it point to a relative significance issue. Moreover, I believe that the relative significance issue suggests that both of these explanatory frameworks will survive in evolutionary biology rather than form a synthetic theory that explains all of the phenomena in the heterogeneous domain. Again, my claim that the relative significance issue indicates that both frameworks will continue to develop unsynthesized says nothing of the possibility of a synthesis, and my claim need not be interpreted as staking a claim on whether neo-Darwinism and evo-devo are compatible. Instead, my claim, built using the conceptual tools of the ongoing debate, employs what is agreed upon within the debate, namely, that both well-supported frameworks explain different evolutionary phenomena, to address what I take to be the true underlying concern of the debate: the likely direction of neo-Darwinism and evo-devo.

4. Relative Significance and Synthesis

Beatty, who introduced and expanded upon the nature of relative significance controversies in the 1990s, argues that a plurality of evidentially supported explanatory frameworks[8] may be required to account for the different phenomena that comprise heterogeneous scientific domains. In other words, it is sometimes the case that the evidence suggests that bodies of related but

8. Beatty uses *theory*, *mechanism* (e.g., 1995, p. 65), and *models* (e.g., 1997, p. S432) to refer to those scientific constructs that account for items in scientific domains.

different phenomena, or heterogeneous domains[9], cannot be accounted for by a single explanatory framework. In such a case, a relative significance issue may exist. Instead of taking issue with which framework is the ultimately correct framework in a winner-takes-all scenario, debates over relative significance concern the significance of one well supported framework relative to the other(s) where significance is assessed, roughly, in terms of "the proportion of phenomena within the domain" that is correctly accounted for by the framework (Beatty 1997, P. S432). Put differently, in domains where a variety of phenomena are accounted for by a number of evidentially supported frameworks rather than a single framework, the question of a relative significance dispute is the extent of applicability of one framework relative to another (Beatty 1995, p. 66).

Beatty contends that relative significance controversies are prevalent in the biological sciences and can be found at all levels of biological investigation (1997, P. S434). In fact, Beatty claims that "there are reasons to be a theoretical pluralist with respect to *every* domain of distinctly biological phenomena, and reasons to anticipate relative significance controversies within every domain" (1995, p. 67, italics original). He argues that one reason for this is the highly contingent nature of evolutionary outcomes[10], an aspect of evolution and biology more generally that distinguishes it from physics where universal generalizations hold throughout a domain. To say that evolutionary outcomes are contingent is to say that nature does not necessitate a particular evolutionary outcome; starting with the same set of initial conditions, evolution can result in a variety of outcomes that are contingent upon the details of particular evolutionary histories (1995, p. 57). Beatty explains that evolution has produced various gene regulation mechanisms, various reproductive systems, and various speciation

9. Dudley Shapere (1974) provides a detailed discussion of scientific domains, which he describes as bodies or areas of related items that are objects of scientific investigation. Shapere states that the 1974 paper "will not provide a systematic examination of reasons for associating items into domains, or for associating domains into still larger domains" (p. 526), but he is clear that the generation of domains depends in part on the relationships between items of the domain being well grounded and significant (p. 526). It is also clear from the preceding quote and the rest of Shapere's paper that the scope of any given domain may vary relative to another. This is consistent with Beatty's use of the term. Beatty's domains are of evidentially related phenomena that are the objects of scientific explanation.

10. Beatty (1997) is careful to distinguish what he sees as a lack of laws in biology from the contingent nature of biology in his discussion of the reasons for the prevalence of relative significance controversies in biology. He says to attrubute the prevalence of relative significance issues in biology to the lack of biological laws is a restatement of the problem rather than an explanation of it (1997, p. S435). Beatty (1995) is clear that his thesis and argument are a further elaboration and defense of Stephen Jay Gould's claims about what he refers to as the "contingent details" of evolution in *Sexual Selection* (1989).

mechanisms (1997, p. S436), all of which are the contingent results of their own distinct evolutionary histories and all of which are accounted for by different theories and models. He acknowledges that while extreme phylogenetic conservatism and/or extreme parallel evolution could result in single accounts of the phenomena within biological domains, evolutionary outcomes are more often not so constrained or conserved (1997, p. S436). So, Beatty concludes that "[t]o the extent that the outcomes of evolution are not so constrained, then, biologists will often be faced with a variety of alternative mechanisms, described by a variety of alternative theories or models, and they will be forced to deal with issues of relative significance" (p. S436). Richard Burian (1988) argues similarly that the contingent nature of evolution suggests that a unifying synthetic theory of evolution may not be possible despite the widespread and long-running curse of "physics envy", which "expresses itself in the desire for a grand unifying theory" (p. 257).

Where relative significance controversies exist, there is no presumption of the possibility of a synthetic theory like in physics. Instead, relative significance controversies are indicative of a kind of theoretical pluralism[11] that exists when the evidence supports the accommodation and pursuit of more than one explanatory framework within a single scientific domain (Beatty 1997, p. S432). That is, the theoretical pluralism reflected by relative significance controversies is one where a plurality of different explanatory theories, models, mechanisms, etc. is well supported by the evidence relevant to the different phenomena of a heterogeneous domain. Given empirical support, different models are investigated and expanded. To flesh out what he means by theoretical pluralism, Beatty provides an example from molecular genetics of the pursuit of more than one model of gene regulation, such as models of negative induction, negative repression, positive induction, positive repression, and attenuation (1997, p. S433). There is a wealth of evidential support for each of the regulation models, and molecular geneticists do not question which is the universally correct model of gene regulation while pursuing individual models. Beatty states, "[t]here is general agreement that each theory accounts for at least some instances of gene regulation, although the issue remains as to *what proportion* of cases each

11. Beatty distinguishes what he means by *theoretical pluralism* from other kinds of theoretical pluralism present in the literature in his 1995 paper, notes 22 and 23 and in the second section of his 1997 paper. What he has in mind is different from the kind of pluralism described by Sandra Mitchell (1992) that "refers to the incorporation of multiple, coacting causal agents within one theory: a developmental theory that includes genetic and environmental factors, an evolutionary theory that includes selection and drift, etc." (Beatty 1997, p. S433). Beatty's theoretical pluralism, according to him, is also different from the kind of pluralism advocated by John Dupré (1993).

theory correctly describes, or in other words, the *relative significance* of each theory" (1997, p. S433 italics original).

Beatty provides several examples of relative significance controversies in biology, including debates over the extent of applicability of selection theories and neutral theories to microevolutionary change, gradualist theories and punctuated equilibrium theory to macrovevolutionary change, and a variety of theories of speciation to speciation phenomena (1997, p. S434). Following Beatty's lead, other philosophers of biology have argued for other cases of relative significance issues. Michael Dietrich (2010), for example, recasts the debate over the possibility of distinct macroevolutionary causal processes—"significant causal processes that are found only in evolution above the species level" (p. 172)—as one regarding the relative significance of micro- and macroevolutionary processes. Through discussion of both the emergent character approach and the emergent fitness approach to thinking about species selection, largely identified with the works of Elisabeth Vrba (e.g., 1984, 1989) and Elisabeth Lloyd (e.g., 1988) and Stephen Jay Gould (e.g., 1993, with Lloyd) respectively, Dietrich argues that "[s]pecies selection represents the best case for a distinct and unique causal process operating only in macroevolution. Once species selection is recognized, however, the question becomes: how frequently does it occur?" (p. 175). He concludes that relative to microevolutionary processes, well-established macroevolutionary processes currently "are relatively rare and so are of minor evolutionary consequence when the entirety of the domain of evolutionary biology is considered" (p. 176). Dietrich explains that more cases of macroevolutionary processes may be established in the future, and as more cases are established, the relative significance of such processes may increase within the heterogeneous domain of evolutionary biology (p. 176). Indeed, different evolutionary changes, those within populations and species and those above the species level, can be caused, and thus accounted for, by distinctly different kinds of processes, and Dietrich draws attention to the relative significance of these different kinds of processes.

Another example of a relative significance controversy comes from Robert Skipper (2002). Here, Skipper's interest is in what he calls the "heated debates" between Jerry A. Coyne, Nicholas Barton, and Michael Turelli (1997, 2000) and Michael J. Wade and Charles J. Goodnight (1998, 2000) regarding Fisher's and Wright's evolutionary theories described in section 3.1 above. As Skipper explains, Fisher and Wright debated the details of their respective theories from 1929 until Fisher's death in 1962, and Wright continued to refine his theory until his death in 1988 (p. 341). The debate led by Coyne and Wade between 1997 and 2000 "rekindled if not thoroughly reignited the Fisher-Wright controversy," thereby demonstrating the controversy's persistence according to Skipper (p. 341). Skipper conducts a detailed and thorough examination of the argumentative structure of the Coyne-Wade debate to argue that "the reignited Fisher-Wright controversy is what Beatty (1995, 1997) calls a 'relative significance controversy'" (p. 342). That is, Skipper claims that the debate between Coyne et al. and Wade and Goodnight is one over the relative significance of Fisher's and Wright's evolutionary theories.[12] Their arguments do not address which theory captures all evolutionary phenomena; instead, the new controversy acknowledges that both theories account for some phenomena within the heterogeneous domain of evolutionary biology.

I contend that the issue of relative significance exists for neo-Darwinian theory and evo-devo as well. The evidence for such an issue is found within the confines of the current debate over the relationship between the two and the possibility of synthesis. Within this debate, there is no question that both frameworks are well supported by the available evidence. As a group, Amundson, Minelli, Pigliucci and Müller, and Laubichler disagree about the relationship between neo-Darwinism and evo-devo, but they agree that both are strongly evidentially supported. No one denies that both frameworks have developed in light of decades of evidence from an assortment of biological specialties to successfully explain and add to our understanding of evolutionary phenomena differently conceived. This is not to suggest that either framework is without anomalies or that the explanations built using these frameworks are free of problems. Neo-Darwinism and evo-devo are successful in part because they allow for explanations of evolutionary phenomena that are consistent with observations, predictions, and explanatory frameworks from other areas of biology—like paleontology, genomics, and cell biology, for example—and, at the same time, leave room for fruitful remodels of and developments to their existing frameworks.

Relatedly, both explanatory frameworks are applicable within the domain of evolutionary biology—a heterogeneous domain that includes those heritable changes that take place over generational and geologic time in organisms and super-organisms—and again, this much is acknowledged by Amundson, Minelli, Pigliucci and Müller, and Laubichler. The authors engaged in this debate agree that both frameworks explain different evolutionary phenomena. As explained in sections two and three above, the

12. More particularly, Skipper argues that Coyne et al.'s conclusion that Wright's SBT is not explanatorily adequate is based on their assessment of the generality of scope of the SBT in population genetics. This assessment strategy conflicts with how theories are to be assesed in relative significance controversies where explanatory adequacy is assessed based on the scope of application and not the generality of scope. So, Coyne et al.'s assessment strategy conflicts with the argumentative structure of the larger relative significance controversy in which Coyne et al. and Wade and Goodnight are engaged, resulting in a controversy dynamic where the participants "are, to a significant extent, talking past each other" (p. 342).

debate stipulates that evo-devo explains phenomena that are left unexplained by neo-Darwinism, specifically the evolution of phenotypes and developmental entities and activities, such as *Hox* genes, transcription factors, and the regulation of gene expression. Neo-Darwinism does not explain these things, according to this debate, because it black-boxes the developmental nexus that connects genes and phenotypes. This black-boxing, along with the different ways in which each framework conceives of genes and phenotypes, demonstrates that neo-Darwinism and evo-devo explain different evolutionary phenomena. And it is important to note that this debate does not question which of these frameworks is universally applicable; this debate does not resemble the kind of debate that is found in, say, quantum physics where part of what is at stake in the debate over string theory and loop quantum gravity theory is which theory explains all of the properties of quantum gravity, time, and space. Rather, this debate is built around the central understanding that both neo-Darwinism and evo-devo account for or explain some evolutionary phenomena; otherwise, there would be no reason to question whether a synthesis of the two is possible.

There is the question, then, of which framework is more significant, or rather, which accounts for the largest proportion of phenomena within the heterogeneous domain of evolutionary biology. I take this relative significance issue to be evidence of current and future theoretical pluralism in evolutionary biology. To be clear, I have in mind the same kind of theoretical pluralism as Beatty. So, for my purposes here, theoretical pluralism, often advanced as an alternative to theoretical synthesis and reductive or eliminative approaches, obtains when more than one explanatory framework is applicable within a heterogeneous domain. A major component of Beatty's account of relative significance controversies is that they are indicative of theoretical pluralism so construed. Because of the contingency of evolutionary outcomes on the details of particular evolutionary histories, similar phenomena, such as speciation events and gene regulation, are the results of different processes that are explained by different explanatory frameworks. Importantly, in cases where theoretical pluralism obtains, theoretical pluralism itself is supported by the available evidence—each theory is supported by the available evidence, so it is not the case that theoretical pluralism results from insufficient evidence in support of a single synthetic theory (Beatty 1997, p. S434).

Embracing the relative significance issue facing neo-Darwinism and evo-devo requires acknowledging that theoretical pluralism obtains for evolutionary biology. Indeed, I believe that this theoretical pluralism will continue to be the case for some time to come. Regardless of whether a synthesis is possible, the relative significance issue between neo-Darwinism and evo-devo suggests that, in light of supporting evidence, both will continue to be pursued and further developed as individual explanatory frameworks within this heterogeneous domain. As is the case with the relative significance issues discussed above, when two or more frameworks are applicable and evidentially supported within a heterogeneous domain, those individual frameworks continue to develop as relatively distinct frameworks. This point is particularly clear in Beatty's examples of reproductive systems, speciation, and gene regulation models, as well as the example of the "persistent" Fisher/Wright debate discussed by Skipper. As Beatty claims, a variety of models are pursued in order to account for the heterogeneous domain of gene regulation, and these models continue to be pursued in order to flesh out the details and extent of applicability of each. Likewise, as illustrated by the exchange between Coyne et al. and Wade and Goodnight, Fisher's and Wright's models continue to be applied and discussed well after their developers' deaths. At least within biology, the kind of theoretical pluralism associated with relative significance issues tends to remain over time rather than give way to synthesis, reduction, or elimination.

Indeed, I suspect that this will be the case for neo-Darwinism and evo-devo as well. The current debate over the relationship between the two frameworks, waged in order to answer whether a synthesis of the two explanatory frameworks is possible, leads us to question their relative significance in the domain of evolutionary biology. I believe that this relative significance issue, in turn, indicates that both neo-Darwinism and evo-devo will continue to be pursued and developed well into the future.

At the very least, however, I hope to have illustrated that the current debate has missed a line of argument in favor of the possibility that theoretical pluralism will prevail in evolutionary biology. And it is important to give this possibility its due consideration. As Beatty claims, generally speaking, it is in principle possible that a theoretical synthesis may be the resolution to relative significance issues, but "it is by no means clear that progress lies in the direction of a singular theory for each domain" (1997, p. S435). In response to David Hull's (1987) argument that theoretical unity ought to be the aim of biological investigations, Beatty argues that such an aim should be scientifically supported. If extreme phylogenetic conservatism and/or extreme parallel evolution are unrealistic assumptions in biological domains or are not supported themselves, then biologists may not have good scientific reason to adopt a scientific methodology that includes the stipulation that a unitary account ought to be pursued. Beatty also briefly discusses the idea that the pursuit of a single theory may blind investigators to the heterogeneity of their domain of interest and the idea that such pursuits may lead to oversimplifications of complex phenomena and restrict new lines of research (1997, p. S440). To avoid the possibility that the question of synthesis has oversimplified the current debate or blinded it to the alternative of theoretical pluralism prevailing, I offer the preceding argument.

5. Conclusion

In this paper, I have argued that the current debate over the possibility of a synthesis of neo-Darwinism and evo-devo waged by Amundson, Minelli, Pigliucci and Müller, and Laubichler misses the very real possibility that theoretical pluralism may continue to obtain in evolutionary biology. Through analysis of the terms and arguments of this debate, I have argued that a relative significance issue exists between neo-Darwinism and evo-devo, which suggests that these frameworks will continue to develop as unsynthesized individuals. Such is the case with relative significance issues—the theoretical pluralism that they reflect tends to persist in light of supporting evidence. Perhaps because the debate of focus is at least partially motivated by the question of synthesis, it has failed to seriously consider theoretical pluralism as an available alternative to future synthesis. If Beatty is correct about the highly contingent nature of biology and its implications, and I believe he is, then the synthesis debate would be well served by serious consideration of theoretical pluralism instead of synthesis.

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