

Is the Neo-Aristotelian Concept of Organism Presupposed in Biology?

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ABSTRACT: According to neo-Aristotelian ethical naturalism, moral goodness is an instance of natural goodness, a kind of normativity supposedly already present in nature in the biological realm of non-human living things. Proponents of this view appeal to Michael Thompson's conception of a *life-form*—the form of a living organism—to give an account of natural goodness. However, although neo-Aristotelians call themselves naturalists, they hardly ever consult the science of biology to defend their commitments regarding biological organisms. This has led many critics to argue that the neo-Aristotelian account of natural normativity is out of touch with the findings of modern evolutionary biology. One line of response to this objection, presented by John Hacker-Wright and Micah Lott, claims that the neo-Aristotelian concept of a living organism has to be presupposed in evolutionary biology as long as organisms are the subjects of evolutionary explanation. In this paper, I examine this response by tracing the concept of organism in modern evolutionary biology. I first argue that the Modern Synthesis theory of evolution, which understands evolution as change in gene frequencies within a population, does not presuppose the relevant concept of organism. I then explore an alternative view of evolution that has emerged in the past twenty years from advances in evolutionary developmental biology. I argue that this so called 'evo-devo' approach makes room for an explanatory concept of organism that can be reconciled with the neo-Aristotelian view. Moreover, I argue that although the explanatory role of the concept of organism in evolutionary biology is still contentious, the well-established role of this concept in *developmental* biology can be used to defend the biological commitments of neo-Aristotelian naturalism.

1. Introduction

Neo-Aristotelian ethical naturalism attempts to place ethical normativity in the natural world using ideas from Aristotle's teleological metaphysics. Defenders of this view such as Philippa Foot and Rosalind Hursthouse argue for a continuity between the ethical and the natural domain. They argue that ethical normativity is an instance of *natural goodness*, a kind of normativity that they claim can also be found in nature among plants and non-human animals. On this view, the goodness of moral virtues such as justice and benevolence in humans is in an important sense similar to the goodness of deep roots in an oak tree. In the same way that an oak tree is good insofar as it has deep roots that allow it to flourish *qua* oak tree, a human is good insofar as she follows virtue and reason which allow her to flourish *qua* human.

The first step of the neo-Aristotelian project is finding a place for natural goodness in the biological world, i.e., giving an account of what makes the deep roots of an oak tree *good*. A paradigmatic account of natural goodness is offered by Philippa Foot (2001). According to Foot, natural goodness is a form of evaluation that is exclusively attributable to living things and their parts and operations in virtue of their nature as living things and according to their form of life. Foot's understanding of a living thing's form of life is based on Michael Thompson's work on representations of life.

Thompson (2008) argues that there is a distinctive form of thought that we use exclusively in relation to living things, and claims that this form of thought can direct us toward an understanding the nature of life. This is the form of thought that we typically encounter in descriptions that we find in a nature documentary or a field guide about a certain kind of living thing. These descriptions are statements such as "cats have four legs" or "beavers build dams", which do not concern individual organisms and have a generic form. Thompson calls statements of this form *Natural-Historical Judgments*. According to Thompson, natural-historical judgments articulate the characteristic features and activities of the form of life, or the *life-form*, to which individual living things belong. Moreover, he maintains that these judgments can underwrite evaluations of natural goodness and defect.

Thompson argues that natural-historical judgments have a generic meaning that is distinct from universal or statistical generality. They are neither universal generalizations about *all* instances of a kind nor statistical generalizations about *most* instances of the kind. The truth of a natural-historical judgment about a life-form is consistent with some or even most instances of the life-form not matching the general description that is expressed in the judgment. For instance, the natural-historical judgment "cats have four legs" will be true even if most cats lose one of their legs. But, according to Thompson, what we can infer about such non-conforming instances is that there is something defective about these instances. We can say, for instance, that a cat with only three legs is defective in that it doesn't have four legs. Thus, Thompson argues our conception of a life-form, which can be expressed by a set of natural-historical judgments, underwrites evaluative inferences to natural goodness and defect.

Foot (2001) argues that the relevant generic judgments about a life-form are the ones that have a teleological significance and specify what "plays a part" in the characteristic life of the life-form. Take, for instance, the two judgments "the male peacock has a brightly-colored tail" and "the blue tit has a blue patch on its head". Foot argues that these judgments are superficially

similar, but only the former underwrites inference to goodness and defect. This is because a male peacock's brightly-coloured tail plays a part in the characteristic life of the bird by attracting mates in a way that a blue tit's having a blue patch on its head does not (Foot, 30). Hence, evaluations of natural goodness evaluate parts and aspects of an organism based on their function in enabling the organism to flourish, i.e., to exemplify the characteristic life cycle of its life-form. Foot argues that for plants and non-human animals, the life cycle roughly consists of self-maintenance and reproduction. But each life-form has its own characteristic way of achieving these ends, which determines the norms of natural goodness for the bearers of that life-form. Moreover, the evaluations of natural goodness also extend to the human life-form, where they also include evaluations of moral goodness. This is how neo-Aristotelians argue that moral virtues such as justice and benevolence are instances of natural goodness: they "share a basic logical structure and status" with evaluations of plants and animals (Foot, 27).

One of the major objections to neo-Aristotelian naturalism targets this account of natural goodness. Critics turn to evolutionary biology and other biological sciences to argue that the neo-Aristotelians' teleological commitments regarding living things are not tenable in light of what science tells us about the domain of life. Some critics appeal to an evolutionary understanding of human nature to question whether substantial virtues like justice and benevolence are instances of natural goodness in human beings (e.g., Millgram 2009; Andreou 2006; and Woodcock 2006). Others appeal to an evolutionary account of the concept of biological function to undermine the concept of function that underlies the neo-Aristotelian account of natural goodness (e.g., Fitzpatrick 2000; Lewens 2010; Odenbaugh 2017). As I have argued elsewhere (Moosavi 2018), these objections share a basic structure and ultimately raise a problem of *naturalistic credentials* for neo-Aristotelian naturalism. The idea is that, in order to show that the account of natural normativity that they call 'natural goodness' is in fact *natural*, neo-Aristotelians need to show that it is *necessary* for understanding living things and cannot be dispensed with in light of evolutionary biology.

In response to the evolutionary objections, some neo-Aristotelians such as Hacker-Wright (2009) and Lott (2012) have argued that Thompson's concept of a life-form, together with its implications of natural goodness and defect, is necessary for representing a living thing *as living*. This response is based on Thompson's transcendental argument for the life-form concept in his work on the representation of life. According to Thompson (2008), apprehending something as *living* requires viewing some of its parts as *organs* like legs and wings, and some of its activities

and processes as *vital operations* like eating and breathing. But what counts as a leg or what counts as eating differs from one kind of organism to another. For instance, the process of cell division amounts to reproduction in bacteria but constitutes growth in humans. Thompson argues that there is nothing in an individual organism as an entity occupying a certain region of space which determines that an organ is there or a vital operation is happening. What determines the fact that something is an organism, or its parts and processes are organs and vital operations is the ‘wider context’ of the life-form to which it belongs (Thompson, 56). Thus, on Thompson’s account, apprehending something *as living* requires presupposing a life-form concept, which brings with it not just the context required for recognizing organs and operations, but also the related norms of natural goodness and flourishing-based function. For instance, when we recognize an individual living thing as a cat, we already commit ourselves to assessing it against the norms that are implicit in our conception of the cat life-form. Although our conception might be incomplete and we may have to revise some of the natural-historical judgments that we make about the life-form, we always have to presuppose *some* conception of the life-form and taking *some* natural-historical judgments to be true if we are to identify the cat as a living organism.

Based on Thompson’s argument, Hacker-Wright and Lott argue that even an empirical science like evolutionary biology has to presuppose the life-form concept if it is to offer an understanding of living things. The idea is that since biology is the study of living things, biologists need to presuppose the concept of a life-form *before* they can even start doing biology, because the life-form concept is involved in recognizing living things in the first place. Thus, Lott claims that “to so much as have a topic for evolutionary explanation, we must rely on Thompson-Foot judgments of life form” (2012, 375). Hacker-Wright similarly argues that a life-form conception “is always in play when we make a judgment of an organism,” regardless of whether we are doing armchair speculation or evolutionary biology. He points out that “there are plenty of other ways of evaluating organisms, say, from the perspective of adaptive fitness, but the other evaluations depend upon natural normativity because they are evaluations of members of life-forms” (2009, 316). In this way, Lott and Hacker-Wright argue that biology is already committed to the life-form concept, which means that the neo-Aristotelian account of natural goodness has a place in our understanding of living things in biology and is therefore naturalistic.

What is troublesome about this argument, however, is that these claims are made without actually looking at the conception of organism in evolutionary biology to see if the relevant concept of a life-form is at work there. Lott and Hacker-Wright seem to assume that that since

biology is *about* living things, biologists are already committed to the life-form concept that is involved in recognizing living things in the first place. However, as I have argued in Moosavi (2018), the mere consideration that the subject matter of a science is pre-scientifically characterized in terms of a concept is not enough to render that concept naturalistic. The question we should ask is whether the ultimate scientific account of the subject matter remains faithful to the initial pre-scientific characterization. Organic chemistry—the study of organic compounds, for instance, was initially characterized as the study of compounds found in living organisms. What motivated the division between organic and inorganic chemistry was the fact that compounds derived from living things seemed to have distinctive features such as being less stable and more prone to decomposition. It turned out, however, that the very compounds that were the focus of organic chemistry were also obtainable from non-living sources. The subject matter of organic chemistry was thus redefined as compounds that contain a significant amount of carbon, regardless of whether they have a biological origin.¹ Because of this, modern organic chemistry does not lend any support to the idea that living things are distinct from non-living things. As far as this particular science is concerned there is no distinction between living and non-living things (Moosavi, 298). Thus, merely being part of a pre-scientific characterization of the subject matter is not enough to make a concept naturalistic. If neo-Aristotelians aim to defend the naturalistic status of their concept of organism, they need to show that this concept plays an explanatory role in biology, not just as part of the initial characterization of the subject matter, but in the scientific account ultimately provided of the subject.

This is what I aim to investigate in the rest of the paper. My intention is to first argue that the explanatory role of the concept of organism in evolutionary biology is in fact disputed, and then explore ways in which neo-Aristotelians might be able to argue for the explanatory significance of this concept by appealing to research in evolutionary developmental biology.

In section 2, I look at the Modern Synthesis theory of evolution, which is the dominant view of evolution today. I argue that the concept of an organism does not have a place in the Modern Synthesis, which understands evolution as change in gene frequencies within a population over time. In Section 3, I explore an alternative view of evolution that has emerged in the past twenty years from research in evolutionary developmental biology. I highlight the explanatory role of the concept of organism in the so called ‘Evo-Devo’ account, and argue that this view is more

¹ See Klein (2005) for an account of the shifting ontology of chemistry in the 18th and 19th century.

congenial to the claims of neo-Aristotelian regarding the concept of organism. Finally, in section 4, I argue that although the explanatory role of the concept of organism in evolutionary biology is still contentious, the role of this concept in developmental biology is well-established and is better suited to defend its naturalistic status.

2. The Modern Synthesis

In this section, I assess Lott (2012) and Hacker-Wright's (2009) claim that evolutionary biology presupposes the conception of an organism by looking at the Modern Synthesis theory of evolution. I highlight how this theory differs from Darwin's original formulation, and argue that the concept of an organism does not play a role in the Modern Synthesis—neither as the subject of explanation nor as an explaining factor.

Darwin's view in the *Origin of Species* was that organisms arise and develop through the natural selection of small heritable variations that increase their ability to survive and reproduce. His characterization of natural selection was as follows:

[I]f variations useful to any organic being ever do occur, assuredly individuals thus characterised will have the best chance of being preserved in the struggle for life; and from the strong principle of inheritance, these will tend to produce offspring similarly characterised. (Darwin 1859[1872], 102)

Thus, his basic idea was that heritable difference in fitness among organisms results in evolution by natural selection. Darwin understood that evolution by natural selection requires inheritance of parents' traits by offspring, but he had no good explanation of inheritance. The prevalent idea of inheritance in Darwin's time was *blending inheritance*, according to which the traits of offspring would be blends of the traits of their parents. This was problematic for Darwin's theory, because blending inheritance would cause the whole population to converge to the same average for all traits in a few generations, which would eliminate variation—another essential ingredient of natural selection.

This problem was not solved until Mendelian genetics came along and became well-known in the 20th century. Mendel's theory of *particulate inheritance* showed how the traits of parents could be passed on to offspring as 'particles' or separate entities that would remain unaffected in the offspring. Insofar as the offspring's traits are a blend of its parents', that blending happens later, during development. The inherited particles can remain unchanged in a lineage generation after generation, which explains how variation can remain in the population over time. Thus, Mendel's

theory of inheritance filled the gap in Darwin's account of natural selection, and eventually led to the Modern Synthesis, which integrated Darwin's theory with genetics.

As we will see below, however, this integration with genetics resulted in the disappearance of the concept of organism from evolutionary biology—both as the subject of evolutionary explanation and as an explanatory factor. As Daniel Nicholson describes this shift, in Modern Synthesis biology, organisms have no explanatory role to play because they have no autonomous agency of their own. They are mere “liaisons of evolution; a sort of interface between the phenotypic expression of genes and the selecting role of the environment” (Nicholson, 2). It's rather the causal capacities of genes that drives evolution forward, which is why evolutionary explanation must be sought at the level of genes. In the rest of this section, I illustrate this shift in the focus of evolutionary explanation by looking at how evolution is portrayed in standard modern texts in biology and philosophy of biology.

The first thing that I want to highlight is how the *subject* of evolutionary explanation has changed from organisms to genes. The Modern Synthesis reconceptualizes evolution as a change in allele frequencies of a population. The *locus classicus* of this shift is Theodosius Dobzhansky's *Genetics and the Origin of Species*, where he defines evolution as “a change in the genetic composition of populations” (Dobzhansky 1937, 11). According to Dobzhansky, since evolutionary change is essentially genetic change, the study of evolution falls within the province of population genetics. Similarly, if we look at standard textbook accounts of evolution, we will see that the very idea of evolutionary change is defined in terms of change in the frequency of genes. Douglas J. Futuyma's *Evolution*, for instance, says the following:

Because evolution consists of genetic change in populations over time, evolutionary biologists are most interested in those variations that have a genetic basis. (Futuyma 1942, 190)

This characterization of evolutionary change as change in the frequency of genes marks a clear departure from Darwin's original focus on change in the observed characteristics of organisms (i.e., phenotypes) as the subject of evolutionary explanation.

The Modern Synthesis reduction of evolutionary change to genetic change may appear puzzling at first. Even if genes account for inheritance, it still seems that what evolutionary theory has to explain are primarily changes in the phenotype—changes in the anatomy, physiology, and behavior of organisms over time. What we find the most interesting and curious about evolutionary change is how characteristics of organisms change, and particularly how they

become adapted to their conditions of existence. There is something very remarkable about living organisms, namely that they fit their environment quite well. Their characteristics seem to have been carefully designed to enable them to appropriate the world around them. We see, for instance, that an aquatic organism like a fish has fins for swimming, and a subterranean organism like a mole has long claws for digging. The fit of organisms to their environment just seems to be a manifest fact about them that evolutionary theory needs to explain.

However, the Modern Synthesis shifts away from explaining *phenotypic* change and toward explaining *genetic* change for two reasons. The first reason has to do with the *Weismann Doctrine*—the idea that phenotypes acquired in an organism’s lifetime do not modify the genes that the organism’s offspring inherits. Darwin actually believed that the effects of use and disuse on an organism’s body could be inherited. But this Lamarckian view did not sit well with the genetic account of inheritance and the Weismann Doctrine. Weismann (1893) proposed a strict distinction between the *germ line*—cells that will be the ancestors of the organism’s sex cells—and the *somatic line*—cells that form the tissues and other components of the organism’s body. And he argued that while the somatic line originates from the germ line, the germ line remains separate from the somatic line such that no change in the somatic line can be transmitted back into the germ line. This later received confirmation in the so-called ‘central dogma’ of molecular biology, according to which information flows only from DNA to protein molecules and never in reverse.

This is the first reason why the Modern Synthesis focuses on genetic, as opposed to phenotypic, change. The ‘Weismann barrier’ between the genotype space and phenotype space does not allow the phenotypic changes that are ‘acquired’, or ‘environmental’, to enter the genotype space. As a result, any phenotypic changes that are *not* associated with genetic change are considered to be short-lived and not worth focusing on in the study of long-term evolutionary change.² The kind of change that most interests evolutionary biologists and is considered to constitute evolution, according to the Modern Synthesis, is genetic change.

Secondly, although the Modern Synthesis is concerned with explaining adaptations, it does not understand adaptations in terms of how well the characteristics of organisms fit their

² As we will see in the next section, the idea that phenotypic changes do not affect the long-term course of evolution is later challenged by more recent research programs such as Evo-Devo (West-Eberhard 2003; 2005) as well as Niche Construction Theory (Odling-Smee et al. 2003). But even though the Moderns Synthesis incorporates some of these criticisms in refining its explanation of evolutionary change, its characterization of evolutionary change as genetic change remains firmly in place.

environment. Instead, since adaptations are viewed as resulting from natural selection, they are simply defined as characteristics that have evolved by natural selection, i.e., by the differential success of genes in replicating themselves (see Futuyma 1942, 247-248; Sober 2000, 84). In fact, the Modern Synthesis denies that there are any design-like characteristics to be explained. There is only an *appearance* of design, which is explained away by uncovering the mechanism through which it is created. Futuyma's text, for instance, tells us that the remarkable nest building behavior of weaver ants (*Oecophylla*)—where workers cooperate and use larval silk to weave together leaves—is merely a genetically determined behavior resulting from many random mutations:

[T]he weaver ant's behavior has the appearance of design because among many random genetic variations (mutations) governing the behavior of an ancestral ant species, those displayed by *Oecophylla* enhanced survival and reproduction under its particular ecological circumstances. (Futuyma, 250)

So the improved survival and reproduction of organisms—which has the appearance of design—is viewed as merely a by-product of molecular processes at the level of genes. Because of this, the adaptations that standard evolutionary theory aims to explain are fully characterized in terms of genes and populations. In other words, it is simply not true that organisms or their observed characteristics constitute the subject of evolutionary explanation in Modern Synthesis biology.

Although organisms are not the subjects of evolutionary explanation, one may wonder whether they appear in the *content* of explanation as explaining factors. So the next thing that I want to look at is the role of organisms in the explanations that are given of evolutionary (genetic) change.

Futuyma's text, which provides a nice illustration of the standard Modern Synthesis account, describes evolution as a two-step process: (i) the origin of genetic variation, and (ii) change in the frequencies of genes caused by genetic drift or natural selection (Futuyma 1942, 270). The first step, which is the origin of genetic variation, is considered to be “the foundation of evolution” and responsible for long-term evolutionary changes (Futuyma, 189). Darwin's formulation in fact required phenotypic variation to exist in a population, but Darwin did not offer any account of the origin of such variation. He only postulated “a tendency to vary, due to causes of which we are quite ignorant” (Darwin, 107). The Modern Synthesis, in contrast, focuses on genetic variation, and offers two sources for this variation which are both genetic processes: mutation and

recombination. In other words, the Modern Synthesis identifies what Darwin characterizes as the organisms' "tendency to vary" with molecular processes at the level of genes.

The second step in the process of adaptive evolution is change in the frequency of genes in a population due to natural selection. According to Lewontin's (1970) well-known formulation, evolution by natural selection occurs when there is *heritable variation in fitness*. This requires that three basic components are in place:

1. Different individuals in a population have different morphologies, physiologies, and behaviors (phenotypic variation).
2. Different phenotypes have different rates of survival and reproduction in different environments (differential fitness).
3. There is a correlation between parents and offspring in the contribution of each to future generations (fitness is heritable). (Lewontin 1970, 1)

To see how this 'recipe' leads to evolution by natural selection, consider an example from Sober (2000). Suppose we have a herd of zebras in which there is variation in running speed (phenotypic variation). Suppose also that faster zebras are better able to survive because they are better able to evade predators (differential fitness). Further, suppose that running speed is inherited, and offspring take after their parents (fitness is heritable). Given these three conditions in place, we can see that because faster zebras have better success with survival and reproduction and thus replicating their genes, and because their genes are inherited by their offspring, the average running speed in the herd will increase over time.

Now, there is no question that organisms are more or less successful in survival and reproduction because of their phenotypes. In our example, some zebras have differential fitness because of variation in their running speed. It is the interaction of the organisms' phenotypes with the environment that determines which organisms can ultimately pass on their genes to the next generation. So one might think phenotypes do play a causal role in natural selection after all, because they are the factors that are actually screened and selected by natural selection.

However, for the same reason that phenotypic change without underlying genetic change is not the subject of evolutionary explanation, phenotypic variation without a genetic basis is also largely considered to be irrelevant as an explanatory factor in the Modern Synthesis. The textbook account, for instance, claims that although phenotypic variation is sufficient for natural selection to occur, it "can have no evolutionary effect unless phenotypes differ in genotype" (Futuyma, 270). The idea is that if phenotypes vary despite being genetically identical, they will be subject to

selection. But assuming that there cannot be inheritance without a genetic basis, this kind of selection cannot have long-term evolutionary consequences.³ Because of this, the Modern Synthesis focuses on the fitness of *genotypes*, even though “genotypes differ in fitness only because of differences in phenotypes” (Futuyma, 270). In other words, the Modern Synthesis simply abstracts away from the role of phenotypic variation. It explains evolutionary change solely in terms of genetic variation.

My discussion of the Modern Synthesis in this section shows that the current paradigm of evolutionary theory understands evolution as change in gene frequencies within a population over time, and explains it in terms of molecular properties of genes and statistical properties of populations. Thus, the neo-Aristotelian concept of an organism does not seem to have a place in the Modern Synthesis, neither as the subject of explanation, nor as an explanatory factor.

3. The Evo-Devo Approach

Although the Modern Synthesis is a widely influential view, it is not the only conception of evolution that has been put forward. In fact, in recent years, the Modern Synthesis has been seriously challenged from various fronts. Empirical advances in the understanding of evolutionary novelty and selection (West-Eberhard 2003; 2005), biological development (Oyama 2000; Oyama, Griffiths, and Gray 2001), and epigenetic inheritance mechanisms (Jablonka and Lamb 1995; 2005) have exposed many theoretical problems of the Modern Synthesis and its *genocentric* approach. As a result, some biologists and philosophers of biology have called for “the return of the organism” (Nicholson 2014), suggesting a very different understanding of evolution. On this *organocentric* view, organisms are the primary agents of evolutionary change, and the main processes of evolution are consequences of the distinctive capacities of whole organisms such as their plasticity and robustness (Walsh 2016; Pigliucci and Müller 2010; Huneman 2010).

In this section, I focus on the evolutionary-developmental account of evolutionary change offered by West-Eberhard (2003; 2005). Evolutionary-developmental biology, or as it is colloquially called ‘Evo-Devo’, is a discipline that is concerned with discovering and understanding the role of developmental mechanisms in evolution (Hall 2003). What is interesting about Evo-Devo is that by identifying the role of developmental mechanisms in evolutionary change, it restores the place of organism in evolutionary theory.

³ Again, as we will see in the next section, this is one of the tenets of the Modern Synthesis that is later challenged by Evo-Devo among other recent theoretical approaches.

West-Eberhard's evolutionary-developmental account of evolutionary change ascribes a significant explanatory role to the phenotypic and developmental plasticity of organisms in evolution. What is meant by the *plasticity* of organisms is their ability to change in response to external or internal environmental inputs during their development. An illustrative example of this ability is the real-life case of a two-legged goat described in 1942 by morphologist E. J. Slijper. This goat was born without forelimbs, but it adapted to its condition in unexpected ways, and developed peculiarities such as enlarged hind limbs, a curved spine, and a large neck. As a result, the goat learned to walk and run by using its hind legs alone. As West-Eberhard (2005) explains, the correlated shift in the goat's morphology and behavior led to "the well coordinated production of a complex and individually advantageous adjustment, producing a novel phenotype with little or no genetic change" (West-Eberhard 2005, 6545).

West-Eberhard argues that plasticity is an evolved property of living things that is universal among them and has implications for our understanding of evolution. She claims that evolutionary biologists since the 19th century have been mistaken to dichotomize development and selection. In her account of adaptive evolution, development plays a major causal role, most notably in originating evolutionary novelty. The two steps of the process of adaptive evolution on her account are (i) generation of variation by development, and (ii) screening of variation by selection (West-Eberhard 2003, 139). Thus, West-Eberhard's Evo-Devo account disagrees with the Modern Synthesis about the origin of variation. The Modern Synthesis was merely concerned with genetic variation, and considered mutation and recombination to be the only sources of variation. As stated earlier, this was due to the fact that variation needs to be inherited in order to be evolutionary and have long-term effects. In contrast, in the Evo-Devo account, the fact that phenotypic variation is what is screened by selection is taken to be more significant, and the role of development in generating phenotypic variation is acknowledged.

The fact that West-Eberhard takes phenotypic variation to be significant is not because she neglects the importance of genetic variation for long-term evolution. Unlike some other advocates of the Evo-Devo approach (e.g., Johnston and Gottlieb 1990; Walsh 2015), West-Eberhard does not contest the conception of evolutionary change as genetic change. What she rejects, however, is the claim that genetic variation is the *origin* of evolutionary change. Her idea is that, just because phenotypic variation needs to be *heritable* to be evolutionary, it does not follow that it needs to be *inherited*. In fact, West-Eberhard rejects the distinction between inherited and acquired phenotypes. Following Johnston and Gottlieb (1990), she argues that *all*

phenotypic characters arise in development as a result of an interaction between the organism and its environment. The fact that genes play a role in this interaction does not mean that they directly determine any phenotypes. There is no such thing as a ‘normal’ or merely permissive environment in which genes get to generate phenotypes that are fully inherited. Thus, West-Eberhard takes it to be misleading to ascribe the origin of variation to the properties of genes. She argues that even though phenotypic variation resulting from development is *acquired*, it can still be *heritable* and have long-term evolutionary effects.

According to West-Eberhard, the “evolutionary potential of a developmental novelty” depends on two factors: *recurrence* and *heritability*. Recurrence refers to the formation of a population of individuals expressing the trait, and is necessary for a developmental novelty to lead to selection. Heritability, on the other hand, is a measure of how much an offspring’s traits resembles the parents’—independently of whether this involves the transmission of genes⁴—and is required for selection to lead to evolutionary genetic change. West-Eberhard argues that developmental novelties can be recurrent and heritable regardless of whether they are initiated by a genetic or environmental change. Her argument for heritability of environmentally-induced novelties relies on the observation that there is virtually always genetic variation among traits that are phenotypically similar. This hidden genetic variation, which on its own does not constitute any phenotypic variation, can be ‘exposed’ when an environmental change induces phenotypic variation. And since the resulting phenotypic variation that is subject to selection will be accompanied with preexisting genetic variation, it can be inherited.

Let me illustrate this with a classic example from C. H. Waddington’s (1953) experiments on *Drosophila*. In these experiments, Waddington applied a temperature shock during the egg stage of *Drosophila*, which caused a bithorax-like phenotype in adult flies. This phenotype was exhibited in various degrees among the flies, and responded quickly to artificial selection when Waddington crossed the bithorax individuals for a few generations. What Waddington observed was that even though the bithorax phenotype was induced environmentally, it was “genetically assimilated” and resulted in long-term evolutionary change. In fact, the novel phenotype ultimately remained in the population even after the temperature shock was removed. Waddington argues that this phenomenon is due to the *canalization*, or robustness, of the developmental processes in *Drosophila*, which is their ability to produce the same phenotype

⁴ Note how this notion of *heritability* diverges from the genetic conception of *inheritance* in the Modern Synthesis.

regardless of variability of genotype or environment. When developmental pathways are canalized, most individuals phenotypically look the same despite having different genetic make-ups. However, canalization can break down as a result of extreme environmental stress, and this would expose the hidden genetic variation. In this case, the pre-existing genetic variation in the population is so extensive that when canalization breaks down, the bithorax phenotype appears in different degrees. These novel phenotypes then provide the material for selection, which can further change the genetic make-up of the population to the point that the original environmental stress is no longer necessary to trigger the phenotype.

Having shown that environmentally-induced phenotypic changes can be heritable in this way, West-Eberhard argues that “the causal chain of adaptive evolution . . . is fundamentally the same whether it starts with genetic or environmental induction” (West-Eberhard 2003, 144). In fact, she argues that environmentally-induced changes are more significant than genetically-induced ones, because they are more likely to be recurrent and so they get incorporated into development more often. But regardless of whether a novel phenotype is induced genetically or environmentally, West-Eberhard distinguishes between the *initiation* and the *origin* of novelty. On her account, the origin of novelty requires two events: (i) initiation by a new input in the form of a genetic mutation or an environmental change, and (ii) a developmental response that produces a new phenotype. In other words, genetic or environmental changes merely provide the initial input, to which the organism responds, and it is this response that is the origin of evolutionary novelty. This is a considerable conceptual shift from the Modern Synthesis account. Not only the effects of environment are brought into light, the effects of genes are placed on a par with them as mere inputs. It is ultimately the organism’s *response* to these internal and external inputs that results in the novel phenotype.

West-Eberhard thus proposes that adaptive evolution involves the following events: (i) trait origin, or phenotypic novelty due to genetic or environmental input, (ii) phenotypic accommodation, or the adaptive adjustment of various phenotypes in the organism to accommodate the phenotypic novelty (as seen in the example of the two-legged goat), (iii) initial spread due to the recurrence of the initiating factor, and finally (iv) genetic accommodation, or gene-frequency change due to selection (West-Eberhard 2003, 140).

West-Eberhard then draws our attention to what is striking about this account: “gene-frequency change follows, rather than initiates, the evolution of adaptive traits” (West-Eberhard 2003, 158). Genes are *followers* rather than *leaders*, and their most important role is not so much

in the origin of novelty as in making a store of genetic variation available for gradual change under selection. What is significant about this result is that on this account, adaptation does not wait for lucky mutations to come along. The novel phenotypes that are available for selection result from developmental plasticity of an already highly adapted organism, which ameliorates many negative effects. This means that novel phenotypes are “not completely random with respect to adaptation,” even though their inducing factors may be (West-Eberhard, 158). Thus, on West-Eberhard’s account, evolutionary novelty does not consist in the random mutation of genes, but is rather biased by the adaptive response of development to the organism’s conditions. This is why, it is the *organism*—and not its genes—that is viewed as the principal cause of evolutionary novelty and thereby the driver of evolutionary change.

This overview of West-Eberhard’s account of evolution is meant to illustrate how recent approaches to understanding evolution challenge the Modern Synthesis in ways that suggest there can be room for an explanatory concept of organism in biology. The Evo-Devo account gives an important explanatory role to phenotypic plasticity, which is a property of *whole* organisms and cannot be reduced in terms of the molecular properties of genes or statistical properties of populations. Admittedly, the argument I have presented here is schematic, and only includes part of the story. I have not discussed many other empirical and theoretical advances in the understanding of evolution that have called for “the return of the organism as a fundamental explanatory concept in biology” (Nicholson 2014).⁵ But if neo-Aristotelian naturalists aim to defend the life-form concept by appealing to the explanatory role of the concept of organism in evolutionary biology, the Evo-Devo account of evolution seems to provide a promising starting point.

4. In Search of the Concept of Organism in Biology

Although Evo-Devo is rapidly growing as a field of biological research, the implications of its findings for evolutionary biology still remain contentious. The exact role of development in evolutionary explanations is currently a hotly debated issue, as can be seen a 2014 exchange in *Nature* about whether evolutionary biology needs a revision. While some biologists respond by an emphatic “Yes, Urgently,” others still do not feel such an urge and respond “No, All Is Well” (Laland et al. 2014). Some biologists are skeptical of the claims of Evo-Devo for reasons having to

⁵ See also Walsh (2016) for a particularly thorough argument for an organocentric view of evolution.

do with the insufficiency of empirical evidence. They argue that few cases of phenomena like Waddington's genetic assimilation have been documented outside the laboratory, and the evidence for the role of phenotypic plasticity in evolution has to be strengthened. Some biologists and philosophers alternatively question the theoretical significance of Evo-Devo for evolutionary explanation. They argue that although development influences a range of traits that natural selection can act on, what matters for evolutionary explanation is ultimately the heritable difference in traits, not the extent of trait variation or how they are caused. Thus, they insist that gene centrism is still "the most powerfully predictive, broadly applicable and empirically validated component of evolutionary theory" (Laland et al., 163).

The idea that evolutionary explanation does not have to cite the developmental causes of variation can be traced back to Ernst Mayr's distinction between *proximate* and *ultimate* causes. Proximate causes are the immediate and mechanical causes that mediate between genotypes and phenotypes, while ultimate causes are responsible for long-term change from one population to the next. Mayr (1961) recognizes two distinct sub-disciplines of biology. The first is functional biology, which studies "the operation and interaction of structural elements, from molecules up to organs and whole individuals". In other words, it is concerned with the 'how' question of proximate causes. The second is evolutionary biology, which studies "the causes for the existing characteristics, and particularly adaptations, of organisms". These are Mayr's ultimate causes, which answer the 'why' question and include natural selection and other evolutionary processes such as drift (Mayr 1961, 1502). The idea is that to the extent that evolutionary explanations are not asking the 'how' question, they are not concerned with the proximate causes of development, which are just gory mechanistic detail.

Proponents of the organocentric approach have questioned the extent to which the proximate-ultimate distinction and the separation of development from evolutionary explanation can be maintained in light of the findings of Evo-Devo (Laland et al. 2013). Walsh (2015), for instance, explicitly argues against what he calls the 'fractionation' of evolution, which consists of thinking of the components of evolution such as development, adaptive change, inheritance, and the generation of novelty as discrete and autonomous. He argues that these processes don't have separate and distinctive causes, and cannot be observed and studied in isolation from one another (Walsh, 159). But this is an ongoing debate that may need further empirical and theoretical investigation to be resolved. What is far more widely accepted, however, is the explanatory role of phenotypic plasticity and other distinctive properties of organisms in *developmental* biology. Even

if it turns out that organisms can be black-boxed in the study of evolutionary change, research in Developmental Systems Theory suggests that what happens during development cannot be explained solely in terms of the properties of genes (see Oyama 2000; Oyama et al. 2001). It is increasingly accepted is that the developmental process is not merely the unfolding of a genetic program, and that the properties of an organism as a unified whole play a significant role in development (Nicholson 2013; 2018).

If this view of development is correct, then at the very least, the concept of organism has a place in developmental biology. The evolutionary objection to neo-Aristotelian naturalism assumes that evolutionary biology is the only relevant area of biology where organisms could possibly be found. Responses to this objection have similarly assumed that what makes organism a naturalistic concept is its explanatory role in evolutionary biology. But this focus on evolutionary biology is unnecessary. As I argued in the previous section, there might be a case to make for the role of the concept of organism in evolutionary biology. But even failing that, there is reason to think the organism can be found alive and well in the field of developmental biology, where it has a much more well-established place, and can potentially lend support to the neo-Aristotelian concept of life-form.

Of course, arguing that the concept of organism plays an explanatory role in developmental biology is not enough to show that developmental biology presupposes the neo-Aristotelian concept of *life-form*, which involves a particular conception of living organisms. As we saw in section 1, the concept of life-form denotes the *form of life* of an organism, and neo-Aristotelians maintain that this form of life can be articulated in a particular, generic form of thought manifested in natural-historical judgments. Because of this, the neo-Aristotelian concept of life-form involves a commitment to the ascription of a characteristic flourishing and flourishing-based functions to an organism and its parts and aspects. So just because the concept of organism plays an explanatory role in developmental biology, it doesn't immediately follow that the particular, neo-Aristotelian conception of a living organism is correct. There is a further question whether the explanatory concept of organism in developmental biology or other branches of biological science commits us to a suitable notion of flourishing and flourishing-based function. However, while I have not offered a complete defence of the neo-Aristotelian concept of life-form in this paper, I hope to have taken the first step toward offering such an argument by first explaining why this argument cannot be made *a priori*, and then identifying an active research program within biology that provides a promising starting point for such an argument.

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