

## *Explanatory Internalism: Challenging Selected-Effect Functions*

Tiago Rama  
 Department of Philosophy  
 University of the Republic of Uruguay  
 Montevideo, Uruguay  
 trama.folco@gmail.com  
<https://orcid.org/0000-0002-1531-7233>

**Abstract:** Explanatory Externalism states that the only adaptive force in evolution is natural selection. Explanatory Externalism is a central thesis of the Modern Evolutionary Synthesis. The etiological theory of natural selected-effect functions also advocates Explanatory Externalism. According to this theory, natural selection is the process responsible for determining the proper natural functions of traits. However, I will point out several challenges to Explanatory Externalism that are proposed primarily by developmental biology and its various subfields. Based on these challenges, this paper will argue why biological functions cannot be fully explained by the selected-effect theory, i.e., that a theory of biological functions must adopt some kind of Explanatory Internalism. At the end of this paper, I will discuss whether or not Explanatory Internalism entails a pluralistic view of biological functions, and how this discussion is related to the different explanations of fit and diversity found in evolutionary biology.

**Keywords:** Explanatory Externalism; Explanatory Internalism; Selected-Effect Functions; Developmental Turn; Functional Pluralism; Evolutionary Forces.

### 1. Introduction: Explanatory Externalism and Selected-Effect Functions

Biological functions are intensely debated in the philosophy of biology (see Ariew et al. 2002; Garson 2016, for some introductions to the topic). Among the alternative explanations for biological functions, the etiological theory of function is probably the one that has gained more adherents. The seminal work on etiological functions is the work of Larry Wright (1973). According to this theory, the function of a trait is defined by its effects. If the effect of the heart is blood circulation, then blood circulation is the proper function of the heart. Of course, etiological functions can be applied to both living and non-living systems. Moreover, there can be different etiological theories for living systems, i.e. different explanations for biological functions that are etiological. In this sense, the biological theory has different etiological functions. However, the best-known and most widely used is the so-called Selected-Effect Theory of Function (henceforth: SETF). In this paper, *I will discuss etiological functions under the interpretation of the SETF.*

The etiological theory of selected-effect functions was developed mainly by Millikan (1984, 1989) and Neander (1991a, 1991b) -see also Ayala (1970) and Ruse (1973). In short, according to the SETF, the function of a trait is to do what it was selected to do by natural selection in the course of evolution. A trait must fulfill the causal role that it has played and that has led to its spread and maintenance in a population by natural selection. As we can see, this is an etiological view of functions: the *effects* of a trait on the fitness values of a population during the processes of selection determine the function of the trait. The function of the heart is to pump blood because the *effects* of pumping blood have led to the selection of hearts in natural evolution. It is important to point out that not all etiological theories of function rely on natural selection. Etiologists define functions based on the effect of a particular process. The SETF invokes the processes of natural selection, but other etiological theories are based on other processes, such as physiological, developmental, or design-like processes. Nicholas Shea's *varitel theory* (2018), for example, argues that in addition to the SETF, those theories of function based on learning processes and persistence mechanisms are also etiological theories. With this clarification in mind, I will focus here exclusively on the SETF. As I will explain in detail below, the SETF is based on a central thesis of biological theory: Explanatory Externalism.

*Explanatory Externalism* (Godfrey-Smith 1996, Walsh 2015) is the thesis that the external forces of a system explain the activity of the system. Just as there are different etiological theories of functions, there are also different types of externalism in biology. The best-known Explanatory Externalism is defended by the Modern Synthesis concerning evolutionary processes and is the one I will mainly discuss here. But there are also other externalist positions in the analysis of other organic processes, such as physiology or development (e.g. McShea 2012; Babcock and McShea 2022). Here I will use the expression Explanatory Externalism to refer to the idea that the only cause of adaptive evolution in nature is an external force: natural selection.

In this view, natural selection -the external causal pressure that selects traits during the evolutionary processes- is seen as the only adaptive force in evolution. The external environmental conditions of organisms determine their adaptive value in the population and thus the future of species. Natural selection is therefore responsible for populations evolving towards adaptive peaks or desolate troughs. This idea is expressed by Huxley in a letter to Mayr, two of the main architects of the Modern Synthesis: “*Natural selection*, acting on the heritable variation provided by the mutations and recombination of a Mendelian genetic constitution, is the *main agency* of biological evolution” (quoted in Huneman (2017, 71, emphasis in original)). Or by Mayr himself: “It [natural selection] acts as a positive force that pays a premium for any contribution toward an improvement, however small. For this reason profound thinkers about evolution, such as Theodosius Dobzhansky, Julian Huxley, and G. G. Simpson, have called selection ‘creative’” (Mayr 1988, 45-46).

The connection between the SETF and Explanatory Externalism is quite obvious. It is not just the fact that most proponents of the SETF have explicitly and implicitly adopted the Modern Synthesis framework. The most important connection concerns the externalist position of the SETF, that is the central role that natural selection plays in determining the functions of traits, which makes Explanatory Externalism a central commitment of the SETF. Functions are determined by selection histories. The effects of a trait that has helped to overcome external pressures make a trait being selected by natural selection. SETF advocates Explanatory Externalism: natural selection is the driving force of evolution and is also responsible for ascribing functions to organic structures. The emphasized connection between the SETF and the Modern Synthesis framework makes the SETF a robust explanation of biological functions. The SETF inherits the scientific legitimacy of the Modern Synthesis as a sound and robust biological approach to trait functions.

So far so good, what is the purpose of this article? The main motivation for this article is that Explanatory Externalism (in its evolutionary version as defended by the Modern Synthesis) has been challenged in recent decades. The monolithic conceptual structure of the Modern Synthesis, which has integrated different disciplines under a common biological framework, has been criticized from various sides due to the experimental and conceptual improvements of the last decades. With this in mind, the main idea of this paper is that the challenge to the Explanatory Externalism of the Modern Synthesis has direct implications for the SETF. Since one of the pillars of SETF is Explanatory Externalism, the attacks on Explanatory Externalism destabilize the foundation of SETF. In this paper, I will highlight several issues facing the Modern Synthesis and how they directly impact the biological foundation of SETF.

An important tenet of the Explanatory Externalism of the Modern Synthesis is the explanatory vacuity of developmental processes in evolutionary theory (see Walsh (2015) for a critical analysis). Shortly, what happens during individual development and the intrinsic properties of organisms are not an adaptive force in evolution. The irrelevance of developing organisms has been forged since the early 20th century. Since then, *Explanatory Internalism* -the thesis that developing organisms and their intrinsic processes are an adaptive force in evolution- has been denied. However, as we will see later, Explanatory Internalism has re-emerged in biology. The challenges to the Modern Synthesis come primarily from developmental biology and are motivated by the central causal role of individual-level intrinsic processes in evolution. In this sense, the disputes over biological functions are linked to the resurgence of the debate between internalists and externalists in contemporary biology.

Having established the link between Explanatory Externalism and the SETF, I will proceed with my analysis as follows. The next section consists of six subsections. In each subsection, I present a challenge to Explanatory Externalism and a consequence for SETF. Each challenge is relatively independent of the other. In all cases, however, the challenges are motivated by Explanatory Internalism and the central evolutionary role of intrinsic/individual-level processes. In this sense, we can find certain connections between them, which we will address in the course of this essay. Having presented all the challenges, I will draw some conclusions in section 3. First, the externalist position advocates a

Newtonian Paradigm and treats organisms as objects in its explanations, whereas the internalist position advocates an Agential Paradigm and treats organisms as subjects in its explanations. Moreover, the discussions on the nature of biological functions and the many theories of function that have been developed are linked to the internalist and externalist debate on the explanation of fit and diversity. In other words, different understandings of what causes fit and diversity in nature lead to different theories of function. The result is that the diversity of theories of biological function is linked to the many explanations of fit and diversity. The coherence between different theories of biological functions is linked to the coherence between different explanations of fit and diversity. I also suggests that these conclusions can be extended to other scientific fields beyond biological sciences, particularly to cognitive science.

## 2. Explanatory Internalism

Explanatory Internalism is the thesis that internal processes of organisms that take place during a single life span have important effects on evolution. Development is not a black box of evolution. Rather, development is a process that produces new phenotypic variations, constantly mediated by multiple inheritance systems, and the fitness values of each organism are constantly adjusted. Nowadays and in the last 30 or 40 years, the importance of the development of organisms is experiencing a revival in evolutionary theory. The main reason for this is that theorists have begun to appreciate the complexity of development such that “the black box [of development] is now being opened to provide a more complete picture of what really happens” (Bateson and Gluckman 2011, 17). I will use the term “developmental turn” to refer to the group of views that oppose the Modern Synthesis and converge on the idea that developing organisms are an important force in adaptive evolution. The revival of developing organisms (Baedke 2019; Bateson 2005; Nicholson 2014; Huneman 2010) gave rise to different critiques of the Modern Synthesis and attempts to provide a “development first” view of evolution. The developmental turn encompasses many fields and theories, such as Evo-Devo, Eco-Devo, Developmental Systems Theory, Developmental Psychobiology, Niche Construction Theory, Extended Systems of Inheritance, Systems Biology, and others. I will directly present six challenges to Explanatory Externalism in each subsection and assess their implications for SETF.

### 2.1 By-Products and Developmental Constraints.

A seminal work against externalist thinking was the 1979 paper by Gould and Lewontin. There are several arguments against the adaptationist thinking of the Modern Synthesis. One of the main arguments concerns evolutionary by-products. They illustrate biological by-products with a well-known analogy. Imagine an architect designing a church. As with most churches, their design would include columns and arches. A direct consequence of this design is that the church would also have what is known in architecture as a *spandrel*. A spandrel is the area created when the column meets the ends of the two connected arches. Spandrels are a “formal” requirement; if you design arches and a column, you get a spandrel. Importantly, spandrels were not part of the original design (the architect’s intentions), even if they could be used for a specific purpose (e.g. for painting religious images). Spandrels are a by-product of architectural design. This example has parallels with biological by-products. “Biological spandrels” are those organic entities that are a necessary structural or developmental consequence of evolutionary design. Just as the architect does not design spandrels, natural selection does not select biological spandrels. In this sense, the evolutionary history of by-products cannot be explained solely by external causes; rather, their explanation must lie in the internal properties of the system -that is, in the properties that make by-products a necessary element of an organism- just as spandrels are necessary elements for any church with pillars and arches. By-products cannot fit into externalist explanations; they are part of internalist explanations.

The work of Gould and Lewontin has generated a lot of discussion about adaptationism. The idea of “biological spandrels” has been taken up by various disciplines and concerning different natural phenomena. In particular, part of the evo-devo research agenda is dedicated to analyzing the evolutionary consequences of *developmental constraints*. In short, developmental constraints concern the limits of the repertoire of possible phenotypic outcomes that can be constructed. The existence of developmental constraints means that not all phenotypic variations are possible. Phenotypic variation is finite, i.e. not all variations are possible. In other words, the existence of developmental constraints means that only some phenotypic outcomes are possible, i.e. some variations are possible.<sup>1</sup>

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<sup>1</sup> In the evo-devo literature, the repertoire of possible (morphological) outcomes enabled by certain developmental resources was termed morphospaces by Pere Alberch (1991). Morphospaces are a consequence of the intrinsic properties of developing organisms the morphospace is defined by the morphologies that can be constructed based on specific developmental resources.

The message we can take away concerns the need for internalist explanations for the structural properties of a system. There are several properties of organisms for which a functional explanation is required. In the context of the externalist framework, the functional role of a trait determines whether or not the trait is maintained and spread in the population. However, not all traits deserve this functional explanation. Several natural phenomena occur in nature not because of their functional role but because of the structural conditions of the systems themselves, such as evolutionary by-products (Novick 2023). The presence of a particular outcome can only be a consequence of the intrinsic restructuring of the system during ontogeny or a necessary structural condition for phenotypic development. The material conditions of the developing system -physical, chemical, biological or social conditions- enforce and require certain traits that fall outside the scope of selection: they are non-negotiable for natural selection.

This challenge can indeed be illustrated by Sober's famous distinction between selection for and selection of (Sober 1984). The difference between *selection for* and *selection of* is based on the causal role of a trait in natural selection. When the function of a trait has played a central causal role, this distinction can be illustrated using the following example (Rama 2022). Imagine a salt shaker with two types of salt, thin and white salt and thick and pink salt. When you season your dish, the first type can fall through the holes of the shaker, but the second cannot. In this case, we should say that there was *selection for* thin salt, as the thin made the *causal difference* in the process of selection (passing through the holes of the shaker), while there was *selection of* white salt, as the white *did not cause* the salt to be selected to flavor the food. This example illustrates the criticism that is leveled at the SETF as soon as developmental constraints are considered a causal variable in evolutionary dynamics. For example, consider a scenario in which being white salt causes being thin salt, i.e. that being white is a necessary condition for being thin (e.g. due to certain molecular reasons). In this context, whiteness plays a central role in selection for thinness, even if it is not directly linked to selection pressure. Thus, the presence of white salt cannot be explained from a purely externalist position. All in all, the presence of developmental constraints and evolutionary by-products means that the traits that *-prima facie-* do not play a causal role in a given environment (the traits that are *selected of*) cannot be explained from an externalist position. We need to look for intrinsic causes; we need internalist explanations.

## 2.2 Exaptations and Evolutionary Mismatches

Another phenomenon relevant to our discussion, first introduced by Gould and Vrba (1982), is that of *exaptations*. In short, the current function of a trait is not necessarily the function the trait had when it was selected. Imagine an evolved trait that is suddenly confronted with a new environment. The feature can adapt to this change and construct a new function. In this case, the current function does not match the evolutionary function. In this sense, exaptations occur when a trait has "evolved for other usages (or for no function at all), and later 'coopted' for their current role" (Gould and Vrba 1982, 6). Rapid adaptations, drastic environmental changes, or internal changes can mean new functions. In these cases, these functions have not arisen through a slow process of gradual, cumulative natural selection, but spontaneously as a result of the internal adaptation of organisms to the new environment (through various means, which are presented in sections 2.3, 2.4, and 2.5).

Furthermore, exaptations are associated with the existence of *Evolutionary Mismatches* (Lloyd 2021), i.e. when "a trait that evolved in one environment becomes maladaptive in another environment" (Lloyd 2021, 32). There could be a mismatch between evolutionary history and current functionality. New, sometimes abrupt, environmental changes -such as species invasion or climate change- alter the functionality of a particular trait in such a way that adaptation is required to overcome unfavorable conditions. Current maladaptations could be a consequence of changing external conditions without natural selection adapting to such new situations.

Exaptations and evolutionary mismatches point to a central problem in some externalist explanations advocated in evolutionary psychology and sociobiology, among others. In particular, we should reconsider the idea that we can figure out the function of a trait by looking at the environmental conditions that the ancestors faced during evolution, since the current function may not match the old environment. The reverse logic, known as reverse engineering, does not work either: the present environment need not shed any light on the functions of a trait during the evolutionary process. Perhaps the evolved function is not the same as the current function, insofar as the ancestral scenario is not the same as the current one. In this sense, Explanatory Externalism is limited; we cannot assume that function and environment are

the same across the evolutionary time scale. It is not a conceptual truth that can be applied to every case, as if just by looking at what we do with our trait we can define the correct function.

### 2.3 Self-organization: autonomy and inherency

Nowadays, it is widely accepted that self-organization is a fundamental phenomenon in the living realm. Living systems are autonomous, self-organized entities. They regulate their interaction with the environment and their internal organization to stay alive. Each part of the system has a functional relationship with other parts to maintain, reconstruct, and reproduce the system during life. This ability is central to finding a balance between two opposing and essential properties, *openness and closedness*. Living systems are *thermodynamically open* (Bertalanffy 1969); they exchange matter and energy with the environment to sustain and reproduce life. However, organisms are also separated from the environment. The functioning of the different parts of an organism represents an *operational closedness* (Maturana and Varela 1980) that makes it a distinct entity from its environment. Regulation of both internal organization and coupling with the environment is crucial for adaptation to different environmental scenarios throughout the lifespan. The adaptive regulation of living organisms allows them to oscillate between the stability of their internal structure and the malleability for different external scenarios. Organisms can adapt to different environments while maintaining their own internal identity, maintaining their structure itself while a stream of energy and matter flows over them, i.e. life occurs at *the edge of chaos* (Kauffman 1995).

Various authors argue that self-organization is crucial for evolutionary theory (e.g. Kauffman 1993, 1995; Goodwin 1995; Camazine et al. 2003; Newman and Muller 2002; Gilbert and Sarkar 2000). The origin of a trait may be the product of the role it has played in the overall system. We will distinguish between two types of self-organization processes that take place during ontogeny and that are relevant to evolutionary theory. We can distinguish between *adaptively directed* self-organization processes and *non-adaptively directed* self-organization processes, i.e. those that are directed to produce a certain functionality in the system and its environment, and those that arise due to non-functional (i.e. structural) means. The former refers to the *autonomy* of the living organization, while the latter concentrates on the phenomenon of *inherency*. The boundaries between the two are problematic, and usually, both types are simultaneously involved in most phenomena explained by self-organization. For the sake of clarity, however, I will say a few words about both here, recognizing that the conclusion is the same in both cases: there are internalist reasons for producing a particular organization of the system.

Newman (2022b) defines “physical self-organization” as the property of systems in which emergent patterns can be explained by the physicochemical properties of their parts. In his view, physical self-organization is generated by “generic mechanisms” (Newman and Comper 1990) that are present in any system subject to physical laws. The consequences of generic physical mechanisms in living systems were developed by Stuart Newman under the concept of *inherency* (Newman 2021) and are supported in many empirical studies. According to his definition, “inherency means that certain structural motifs (e.g. tissue layers, lumens, segments, appendages) can be readily generated by physical organizing forces acting on tissues masses” (Newman 2021, 121).

Therefore, generic physical mechanisms become crucial to the evolutionary origin and development of many traits. The crucial point here, following Newman, is that the generation of phenotypes due to generic physical mechanisms is independent of any externalist or functional consideration. Physical, self-organized (anatomical) patterns emerge as a consequence of the physicochemical composition of their parts. They are not the result of selection processes, but of the intrinsic dynamics of developmental systems: “If morphological novelties arose by means other than cycles of gradual change, evolution of form cannot mainly be a question of fitness and relative advantage, but rather of development and its transformations” (Newman 2022a, 199). In other words, the evolution of many traits cannot simply be reduced to understanding their causal contribution to fitness maximization during selection processes (as the SETF claims). The physicochemical constitution of living things can provide an alternative, non-etiological answer to the presence of a trait in nature, insofar as “major pathways of evolution are determined by physical law, or more specifically by the self-organizing properties of biomatter, rather than natural selection” (Edelmann and Denton 2006, 578-580). The fact that different traits arise during evolution and development as a result of generic mechanisms acting on the physicochemical basis of cells cannot be explained by a selectionist-externalist picture. The origin of self-organized patterns during evolution and development does not fall within the realm of Explanatory Externalism, but of Explanatory Internalism: “Self-organized order is spontaneous pattern from within; the order of selection is additive

order from without” (Edelmann and Denton 2006, 588). For this reason, Newman comes to the conclusion that “inherency is not merely complementary to the Darwinian paradigm, but is at odds with it” (Newman 2021 130).

Apart from the self-organization processes caused by the internal dynamics of a system’s physicochemical substrate, living systems in particular exhibit a special kind of self-organization process that makes them unique. While many non-living systems generate self-organized patterns and are able to differentiate themselves from the environment (such as Bénard Cells), living systems seem to be able to regulate their interaction with the environment in order to maintain their internal organization. In other words, the regulation of coupling with the environment through different actions seems to be a special ability of living organisms. This ability is usually associated with the *autonomy* of living organisms (Moreno and Mossio 2015), understanding that an “autonomous agent is a physical system that can act on its own behalf in an environment” (Kauffman 2000, 8). In this framework, organisms are able to regulate their own life state by adaptive means, to change the internal or external configuration to maintain a viable state (Barandairan et al. 2009). The picture that emerges is that organisms are a complex whole made up of different interconnected parts that perform specific functions to maintain the life system. This holistic view and its organicist foundations (Nicholson and Gawne 2015) explain how organisms manage to integrate their open and closed conditions adaptively.

The connection between the different parts of the system and the interdependence between them, which is necessary for the maintenance and construction of life, is at the center of the different biological processes. The autonomous regulation of living conditions may lead to various morphological, anatomical, physiological, cognitive, or immunological modifications. A good example of morphology is the study of the so-called *two-legged effect* examined by West-Eberhard (2003, chapter 3). It is about a goat that was born with two legs due to a genetic disorder. Interestingly, this impairment led to an enormous change in its column. Thanks to these morphological modifications, the goat was able to stand upright and walk with two legs. In this example, a drastic morphological change in the column occurred as a result of another change in the system (two legs instead of four). This example only illustrates how different traits can arise for organizational reasons. This deserves to look what is going on inside the organism. It is about organizing one’s structure to function properly in a particular environment. The idiosyncratic properties of living systems *qua* living systems are an important factor in the emergence of novel traits functions.

#### 2.4. Developmental plasticity

Developmental plasticity refers to the ability of developing organisms to adapt phenotypic outcomes according to their developmental contexts. Developing organisms can accommodate their phenotypes and adaptively control different phenotypic trajectories, i.e. adapt to their circumstances. West-Eberhard (2003, 33) defines plasticity as “the ability of an organism to react to an environmental input with a change in form, state, movement or rate of activity.” Various authors have recognized the evolutionary role of developmental plasticity and it is now recognized as “a ubiquitous and probably a primal phenomenon of life” (Wagner 2011, 216).

But does developmental plasticity contradict Explanatory Externalism? Certainly, there is an interpretation of plasticity that could fit an externalist view. Although plasticity was well recognized in the 20th century by biologists such as Baldwin, Waddington, and Schmalhausen, the Modern Synthesis found a way to accommodate plasticity within its framework. The strategy was to reduce plasticity to the level of genes (Amundson 2005). The strategy was to view the plasticity of phenotypic outcomes as the result of prior selection processes of genes (see Futuyma (2017) for a contemporary defense of this idea). In the Modern Synthesis, plasticity can be explained at the genotype level by postulating genes that are able to provide a repertoire of phenotypic outcomes in different environments (also called the *norm of reaction*). If this reduction is possible, natural selection is responsible for the explanation of plasticity, and consequently developmental plasticity is not controversial for the Modern Synthesis and could also be explained from an externalist point of view. Phenotypic plasticity is the result of the plasticity that genes have to produce different outcomes, and the plasticity of genes is explained by natural selection, i.e. by an external force.

A central thesis behind this position concerns a particular way of understanding the role of genes in development and evolution. According to this view, genes code for traits; phenotypic outcomes are specified in DNA sequences in such a way as to produce a robust Genotype-Phenotype map. The development of cells is orchestrated by its genetic underpinnings. This view of genetic activity was developed by Weissmann and Heackel, later modernized by Crick under the name Central Dogma in Molecular Biology (Crick 1958), and finally popularized by Dawkins (1976). Under this dogma, we can understand how phenotypic plasticity can be understood in terms of genetic plasticity. If the

construction of a trait depends on a genetic blueprint, the reaction norm of the system defines the repertoire of possible phenotypes that can be constructed. As Brigandt (2013, 84, emphasis in original) asserts, “a selection-based explanation of phenotypic evolution merely requires *that* genetic differences result in phenotypic differences (so that variation is heritable), and it is irrelevant *how* genetic differences developmentally lead to phenotypic differences.”

The problem, however, is that the above view of genetic activity was challenged when the complexity of genetic activity, genomic regulation, and genetic networks began to be understood. An important event for this realization was the Human Genome Project. As many have noted (Keller 2002; Lewontin 2000; Reid 2007), the main conclusion of this project was the rejection of its main goal: to understand development just by sequencing DNA strands alone. On the contrary, DNA sequences are not sufficient to understand development. Development is much more complex than the central dogma makes it out to be (for various introductions to this conceptual and experimental shift in molecular biology, see Keller 2002; Rheinberger and Müller-Wille 2018; Griffiths and Stotz 2013; Moss 2003; Sarkar 2005). Genetic activity can only be understood in the context of cells. The coding regions are only a small part of the genome. Genomes are equipped with a rich apparatus of genetic regulation that is still unknown. The expression or recession of genes cannot be understood independently of the genome. Moreover, genomes are located within the cell. Many processes of cellular regulation of genetic activity remain to be studied. The picture that emerges in molecular developmental research should not be encoded in classical molecular genetics. Rather, the so-called *post-genomic era* (i.e. after the Human Genome Project) understands genetic activity as part of molecular epigenetics. The post-genomic era places the developing organisms above the genes in ontogenesis. The mantra of post-genomics is that the cells have custody of the genes and not the other way around.

The post-genomic view denies the possibility of reducing plasticity to the genetic level. From this point of view, the organismic dimension of phenotypic plasticity comes to the fore. Plasticity is a property of developing systems and cannot be explained solely at the level of genes; as Bateson and Gluckman (2011, 43) emphasize in their book, “the central elements underlying many forms of plasticity are epigenetic processes”. This view has motivated the “plasticity-first” view of evolution, strongly advocated by West-Eberhard (2003). According to this view, no genetic changes are required to drive evolution: “Plasticity is the basis of phenotypic change in the absence of genotypic change” (Bateson and Gluckman, 2011, 100). Developmental plasticity can give rise to new variants. Such variants can be epigenetically inherited and “genetically accommodated” to be reconstructed in each generation. In this sense, adaptive heritable variants occur without genotypic evolution. As West-Eberhard (2003, 29) puts it, “genes are usually followers, not leaders, in evolutionary change.” To summarise, the net result of the study of plasticity in the post-genomic era is that “plasticity is an *intrinsic property* of organisms” (Sultan 2021, 6, emphasis added), it cannot be explained by an extrinsic force acting on genes. Phenotypic plasticity and its epigenetic interpretation provide another reason in favor of an internalist factor in evolution and the construction of trait functions beyond selective reasons..

## 2.5 Niche Construction

Another discipline that has been confronting Explanatory Externalism is niche construction theory (see Odling-Smee et.al. (2013) for a classic book on this topic). The core idea is the following. Faced with environmental problems, organisms can overcome them by *changing the environmental scenario*; in other words, solve the problem (the environment) by changing it. The theory was developed at the beginning of this century. However, many of the central ideas have already been set out by Richard Lewontin (2000, 2007, see also West and King (1987)).

Lewontin’s remarks refer to how niches and adaptations are represented in the Modern Synthesis. Adaptations are the better solutions that various traits provide to problems in the environment. The environment poses problems and natural selection chooses the best solution promoted by random genetic changes. Adaptations are those phenotypic variations that fit the environmental conditions. In this view, niches are seen as pre-existing places, they are the scenario that the organism passively deals with. The way that the Modern Synthesis understands niches was described by Lewontin as the *Autonomy of the Environment*. The environmental conditions that organisms inhabit are autonomous from the organism itself. The Autonomy of the Environment and Explanatory Externalism are aligned under a similar point of view: the key driving force in evolution is the external selection of phenotypes; organisms are passive repositories of genetic variants waiting to be selected or discarded by natural selection, as Lewontin nicely summarizes:

According to Darwinism, there are mechanisms entirely internal to organisms that cause them to vary one from another in their heritable characteristics. In modern terms, these are mutations of die

genes that control development. These variations are not induced by the environment but are produced at random with respect to the exigencies of the outside world. Quite independently, there is an outside world constructed by autonomous forces outside the influence of the organism itself that set the conditions for the species' survival and reproduction. The inside and outside confront each other only through the selective process of differential survival and reproduction of those organic forms that best match by chance the autonomous external world. Those that match survive and reproduce, the rest are cast off. Many are called but few are chosen. (Lewontin 2007, 230)

In contrast to this view, niche construction theory comes to the fore. The core idea is that an organism can also be actively involved in the dynamics of selection. Rather than viewing the environment as something autonomous from the environment, the organism and its environment are so intertwined that the intrinsic processes of organisms are active agents that determine the niche that they face. Importantly, there are two types of niche construction processes, both of which are suitable for understanding the critique of externalism and the alleged autonomy of the environment. One process of niche construction is usually referred to as *material niche construction*, the other is named *experiential niche construction*.

In material niche construction, organisms are able to deal with the environmental conditions in which they live by directly modifying their environment. Material niche construction concerns the activities that organisms carry out to change their environmental conditions. These include the construction of the niche in which they live, the modification of certain elements, migration, or invasion. Once these phenomena are recognized, external circumstances are no longer the only factor in the process of selection. The construction of the material niche alters the fitness values of organisms and must therefore be regarded as an intrinsic, organic phenomenon that contributes to the processes of adaptive evolution. Adaptations are not just new, random phenotypic solutions to earlier environmental problems, but can be the result of the adaptation of environmental problems to earlier phenotypes.

Secondly, there is a (philosophically deeper) concept of niche construction. It concerns the inherent ability of each organism to determine which aspects of the world are relevant to it (Lewontin 2000; Rama 2021; Rama forthcomingb). Sultan (2015) proposes the term experiential niche construction to refer to the idiosyncratic ability of each organism to construct its environment based on its sensory abilities. "The concept of niche construction", as Sultan (2015, 37, emphasis added) claims, "can be further extended to include phenotypic adjustments that permit the organism to *experience* a given set of conditions as more favorable, without either changing those conditions or moving to different ones." Definitely, not all organisms are related to the same part of the world. This is partly because they inhabit different places. But apart from that, each organism has a specific niche, which is defined as the elements that are relevant to the organism and to which it is receptive. This notion of construction has an epistemic component, it is about what a system is "aware" of. Even unicellular organisms are context-dependent beings. The organism is only connected to those things that affect its system in some way -perceptually, physically. The context-dependent ability of living organisms is crucial for them to be able to regulate their living conditions. To enable adaptive direct phenotypic change -through plasticity, self-organization, or material niche construction- organisms must be able to perceive their living conditions. The adaptability of organisms *qua* agents requires a context-sensitive ability that indicates to the organism what is going on in its environment, i.e. how the organism experiences its niche.

All in all, material niche construction and experiential niche construction pose a major challenge to Explanatory Externalism. The internal ability of organisms to change the material configuration of the environment and experience it in a particular way means that organisms are not passive objects subject to selection pressures, but active agents that find adaptive solutions. "The organism cannot be regarded simply as a passive object of autonomous internal and external forces; it is also the subject of its own evolution" (Levins and Lewontin 1985, 89). The environment is not independent of the organisms but is in a reciprocal relationship with each other and defines each other.

## 2.6 Statisticalism: function without causes?

The following challenge is entirely theoretic and concerns the nature of explanations by natural selection. It arises from the question of whether natural selection is capable of fulfilling the explanatory role that any natural theory of biological functions must fulfill. In other words, if we define the natural proper function in terms of natural selection processes, can we fulfill a central *desideratum* that any theory of biological functions must fulfill? It is necessary to first formulate such a *desideratum*.



The *desideratum* concerns an explanatory role for biological functions, which Cummins (1975, 741, emphasis added) expresses clearly: “The point of functional characterization in science is to explain the *presence of the item* (organism, mechanism, process, or whatever) that is functionally characterized.” That is, a theory of biological functions must explain why a biological object exists in nature as a consequence of the functions it has. A biological theory of function must explain why the functions of, say, hearts lead to hearts being part of nature. In principle, SETF can fulfill this *desideratum*: hearts exist insofar as they have been selected during evolution, i.e. insofar as an external pressure perpetuates hearts and distributes them over time. However, this *desideratum* has another ingredient. The functional explanation that explains the existence of a trait must be *causal*; a causal concept of function is essential to the naturalistic goal of viewing biological functions as real parts of nature and not mere idealizations of scientific discourse. A theory of biological function must *causally explain the existence in nature of the features that are functionally characterized*. Does the SETF have the causal support expected of a biological theory of function? According to its proponents, the SETF can fulfill this *desideratum*: “Selection does more than merely distribute genotypes and phenotypes ... *by distributing existing genotypes and phenotypes it plays a crucial causal role in determining which new genotypes and phenotypes arise*” (Neander 1995, 585, emphasis in the original). Even, the alleged explanatory adequacy of the SETF is a reason to support it and reject other theories of functions (such as Cummins’s one):

...functions are explanatory. One peculiar feature of functions is that, when biologists attribute a function to a trait, they are often trying to give a *causal explanation for why that trait exists*. One virtue of the selected effects theory is that it makes sense of this explanatory aspect of functions. (Garson and Papineau 2019, 36, emphasis added)

It is therefore expected that the SETF regard the explanation by natural selection as a *causal explanation*. This is indeed what we find in the literature. Most etiologists explicitly invoke Elliot Sober’s terminology (Sober 1984) to support a causal view of natural selection (e.g. Millikan 1993; Neander 2017; Artiga 2021; Garson and Papineau 2019). As noted before, Sober’s notion of *selection for* refers to a causal process (natural selection) acting on populations throughout history: “If there is selection for one trait and selection against another, the traits make a *causal difference* in survival and reproductive success” (Sober 2013, 339, emphasis in original). Following this idea, the actual function of a trait according to the SETF is defined by the causal processes of natural selection that ensure that a trait under selection plays a particular causal role: “On an etiological theory, functions are what entities were selected *for*. Mere selection *of* a trait is not enough to confer a function on it” (Neander 2017, 132, emphasis in the original). Selected for effects refers to the causal role that certain trait *types* have played in the course of natural evolution, so that these traits are selected, i.e. are part of nature. All in all, the biological roots of SETF make it an explanatorily adequate to fulfill our *desideratum*: the *causal explanation of natural selection* processes explains the existence of those traits that are functionally characterized.

The challenge of this subsection is rooted in an ongoing debate about the causal structure of natural selection (see Pence (2021) for a recent introduction to the topic and key references). On the one hand, we find the Causalist School, inspired by the work of Elliot Sober and other followers. On the other side, we find the Statisticalist School. According to this position, explanations by natural selection are not causal, but statistical explanations. If this is so, selected-effect functions do not seem to explain the *desideratum* mentioned above. The SETF is not a causal theory of biological function, but a statistical theory of biological functions (see Rama (2023) for a detailed argument).

The statistical view was proposed in 2002 by Walsh et al. (2002) and Matthen and Ariew (2002), and since then other works have further developed its main principles (Ariew 2003; Walsh 2003; Walsh 2007; Walsh 2019). The core idea is that the explanation by natural selection involves an abstraction of what is going on at the individual level to the population level. Describing changes in the population in abstract terms is done by resorting to statistical analysis. In particular, it is important to distinguish between two interpretations of *fitness* (the central concept in the explanation by natural selection), *trait fitness* and *individual fitness* (Ariew and Lewontin 2004). The latter refers to the fitness of each individual as a function of the phenotypes it possesses in a given environment, while the former is “the average survivability of a group of individuals possessing a type of trait” (Ariew 2003, 562). In other words, trait fitness is a statistical measure used to describe populations that are abstracted based on the individual fitness of the members of those populations; trait fitness is a population-level abstraction of what is going on at the individual level. This abstraction is an average, a mathematical analysis that explains how a population changes as a result of differences in trait fitness.

In short, natural selection occurs only when the relative frequency of trait types changes in a population as a consequence of differences in the *average* fitness of individuals in different trait-classes. This is what we call the statistical interpretation of natural selection. (Walsh et al. 2002, 464, emphasis in the original)

The Statisticalist School is based on the type of terminology used in explaining natural selection and the method used to explain population change. Indeed, statisticians' claim is closely related to the debate between externalists and internalists in this paper. The central conclusion is that natural selection is not, as Sober claims, a causal process acting on populations; natural selection is not a populational force. On the contrary, the conclusion is that "*all causes of evolution are individual-level causes*: "[t]here is one level of causation; *all the causes of evolution are the causes of arrival and departure* (the 'struggle for life') ... It is 'proximate' causes all the way down" (Walsh 2019, 238, 242, emphasis in the original). Thus, if evolution is caused by processes at the individual level -as statisticalism supports- then the intrinsic properties of individuals become central to evolutionary theory; individual processes provide the causal reasons for evolution, and they causally determine individual fitness. Conversely, if evolution can only be explained by the heritable variations in fitness in a population, then we can dispense with the study of individual-level processes, i.e. "the details concerning the individuals who are parts of this whole are pretty much irrelevant" (Sober 1980, 370). Explanatory Internalism is central to the Statisticalist School but is at odds with the Causalist School, while Explanatory Externalism fits the Causalist School but it is inadequate for the Statisticalist School. The advocacy of an internalist position, as outlined in this paper, motivates a statistician stance and consequently a critique of the SETF. To summarise, the SETF is not a causal theory of function. The SETF cannot causally explain the presence of features in nature.

### 3. Discussion: forces and functions

Let us summarise the ideas presented here. I have begun by explaining Explanatory Externalism and its connection to SETF. Explanatory Externalism, which is at the core of the Modern Evolutionary Synthesis, states that external selection pressures are the only adaptive force in evolution. The SETF is rooted in Explanatory Externalism. The SETF is defined in terms of the selection pressures that a trait function has helped to overcome during the evolutionary process. Since natural selection is a process that guides nature to adapt, it also defines the functions of its phenotypic products.

My strategy was to examine the current debate in biology and the philosophy of biology about Explanatory Externalism. The developmental turn forms a group of theories, disciplines and research areas that pursue Explanatory Internalism. The argumentative logic is that disputes about externalism and internalism in biology have direct implications for debates about the SETF. With this in mind, I have pointed to various phenomena that take place at the individual level that give rise to adaptive variation and have a central impact on the direction of evolution, such as phenotypic plasticity, niche construction, or self-organization. As can be seen, much of the debate about internalism and externalism revolves around the origin of phenotypic variation, which is the source of directionality in evolution (Novick 2023). The first conclusion is that the arguments between externalist explanations and internalist explanations are closely linked to the ongoing debates about the status of the Modern Synthesis.

In the introduction to this essay, I clarified the term used here by pointing out that my analysis refers to the Explanatory Externalism of evolutionary theory, even though I noted that there are other externalist positions. Although these externalist positions are not necessarily the target of the attacks of the developmental turn, these positions suffer from some problems common to all externalist positions. One clear case is the externalism proposed by Daniel McShea (Babcock and McShea, 2021; McShea 2012). His proposal is named *field theory*. Without going into the details of his theory, it states that the environment acts as a field that controls the activity of organisms. In particular, he constructs a field theory for physiological and developmental processes beyond the evolutionary level. In these processes, according to field theory, "guidance always comes from the outside, from some larger external entity in which the guided entity is embedded" (Babcock and McShea 2021, 8). All physiological and developmental processes can be explained by an external elements that orient their trajectories. The problem behind any externalist position is the denial of the agency of organisms. If physiological or developmental processes are governed by external factors, the directive force in nature is not explained by the agentive properties of organisms, as is partly stated in the developmental turn. In other words, in an externalist framework, organisms are treated as objects adrift to external forces. This framework has been called the

Newtonian Paradigm: the idea that we can explain the processes of a particular entity by citing external forces acting on it, without ascribing an explanatory role to internal causes. The developmental turn pursues an Agential Paradigm: the entity itself (organism) to be explained is an element that belongs to the given explanation; organisms provide causes that explain their own processes. If the explanatory goal is to understand the fit and diversity of living organisms, the externalist position of the Newtonian Paradigm would not include organisms in its *explananda*, whereas the internalist position of the Agential Paradigm would treat the internal processes of organisms as a fundamental guiding force explaining fit and diversity.

If we embed the debate between internalist and externalist explanations in the arguments about the origin and direction of phenotypic evolution, we can clarify certain controversies that may arise. Basically, it seems quite clear that there are externalist explanations that introduce internal elements (e.g. Mc'Shea's *field theory*), and there are internalist explanations that introduce external variables (eco-devo explanations). However, this is not problematic. The fact that an externalist theory introduces internal variables does not mean that this variable acts as a directive force in evolution, but only as a mere bias. This is indeed a common and misleading interpretation of evo-devo. According to this view, held by neo-Darwinists, development introduces a bias to selection. It is not a guiding force, but only a constraint. Evo-devo, on the other hand, views developmental constraints as a creative force that can produce new traits (Amundson 1994, cf. Section 2.1). Similarly, the eco-devo explanations and the studies on phenotypic plasticity introduce an external variable. The central claim is that developmental processes are context-dependent. However, I do not see any remnants of externalism here. Even if an externalist element is involved, the directive force lies within the organisms. The crucial idea in this case is that the organism manages to regulate its coupling with the environment. To summarise, while the developmental turn takes a holistic view of development in which external variables play a role, the distinction between internalist and externalist explanations relates to the source of directedness in evolution, specifically the origin of variation.

A possible counter-argument to the ideas presented here is that many SETF theorists accept the existence of ontogenetic functions (e.g. Shea 2018; Millikan 1984; Neander 2017; Papineau 2017, see Rama (forthcoming) for a discussion); that is, most selected-effect theorists accept both evolutionary and ontogenetic functions. Thus, etiologists are well aware that the explanation of biological functions is not exhausted by natural selection alone. However, this counter-argument does not seem to work. The main reason for this is quite simple. The existence of ontogenetic functions is not the target of this article. I am not just saying that some biological functions are not explained by evolution but by ontogenesis. On the contrary, I want to show how ontogenesis influences evolution. Accepting ontogenetic functions is not the same as recognizing the role of ontogenetic functions and ontogenetic processes in evolution, i.e. how ontogenetic processes give rise to evolved functions by internal means. The existence of ontogenetic functions can be coherent with Explanatory Externalism. For example, we can say that evolved functions are explained extrinsically, but some functions are explained by ontogenetic functions for intrinsic reasons. This is a classic dichotomy between individual causes and populational causes that underlies the debate on nature and nurture. Indeed, this is the position held by various supporters of the SETF: evolved functions are explained by natural selection and are innate and species-specific traits, whereas ontogenetic functions are achieved through processes of acquisition and are produced by nurture (Keller 2010). This is not the view we take here. We have shown several ways in which ontogenetic processes triggered by intrinsic causes give rise to evolutionary functions. Once ontogeny puts its hand in adaptive evolution, Explanatory Externalism should be abandoned. Consequently, the existence of ontogenetic functions can be coherent with the SETF, but once ontogenetic functions play a central role in evolution, the SETF must be reconsidered.

This clarification leads us to a central issue concerning the link between theories of biological functions and explanations of fit and diversity. The main message of the developmental turn is that ontogenetic causes are relevant to evolutionary theory and the explanation of fit and diversity. As with all the challenges posed in section 2, ontogenetic and intrinsic causes are crucial to the history of species. Beyond the explanation of natural selection, we need further analysis to properly understand the evolution of species -their fit and diversity. A central conclusion of this paper therefore concerns the relationship between biological functions and the explanation of fit and diversity. From this analysis, it is clear that the different explanations and causes of fit and diversify discussed here are related to different theories of biological functions. This is also what we find in the literature. As explained above, the SETF is based on the idea that natural selection is the only adaptive force in evolution that is responsible for producing fit and diversity. However, most evo-devo account of functions as well as various theories focusing on internalist processes from a structuralist stance provide non-teleological theories of functions (Amundson and Lauder 1994; Balari and Lorenzo 2013; Love 2007). The criticism of evolutionary mismatch is usually related to the so-called modern-history account of

biological functions. (Godfrey-Smith, 1994; Griffiths, 1993). The challenges based on self-organization led to organizational accounts of functions (Christensen and Bickhard 2004; McLaughlin 2000; Moreno and Mossio 2009). The agentive view of development, which has to do with phenotypic plasticity and niche construction, leads to various approaches on how functions are generated by epigenetic processes (Rama 2022; Walsh 2015). To summarize, the possibility of coherence between these theories of functions is related to the coherence between the different explanations of fit and diversity. In other words, support for a pluralist viewpoint regarding biological functions requires the adoption of a corresponding pluralist viewpoint regarding the explanation of fit and diversity.

A final comment for further discussion concerns the possible application of the ideas examined here in areas other than biology. As already mentioned, the externalist position is not exclusive to evolutionary biology; other areas of biology also hold an externalist position. Interestingly, there are also externalist positions outside of biology. One clear case is cognitive science and the various disciplines devoted to understanding the mind and behavior. Along the history of these disciplines, there are also different theoretical frameworks. In this example, there is a strong parallel with the current scenario in theoretical biology. During the Cognitive Revolution, cognitive science was launched to provide an internalist framework that surpasses the externalism of behaviorism (see Rama (forthcoming) for a detailed account). In contrast to the input-output model of behaviorism, cognitive science is dedicated to opening the black box of the mind and examining the inner realm and how internal processing produces adaptive behavior. This historical transition in the behavioral sciences is similar to the current scenario in theoretical biology, where the developmental turn seeks to open the black box of development and investigate how the inner world gives rise to adaptive organisms. We can therefore recognize the validity of our central conclusion beyond biology: that different internalist or externalist positions arise as a consequence of different explanations for our target phenomenon. Just as different biological functions arise from different explanations of fit and diversity, different behavioral theories arise from different explanations of adaptive behavior.

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