Function and Selection Beyond Externalism

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Abstract: In the context of evolutionary theory, Explanatory Externalism, one of the pillars of the Modern Evolutionary Synthesis, states that the only adaptive force in evolution is natural selection. However, I will point out several challenges to Explanatory Externalism that are mainly proposed by developmental biology and its various subfields, i.e. by those approaches that call for internalist explanations in evolutionary theory. Based on these challenges, I approach the debate on biological functions with a specific aim: to examine whether the challenges to explanatory externalism affect one of the most strongly established theories of functions, namely the selected-effect theory of functions. My first conclusion is that the selected-effect theory has been closely related to the externalism view, understanding selection as the process responsible for producing trait functions. Therefore, the selected-effect theory is affected by internalist challenges. However, I suggest a possible alternative in which selected functions are reinterpreted from an internalist framework. Under this internalist view of selection, the very capacity of an organism to regulate its environmental coupling produces particular trait functions and consequently determines its selection conditions. Instead of considering selection as the process of creating function in nature – the external force that produces order over random variation – trait function causes traits to be selected. Trait function is connected to the adaptive origins of the trait and thus to its effects on selection. While this conclusion departs from the usual way to understand selected functions, it preserves the idea that selection processes can define (some) evolved functions.

Keywords: Explanatory Externalism; Explanatory Internalism; Selected-Effect Functions; Natural Selection; Agential Paradigm.

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1. Introduction

In *Complexity and the Function of Mind in Nature*, Godfrey-Smith (1996) provides a detailed analysis of various explanatory frameworks in the life sciences. The most widely discussed is the so-called Explanatory Externalism (henceforth EE). Although Godfrey-Smith has dealt with different externalist theses, they are all united under the assumption that "[t]he internal is understood in terms of its relation to the external [...] the channel of causal influence goes 'outside-in' [...] the term 'externalist' will be used for all explanations of properties of organic systems in terms of properties of their environments" (Godfrey-Smith 1996, 30). There are various areas or theories in the life sciences that have adopted an externalist framework. I will limit myself here to the discussion of EE in biology, more specifically in evolutionary theory.[2] The best-known EE in biology discussed by Godfrey-Smith is represented by the adaptationist program of the Modern Synthesis (hereafter MS). The reasons for this are fairly clear: "Adaptationism seeks to explain the structure and behavior of biological systems in terms of pressures and requirements imposed by the systems' environments" (Godfrey-Smith, 1996, 32). Natural selection – an external causal pressure – is seen as the only adaptive force in evolution. The external environmental conditions of organisms determine their adaptive value thus the future of species..

The starting point for this article is that EE has been challenged in recent decades. The monolithic conceptual structure of the MS, 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. These challenges are proposed, therefore, by an internalist framework. Following Godfrey-Smith (1996, 30), "[e]explanations of one set of organic properties in terms of other internal or intrinsic properties of the organic system will be called 'internalist.'" In a biological context, Explanatory Internalism (EI) in evolutionary theory states that organisms – and their internal properties – are a driving force of adaptive evolution.

The first goal here concerns a "meta-metatheoretical" analysis: to connect the metatheoretical analysis of Godfrey-Smith's explanatory framework with different explanatory paradigms that have been conceptualized in different scientific disciplines – the so-called Newtonian Paradigm and Agential Paradigms. This meta-metatheoretical analysis is only intended to shed light on the epistemic properties of internalism and externalism. The second aim of this article is to provide a concise and updated overview of the challenges facing the externalist foundations of the MS. Although the first and second goals are relevant to current biological theory, they are a means to assess our main goal here: to evaluate the selected-effect theory of functions (SE) based on current arguments about EE. This article aims to evaluate whether or not the critique of MS externalism compromises the SE. I argue that the SE has been associated with EE, and this commitment is reflected in various analyses within the SE. However, I will also suggest a way to understand selected functions without associating them with externalism. This in turn means that selection is shifted into the realm of explanatory internalism.

I will proceed with my analysis as follows. In section 2 I present the Newtonian and the Agential paradigms. Section 3 consists of six subsections. In each subsection, I outline a challenge to EE. After presenting all the challenges, in Section 4, I will address the adequacy of the SE in light of the internalist-externalist controversy in evolutionary theory.

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[2] Even though MS's externalism is the main framework for externalism thinking, there are other theories that also take an externalist position. In particular, Field Theory, recently developed by Babcock and McShea (2021, 2023), is an externalist theory in biology that operates at different levels – evolutionary, developmental, physiological. Although this theory has been solidly developed in recent years and deserves careful analysis from a developmental turn perspective, it is not the target of this article.

2. Externalism and Internalism: Different Paradigms

Following the analysis of Godfrey-Smith, what defines externalism is not just the existence of an external force, nor the rejection of internal forces. In the context of biology, EE is the thesis that an external cause is the *guiding* force responsible for explaining the properties of a system. What constitutes externalism is not the rejection of internal causes, but the fact that internal causes are irrelevant to explain why the system has the properties it has. For example, in the context of the old rationalist-empiricist debate, empiricism seems to be an externalist position (without going into the complex details that Godfrey-Smith analyzed) because the features of the environment are responsible for building the mental realm. The external force produces order in the mind, even if internal causes are also involved. Interactivism need not be rejected to support externalism (or internalism). Externalism (or internalism) is defined based on the distinctiveness of a particular cause in an explanatory framework: the cause that explains why the system has the property it has.

MS's EE rests precisely on the distinctiveness of natural selection among other evolutionary causes, an idea easily found in several of the named architects of this synthesis, as expressed, for example, by Huxley in a letter to Mayr: "*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, emphasis added). Natural selection is not seen as the only cause of evolution. It is seen as the only *adaptive* cause.

In particular, natural selection differs from those forces producing phenotypic variation and novelty. Natural selection acts on existing variations. Thus, there must be a process responsible for generating such variations or novelties so that natural selection can pick up the fitter ones. However, the origin of a trait cannot be explained in adaptive terms. Variation, in the MS framework, is *not* produced by a directive force. Variation occurs *randomly*, i.e. traits vary independently of its adaptive consequence. Alternatively, natural selection explains the persistence of a trait not for random reasons, but precisely for adaptive reasons: A trait is selected for its causal contribution to fitness. The origin of the trait could be due to an internal force (e.g. a genetic mutation). But this is not a directive force. The directive force in the MS externalism is about preservation, not origin. I will return to this idea in Section 4.

Lee Smolin (2013) has made a profound analysis of the so-called Newtonian Paradigm in physics, and this characterization has also been applied to biology (Walsh 2018, Kauffman and Roli 2023). Strictly speaking, the Newtonian Paradigm is defined by an EE: the idea that we can explain the processes of a given system by citing external forces acting on it. In this paradigm, the system to be explained plays no role in the explanation. The forces are external and independent of the objects on which they act. The system is regarded as an object that passively "waits" for an external force to act on it. The Newtonian Paradigm thus analyzes "Object Theories". As Walsh (2015, 212) explains,

> Object theories are characterised by what we might call 'transcendence' and 'explanatory asymmetry'. By 'transcendence' I mean that the principles that govern the dynamics of the objects in the theory's domain are not part of the domain itself [...] Because of this transcendence of the principles over the objects, there is an explanatory asymmetry. The principles explain the changes to the objects in the domain, but the objects do not explain the principles.

It is not difficult to recognize the "transcendence" and the "explanatory asymmetry" of the MS: The evolution of a population is not explained by the population itself, but by a property of the environment (selection pressure) and the principle of natural selection explains the change in the population, but the change in the population does not affect natural selection (the selective environment).

An important entailment of MS's EE is the explanatory emptiness of developmental processes in evolutionary theory. The irrelevance of developing organisms has been advocated since the early 20th century. Externalism is secure insofar as the internal source of variation and novelty is not an adaptive force but a random effect. As a result, EI was denied in evolutionary theory. As Maynard-Smith (1982, 6) stated: "It is possible to understand genetics, and hence evolution, without understanding development". However, development is not a black box of evolution. Rather, development is a process that constantly produces new phenotypic variations mediated by multiple inheritance systems, and the fitness values of each organism are constantly being adjusted. Nowadays and in the last 30 or 40 years, the importance of the development of organisms in evolutionary theory is experiencing a revival. The main reason for this is that biologists and theorists have begun to appreciate the complexity of development, so that "the black box is now being opened to provide a more complete picture of what really happens" (Bateson and Gluckman 2011, 17). This has favored an EI in evolutionary biology, whose main claim is that it is "not possible to explain the structure of organic systems, or the course of evolution, by attending simply to the structure of the environment which organisms inhabit" (Godfrey-Smith 1996, 37). I will use the term "developmental turn" to refer to the group of views that oppose the MS and converge on the idea that developing organisms are an important force in adaptive evolution, recognizing that within the developmental turn there is also a plurality of views (Rama 2024b).

In this context, EI is usually enclosed under the idea that "the organism is an evolutionary cause" or that "developmental processes causally affect evolutionary change". The emergence of a developmental turn in evolutionary biology has given rise to the Agential Paradigm, most notably explored by Walsh (2015, 2018). In contrast to the Newtonian Paradigm, the entity itself (the organism) is now required to explain its own properties; organisms are part of both the *explanans* and the *explanandum*. The organism is a force within the realm of the given explanation; organisms provide causes that explain their own processes. Accordingly "Agent Theories":

> … are characterised by what I shall call 'immanence' and 'explanatory reciprocity'. In an agent theory the entities in the domain include both agents and the principles we use to explain their dynamics […] as agents implement their responses to their conditions, they not only alter their own state, they also change the conditions to which their activities are a response. There is thus a dialectical relation between the activities of the entities in the domain, and the principles we call upon to explain them. The activities of the agent can be explained as a response to its conditions, and reciprocally, the change in conditions can be explained as a consequence of the activities of the agent.

Beyond internalism and externalism, Godfrey-Smith also examined another explanatory framework: constructivism. Accordingly,"'[c]onstructive' explanations are explanations of environmental properties in terms of properties of an organic system" (Godfery-Smith 1996, 30). As we will see, constructivist views have played a central role in the challenge to EE, influenced especially by Lewontin's dialectical ideas (Levins and Lewontin 1985). This leads to the following question: should we identify the developmental turn with constructivism or with internalism? The first answer is quite simple: constructivism can be coherent with internalism. The fact that organisms account for some properties of the environment *and* some of its internal properties is not a contradiction, and this possibility was well recognized by Godfrey-Smith. Against EE we can put forward both internalist and constructivist explanations.

Another response is highly critical: constructivism is only problematic *if* it neglects the explanatory privilege of organisms over the environment. It is important to avoid this commitment when interpreting "explanatory reciprocity" in the above quotation. One unproblematic interpretation is that explanatory reciprocity simply means that organisms are embedded agents that constantly act in context-dependent ways. Nonetheless, "explanatory reciprocity" can be interpreted to mean that the organism has no explanatory privilege over the environment. This does not seem compatible with internalism. This blurs the boundaries between internalists and externalists and attempts to explain the relationships between organisms and the environment as a single unit of analysis. However, I believe that this is not an adequate characterization of the developmental turn. Rather, the agent in the Agential Paradigm introduces an *asymmetric* explanatory component. Barandiaran et al. (2009) provide one of the most robust and widely accepted views of natural agency. One of the characteristic features of agents is *interactional asymmetry*: "the condition describing a system as capable of engaging in some modulations of the coupling and doing so at certain times" (Barandiaran et al. 2009, 372). In the next section, I will point out various phenomena in which organisms change their (internal or external) circumstances according to their own needs. This is also the distinctiveness of living systems: living systems can modulate the relationship with the environment in such a way that the system is not controlled by the environment, unlike non-living systems that cease to exist when the environment changes.

I find this clarifying point important insofar as internalism is sometimes rejected on the grounds that development is not an "internal" process (e.g. Oyama 2000, Walsh 2012, 2015). This is correct. Most areas of the developmental turn – see next section – argue that development requires context sensitivity and that ecological factors are central causal factors in development and physiology. But, to reiterate, internalism does not mean that there are no external factors. Internalism entails that external factors are regulated by internal means. Internalism relies on the asymmetrical relationship between organism and environment and not on the fact that development is a "solipsistic" or "isolated" phenomenon. Therefore, I suggest, "explanatory reciprocity" should be complemented by "interactional asymmetry" in the classification of the Agential Paradigm. The identification of the developmental turn with an EI is based precisely on this asymmetry.

3. Explanatory Internalism in Evolutionary Biology: An Overview

I will now spell out six different phenomena and their related field of research that have questioned the EE of the MS.

3.1 By-products and developmental constraints

A seminal work against externalist thinking was the 1979 paper by Gould and Lewontin. One of the main arguments of this paper concerns evolutionary by-products. They illustrate biological by-products with a familiar 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 by external causes alone. Rather, their explanation must lie in the internal properties of the system, i.e. 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.

Furthermore, part of the evo-devo research agenda is devoted in particular to analyzing the evolutionary consequences of *developmental constraints* (Amundson 1994). The existence of developmental constraints means that not all phenotypic variations are possible. Phenotypic variation is finite – as Alberch's (1991) morphospace illustrates. Limits exist insofar as some elements of developing organisms must be a prerequisite for the development of a particular organic structure. The presence of a particular trait may not be due to a selection process, but an internal requirement of the developmental system; something that cannot vary because it is a prerequisite for development – be it a physical, a chemical, or a biological constraint. The most discussed case is the tetrapod limb, a highly conserved structure across species. While a functional-selective explanation would point to the adaptive advantage of tetrapod body plan, there is an alternative explanation according to which the presence of four-limbed body plans is constrained by developmental factors (Carroll, 2005). The message we can take away concerns the need for internalist explanations for the structural properties of a system (Novick 2023). There are several properties of organisms for which a functional explanation is required. 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.

3.2 Self-organization: inherency

Various authors argue that self-organization is crucial to evolutionary theory (e.g. Kauffman 1995, Newman and Muller 2002, Gilbert and Sarkar 2000). The origin of a trait may be the product of interaction between the parts of a system at a particular level of analysis. However, it is important to distinguish between two types of self-organization processes that take place during ontogeny and are relevant to evolutionary theory: *adaptively directed* and *non-adaptively directed* self-organization processes, i.e. those that are directed to produce a certain functionality and those that arise due to non-functional reason. The former is connected to the *autonomy* of the living organization while the latter focuses on the phenomenon of *inherency*. The boundaries between the two might be blurry, and usually, most living phenomena explained by self-organization involve both types simultaneously. For the sake of clarity, however, I will present them separately. Let us begin with inherency, following the work of Stuart Newman.

Newman (2022b) defines “physical self-organization” as the property of systems in which emergent patterns can be explained by the physicochemical relations of their parts. In his view, physical self-organization is generated by “generic mechanisms” (Newman and Comper 1990) that might be found in living and non-living systems. The consequences of generic physical mechanisms in living systems were developed under the concept of inherency (Newman 2021) and are documented 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). Keeping in the context of tetrapod limbs, Newman explored how skeletal elements in vertebrate limbs, like the bones in human arms and legs, form through a pattern formation driven by a mechanism known as reaction-diffusion, where interacting chemical signals generate periodic patterns that direct the development of skeletal structures.

The key point here is that the emergence of phenotypes due to generic physical mechanisms is independent of externalist or functional considerations. The physicochemical nature of living organisms can provide an alternative, non-etiological answer to the presence of a trait in evolutionary history, 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 emergence of self-organized patterns during evolution and development does not fall within the framework of EE but of EI: “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 (2021, 130) concludes that “inherency is not merely complementary to the Darwinian paradigm, but is at odds with it.”

3.3 Self-organization: autonomy

Autonomy also concerns the self-organized quality of living systems, but unlike inherency, to understand autonomy we need to introduce a functional characterization of how the parts of a system contribute to the maintenance of the whole system. Autonomy differs from inherency precisely because autonomy seems to be present only in living systems, whereas inherency is found in non-living systems. The core idea behind the minimal characterization of an autonomous system is that a living system regulates its interactions with the environment and its internal organization to stay alive. Each part of the system is in a functional relationship with other parts to maintain, reconstruct, and reproduce the system during life. This ability is of central importance when it comes to finding a balance between two opposing and essential properties, namely *openness* and *closedness*. Living systems are *thermodynamically open* (Bertalanffy 1969); they exchange matter and energy with the environment in order to maintain and reproduce life. However, organisms are also separated from the environment. The functioning of the different parts of an organism represents an *operational closure* (Maturana and Varela 1980) that makes it a separate entity from its environment.

The regulation of both internal organization and coupling with the environment is a milestone for autonomous agency (Moreno and Mossio 2015). Adaptive regulation of living organisms allows them to fluctuate between the stability of their internal structure and malleability to different external scenarios. Organisms can adapt to different environments while maintaining their own internal identity. While many non-living dissipative systems generate self-organized patterns and can be differentiated from the environment (e.g. Bénard Cells, vortex), living systems seem to be able to regulate their interaction with the environment in order to maintain their internal organization.

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 various biological processes. The autonomous regulation of living conditions can lead to various morphological, anatomical, physiological, cognitive, or immunological changes: The absence of a regulatory gene can lead to a nonlinear change in ontogenetic stages; the modification of a specific enzyme can lead to variants in the amount of protein product; a chemical gradient can influence the timing of gene expression. The networked nature of developmental factors proves that the regulation of their interaction is a crucial factor for the emergence of an adaptively directed developmental outcome. A good example of morphology is the study of the so-called *two-legged effect*, which was investigated by West-Eberhard (2003). 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. Due to these morphological changes, the goat was able to stand upright and walk with two legs. In this example, there was a drastic morphological change in the column as a result of another change in the system (two legs instead of four). This example only illustrates how different features can arise for organizational reasons. This deserves a look at what is going on inside the organism. It is about organizing its own structure so that it functions properly in a particular environment.

3.4 Developmental plasticity

Developmental plasticity refers to the ability of developing organisms to adapt phenotypic outcomes according to their developmental context. 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 stressed the evolutionary role of developmental plasticity and it is now recognized as “a ubiquitous and probably a primal phenomenon of life” (Wagner 2011, 216). A well-documented case of phenotypic plasticity with evolutionary consequences concerns the plant *Polygonum* (Sultan 2015). For example, the invasion of *Polygonum cespitosum* in North America due to new environmental conditions led to drastic plastic changes (allometric, morphological, reproductive, physiological) that affected reproductive success and spread the new variants in short periods.

But does developmental plasticity contradict EE? 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 MS found a way to accommodate plasticity within its framework (Rama 2024c). The strategy was to consider that plasticity can be explained at the genotype level by postulating genes that are able to provide a repertoire of phenotypic outcomes in different environments. *If* this reduction is possible, natural selection is responsible for explaining plasticity, and consequently, developmental plasticity could be explained from an externalist framework (see Futuyma (2017) for a contemporary defense of this idea). Phenotypic plasticity is the result of plastic genes, and the plasticity of genes is explained by natural selection. 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 such that a robust Genotype-Phenotype map emerges. 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' gene-eye view (1976). Consequently, we can understand phenotypic plasticity in terms of genetic plasticity. 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 in greater detail. An important event 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 and evolution by sequencing DNA strands alone. DNA sequences are not sufficient for that explanatory task. Development is much more complex than the central dogma suggests (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). Developmental research should not be enclosed in classical molecular genetics, but rather in the so-called *post-genomic era*. Here, genetic activity is understood as part of molecular epigenetics. The mantra of post-genomics is that the cells have custody of the genes and not vice versa. Genetic activity is regulated by a huge amount of causes emanating from different levels of organization, taking place in the context of complex systems. The explanation of developmental products cannot ignore the non-genetic sources of developmental specificity (Griffiths and Stotz 2013). As a result, in the post-genomic era, the organismic dimension of phenotypic plasticity comes to the fore: "plasticity is an intrinsic property of organisms" (Sultan 2021, 6), it cannot be explained by an extrinsic force acting on genes. As Bateson and Gluckman (2011, 43) emphasize, "the central elements underlying many forms of plasticity are epigenetic processes." Phenotypic plasticity and its epigenetic interpretation provide another reason in favor of an internalist factor in evolution.

3.5 Niche construction

Another discipline that has dealt with EE is niche construction theory (Odling-Smee et.al. 2013). The core idea is that when faced with environmental problems, organisms can overcome them by *changing the environmental scenario* – i.e. to solve the problem by changing it. The theory was developed at the beginning of this century and many of the central ideas were set out by Richard Lewontin (2000, 2007).

Lewontin analyzed how niches and adaptations are represented in the MS. Adaptations are the better solutions promoted by random genetic changes to problems posed by the environment. Adaptations are the 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 the MS understands niches was described by Lewontin as the *Autonomy of the Environment,* and is a clear sign of an Object Theory. The environmental conditions that organisms inhabit are autonomous from the organism itself; organisms are passive repositories of genetic variants waiting to be selected or discarded by natural selection.

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 organism, organisms are actively determining the niche they face. Two types of niche construction processes are relevant, both of which are appropriate for understanding the critique of externalism and the alleged autonomy of the environment. First, 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 in order to change the environment they live in. These include the construction of the niche in which they live, migration, or invasion. Secondly, there is the (philosophically deeper) concept of *experiential* niche construction (Sultan 2015). This involves the inherent ability of each organism to determine which aspects of the world are relevant to it (Lewontin 2000, Rama 2021, Rama 2024a). Experiential niche construction describes the idiosyncratic ability of each organism to construct its environment based on its sensory abilities. Different developmental aspects directly rely on how organisms perceive their environment, such as the effect of the perceived amount of water in an amphibian's niche in the timing of metamorphic changes or sound perception during vocal learning in birds. Certainly, not all organisms relate to the same part of the world. This is partly because they live in different places. But also because each organism has a specific niche it experiences.

3.6 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 trait can adapt to this change and construct a new function. In this case, the current function does not match the evolutionary function. A well-documented case is the feathers of birds, which were originally selected for thermoregulation but then acquired the function of improving aerodynamic performance. Another example is the human tendency to consume sugar, which may have had more positive effects in earlier times when sugar was scarce than in today's world. 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 to drastic environmental or internal changes can produce 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 organisms' internal adaptation to the new environment.

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 might be a mismatch between the evolutionary history and the 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 having adapted to such new situations.

Exaptations and evolutionary mismatches point to a limit in some externalist explanations advocated, for instance, in evolutionary psychology and sociobiology. 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 were exposed to during evolution, since the current function may not fit the old environment. The reverse logic, known as reverse engineering, does not work either: today's environment does not have to provide information about the functions of a trait during the evolutionary process. Perhaps the evolved function is not the same as the current function, just as the ancestral scenario is not the same as the current one. In this sense, EE is limited. I cannot assume that function and environment are identical across the evolutionary time scale; it is not a conceptual truth that can be applied to every case.

4. Rethinking Selection Beyond Externalism

The discussion between externalism and internalism leads to our main topic here, biological functions. The goal is to evaluate whether the challenges to EE affect the selected-effect theory of functions (SE). Biological functions are intensely debated, and various theories and proposals are in play. While the analysis here focuses on SE, there are several biological theories of functions associated with internalism (e.g. Christiensen and Bickhard, 2002, Mossio et al, 2009, Love, 2007, Newman 2022a, Walsh 2014). I will not go into these theories, but before proceeding, it is important to note the following point: Since Darwin, externalist-adaptationist explanations of function provided an alternative to vitalist or creationist views and their anti-scientificity. This was definitely seen as a strength of externalism. But times have changed, and the twentieth century has brought forth a multitude of scientific disciplines – e.g. dynamical system theory, systems biology, cybernetics – that support internalist theories of function. Darwinism is thus no longer seen as the cure for the hidden forces of vitalism, and the reason for the adoption of externalism is not the absence of naturalistic internalism.

Internalist criticism of the SE is not new. The SE has been criticized many times before, and many of these criticisms are biological arguments motivated by the developmental turn. Some critiques are quite recent (e.g. García-Valdecasas and Deacon 2024, Balari and Lorenzo 2013, Rama 2022, 2023, Christie et al. 2021, Bourrat 2021, Bouchard 2021, Mossio et al. 2009, Fodor and Piattelli-Palmarini 2010, Kraemer 2014, Griffiths 2006), while others are present since some decades ago (e.g. Cummins 1975, Bedau 1991). This paper combines many of the elements discussed in this literature and places the analysis in the context of the externalism and internalism debate.

As a result of criticism, the SE has undergone many reformulations and ramifications. Despite their differences, all SE approaches at the evolutionary scale converge on the idea that the function of a trait is defined by the causal role that the trait plays in natural selection. The function of the heart is to pump blood, not to make noise because pumping blood led to hearts being selected while making noise did not. In a recent appraisal of SE, Artiga (2020, 53-53; emphasis in original) provided the following definition of the SE:

T has the function F iff F was an effect of T and the following conditions hold:

> 1) *Heredity*: Individuals reproduce and offspring tend to resemble their parents.
> 2) *Variation*: Individuals differed from one another in whether they possessed a trait T that they performed F.
> 3) *Differential Reproduction*: Individuals that possessed a trait T that performed F were more successful at reproducing than individuals that did not possess a trait T that performed F.
> 4) *Causation*: F causally contributed (positively) to reproduction.

According to it, hearts have the function of pumping blood because population *A* with hearts reproduced differently than population *B* without hearts due to the causal role that hearts played in population *A*. The question raised now is whether or not the criticism of the EE affects the SE. To this end, the relationship between the SE and the EE must be examined. Is the SE beholden to the EE? I will give two answers here. First, I argue that the SE has been closely linked to EE. This means that most SE theories draw on EE in one way or another. In the next section, however, I argue that EE can be defined in a way that is unaffected by the challenges of Section 3. However, this implies a serious reframing of what selection is.

4.1 Selected-effect functions and externalism

To a first approximation, the links between the SE and the EE are fairly clear: the birth of the SE took place in the context of philosophers who explicitly adopted an MS framework – Ruse (1973), Ayala (1970), Millikan (1989), Neander (1991). Hence the SE inherits the explanatory framework of the MS, including externalism. However, apart from the idiosyncratic emergence of the SE, there are also more strictly theoretical reasons that can be found even in today's literature.

A first theoretical link between SE and EE can be found in the (still) repeated use of Sober's *selection-for* concept to characterize functions as selected-effects. Sober (1984) depicted natural selection as a force that causes population change – speciation, extinction, expansion. Selection refers to the causal contributions of a trait type to the selection of the population possessing that trait. In this framework, as Sober has made clear, individual processes are completely irrelevant. The only relevant parameter is the difference in fitness at the population level, and natural selection is presented as an external force acting on the population. Sober's framework is a clear case of a Newtonian Paradigm in biology.

Another externalist feature of SE is based on the adoption of an adaptationist framework by some of its proponents. This can be seen, for example, in Ruse (2003) and Nenader (2017), who present natural selection as a process that "designs" populations. Design-like explanations have found their niche in the adaptationist notion of natural selection as a blind watchmaker that creates order (through selection) where chaos (random variation) previously prevailed. The link between adaptation and selection has been discussed in detail by Sterenly and Griffiths (1999), for example, and recently emphasized by Bourrat (2021). In this vein, if "functions of a biological trait are those effects for which it is an adaptation" (Sterenly and Griffiths 1999, 221), it is not easy to see how the SE could dispense with the evolutionary externalism on which the design-like arguments are based.

The (implicit or explicit) use of Sober's notion of selection-for and adaptationist ideas leads to the clearest point at which we can find an externalist commitment of the SE, namely that selection is needed to produce functions. This idea has been present since the early days of the selected-effect account and is still defended today. According to this view, natural selection is the force that produces functions. As discussed in Section 2, the externalist position of the MS accepts internal causes, such as the causes of variation. But it holds to the external cause (selection) as the only adaptive cause. This is what the SE seems to support: causes of variation do not create functions, selection processes do. For instance, when Garson (2019, 29) analyzes other evolutionary causes driving variation, he argues that functional attribution should not be in play because "selection hasn't yet taken place." The externalist footprint of the SE regards the cause that produces functional organisms. Externalism states it is selection: a trait *T* has function *F* *because* it was selected. Before selection, no adaptive force acted on *T*, so *T* has no function.

The creative role of selection in functional ascription – i.e., no function without selection – is well appreciated in the distinction between function and accidents developed by Garson (2019, 28): "The difference between a function and a lucky accident is that the former explains the existence of the trait in question, through a natural process of selection, and the latter doesn't." His view adopts the common representation of the MS. A trait arose by chance. If selected, it has a function; however, "in the absence of selection, the activity [of that trait] should count as a lucky benefit, and not as a function" (Garson 2016, 51). Variations and novelties, if understood as the result of random forces (i.e. non-directed to fit), should be regarded as a lucky accident. Traits acquire a function through cumulative selection processes.

I have two comments on this. First, using Garson's example, imagine that zebra stripes arose by chance and that zebra stripes were *selected for* deterring flies. If this is the case, it means that the first zebras with stripes *already* performed the causal role of fly deterrence before they were selected. If not, how could the stripes cause differential reproduction? The function that causes a trait to be selected is *already* present before selection. It seems incorrect to say that trait *T* performs a function in a population *P* at time *t*, while this trait performs no function at previous time t-x when in reality they play the same causal role and contribute to differential reproduction. Even if a trait arises by chance, it is a mistake to say that natural selection must produce a function for a causal role that a trait already plays.[3] The second point is even more important and is directly related to our interests: we have sufficient reasons from Section 3 to devise alternative scenarios in which the zebra's stripes did not arise randomly but because of an adaptive response to certain environmental conditions. In these cases, the origin of the trait is linked to the function that the trait performs. This is how the developmental turn usually uses functional explanation. Natural selection cannot be the process that helps us

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[3] It is important to point out that the existence of mutations does not mean that the phenotypic variant produced is also random. First, most mutations or stochastic errors are neutralized by plastic regulatory means (Noble and Noble 2018). Moreover, the presence of a particular mutation at the molecular level does not mean that its effects are adaptively regulated. A mutation can be internally regulated so that the phenotypic variant arises for adaptive reasons (Nuño de la Rosa and Villegas 2022).

distinguish between function and accidents, and that is bad news for SE, insofar as one of "[t]he strongest rationale for SE is that it makes sense of the distinction between function and (lucky) accident" (Garson 2017, 523).

To summarize, I have pointed out two central externalist claims in the SE: first, that selection is the external force that creates functions, and second, that internal causes that produce variation are not a directive, creative force in evolution. This article argues that *if* the increasing importance of internalism in evolutionary biology affects the externalist explanations, *and* the SE relies on EE, *then* the SE is also affected by EI. In this section, I have argued that the links between the SE and EE are clear in different approaches. However, a more general (and complex) question arises: is the SE inescapably linked to EE? Is it possible to accommodate SE within an internalist framework? These questions are important for two reasons. First, to enable a more robust analysis of the SE from the perspective of the developmental turn. Second, to explore the possibility that evolutionary functions can be defined by selection processes

4.2 Selected-effect functions and internalism

Some of the internalist challenges concluded that not all traits merit a functional explanation for their existence. This is of particular importance insofar as those traits that do not evolve for functional reasons (e.g. "biological spandrels") could also have a function. It is not an indication of the functional role of these traits that explains why they exist in nature.[4] However, this is not the case in all the phenomena portrayed in Section 3. A radical and misguided view of the developmental turn might say that selection does not explain evolutionary processes. This is a clear misconception. Rather, the developmental turn seems to suggest a reconceptualization of selection. Many of the internalist explanations we have seen are based on selection processes. Plasticity, for example, is just one way of generating heritable variations that can influence the evolutionary path. As we have seen, the developmental turn would reject the idea that cumulative selection is the only process that creates functions. Developmental processes also do. However, the recipe for natural selection (inherited variations in fitness) introduced by Darwin remains intact and so do the elements in Artiga's definition above. The developmental turn argues that this recipe requires an internalist explanation: the study of developmental processes, organism-environment coupling, self-organization, or other processes that generate inherited variations in fitness. This in turn suggests an alternative view of selection that breaks away from the externalist foundations of neo-Darwinism.

We can picture alternative views of selection by drawing on the differences between the Newtonian and Agential paradigms. According to the characterization made in Section 2, a Newtonian view of selection is defined by two claims. I) *Transcendence*: selection is regarded as a force independent of the domain of analysis (traits functions) – i.e. the external pressure acts on traits to produce their proper functions. II) *Explanatory asymmetry*: selection is the process that causes a trait to have certain functions, while the function of the trait does not modify selection pressures – i.e. environmental pressure changes the traits in a population, but the traits do not change the environmental pressure. The Agential Paradigm invites us to look at selection differently, based on two claims. I) *Immanence*: the environment

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[4] Garson (2016, 2019) has recently argued that the question of whether a trait is a by-product or a selected trait is not a problem for selected-effect theorists, but for biologists; i.e., that the evolution of any trait is a contingency of biologists, not a problem for selected-effect theorists. I understand this argument, but I do not find it convincing. In principle, a biological theory of function is not applied in this way in different contexts. Consider teleosemantics. Should we wait until we know whether the frogs' visual systems have been selected to provide a teleosemantic analysis of the frogs' perceptual representations? Teleosemanticists certainly do not. They apply the SE directly to characterize the function of a trait, regardless of whether they know its evolutionary history. The same is true for other fields such as ethics or medicine. As Wouters (2005, 126) has already argued, "functions are often ascribed in the absence of a historical study". "Biological spandrels" are not just a problem for biologists, as Garson has said. It is a shortcoming for the SE and the explanatory role of functions in various biological disciplines (hence the anti-adaptationism of Gould and Lewntoin was taken seriously by many and various modifications of the SE emerged, notably (Girffiths 1993, Godfrey-Smith 1994)).

and the activities of organisms are interviewed in such a way that the elements of the domain of analysis (traits) are part of the force that explains itself – i.e. selection is the product of the adaptation of organisms' living conditions. II) *Interactional asymmetry*: The reciprocity between organisms and the environment means that the presence of a certain function in an organism leads to the selection of that organism and not the other way around. The Newtonian and Agential paradigms contradict each other about the nature of selection: according to the former, selection is an external cause that produces the functions of a trait; according to the latter, the presence of a function is an intrinsic cause that leads to selection.

Understanding selection from an internalist point of view makes it possible to rethink the SE, even if it differs from the common interpretations. This is something positive, in our opinion, as we are searching for a characterization of evolutionary function beyond externalism. We can still identify the function of some evolutionary traits in the context of a selection process, without neglecting the motivations that lead many in recent decades to an internalist stance. Artiga's definition above can be placed in both an externalist and an internalist framework. While I have argued that externalism is the predominant framework adopted by SE theorists, it is not the only possible option. If the stripes of zebras have the evolutionary function of deterring flies, this means that the stripes were selected during evolution. However, this process is interpreted differently by each paradigm. A Newtonian view would say that the stripes arose by chance without having a specific function and that cumulative selection processes have given the stripes the function of deterring flies. The Agential view, on the other hand, would argue that the stripes arose through a developmental process related to the needs of deterring flies (or it might be said that zebras stripes do not deserve functional evolutionary explanations, as is the case of butterfly spots); that some regulatory developmental process enabled the zebra to produce stripes. Since the stripes are functional to deter flies (and this presumably affects fitness scores), zebras with stripes were selected. This illustration is not about the empirical plausibility of each paradigm in this specific case, but about how these paradigms explain selection and function differently.

A positive aspect of this proposal concerns a central *desideratum* for any theory of function: the explanatory role of functions. Typically (Artiga 2021, Garson 2016), functional explanations aim to explain the existence of a trait, e.g. that zebras have stripes *because* they deter flies. We have already seen that the existence of some traits cannot be explained by functional reasons. But apart from this point, the explanatory role of functions is usually understood specifically: in terms of persistence and not in terms of origins (Neander 1995). In other words, functional explanations are concerned with why a feature persists in nature, rather than why it first comes into nature. I am not going to debate whether effectively functional explanations in biology are related to persistence and not origins (that might just be MS's thinking bias). What we are getting at is that an internalist view of selection is appropriate for both the origin and persistence of traits: since the origin of a trait is functional, we explain i) why it first appears in functional terms (i.e. because it responds adaptively to its developmental context) ii) why it was selected (i.e. because it produces a suitable trait for a given environmental condition). According to the above scenario, the stripes would arise through some regulatory mechanisms. And since they arose in response to an environmental condition, the function of the stripes would result in zebras with stripes being selected. This does not mean that EI substituted population explanation by natural selection. It just means that internalism is suitable to study both the causes that produce a novel trait and those causes that explain why it is selected and preserved.

We can imagine a simple scenario, motivated by the role of plasticity in evolution, in which trait function can be identified as the selected function without assuming the environment as an external guiding force. Imagine that a particular epigenetic change is produced when a particular species is confronted with an environment – a plant that produces a variant T because another species invades its niche. This variant plays a crucial functional role F in the survival of the plant population, and the mechanisms for the development of this new variant are inherited epigenetically. Following West-Eberhard's revival of Waddington's view (West-Eberhard 2003), we can even add that the mechanisms for developing T are genetically internalized, and reproduced across generations with great fidelity. The relevant conclusion is that we can say that T has the function F without assuming that it was the process of selection that produced that function. Rather, it was the epigenetic regulatory capacity of the plants when confronted with invasion. The force that explains the origin and persistence of functions is not explained from an externalist perspective but from an internalist one.

To finish, let's make an important remark that may clarify the ideas exposed here. Most SE theorists are pluralists. This means that they also accept other theories of function (the clearest case is Shea 's (2018) *varitel*; see also Neander (2017) and Papineau (2016)). SE theorists are aware that the explanation of biological functions is not limited to evolutionary functions alone. This means that beyond evolved functions, SE theorists also support ontogenetic theories of functions. This too is problematic, but not for the reason we discuss here (but see Rama (submitted)). What we are getting at is that accepting ontogenetic functions is quite different from recognizing the role of ontogeny in evolution, as the developmental turn aims to do. It is one thing to say that there are ontogenetic and evolutionary (selected) functions; it is another thing to say that ontogeny influences evolutionary functions. Our aim here concerns the latter claim. The tension between EE and the SE cannot be resolved simply by adopting a pluralistic view, as is usually done in relation to ontogenetic and evolutionary functions. To clarify this difference: one thing is to say that the development of behavior gives rise to new ontogenetic functions, and another to say that the development of behavior gives rise to evolutionary functions. No MS biologist would neglect the former; most rejected the latter.

This comment is relevant if we think about different ontogenetic theories based on selection, for instance, Garson (2017), Frisco et al. (2017), or Kingsbury (2008). As said, my target here is selection in an evolutionary context, so we have no space to discuss these ontogenetic approaches. However, the remarks for the internalist-externalist debate discussed here might also be relevant. Principally, the question at play is whether ontogenetic selection processes would be explained based on an external force or an internal force. If we say that ontogenetic selection is the product of the environment eliminating alternative random variants during development – as in classical behaviorist models, we might tend toward an externalist position. However, if an ontogenetic selection process refers to different variants that arise through the adaptive adjustment of the organism to its environmental conditions, then we need an internalist view. Consider a plant that develops two types of leaves – small and large – during its first ontogenetic stages and that only the small leaves are retained in later life stages due to temperature conditions. An internalist explanation would point to the regulatory mechanisms that guide a plant's development towards the production of small leaves through its contribution to thermoregulation, while an externalist explanation would say that the external conditions eliminate the large leaves and maintain the small leaves, without referring to the regulatory mechanisms that produce one or another leave. From an externalist perspective, small leaves have the function of thermoregulation because they were selected during ontogenetic stages; an internalist explanation would rather say that having the function of thermoregulation leads to small leaves being selected during ontogeny.

5. Conclusions

In this paper, I have developed several interrelated analyses. First, I have presented two different meta-theoretical analyses of explanations in biology: the internalist-externalist debate and the Newtonian and Agential paradigms. I have devoted an entire section to showing the externalist roots of the Newtonian Paradigm and the internalist roots of the Agential Paradigm. I continued by outlining several challenges that different areas of biology have posed to EE in evolutionary theory. A first shortcoming is that not all traits merit an adaptationist explanation in terms of the function a trait performs; many traits are in nature due to "formal" or "structural" reasons, as is the case with biological spandrels or inherences. In addition, several areas deal with processes that produce adaptive variation as a result of organisms' agentive regulatory capacities. These scenarios demonstrate the central active role of organisms in evolution as producers of trait functions, depending on how they adapt to changing environmental scenarios. Almost thirty years ago, Godfrey-Smith analyzed the challenges to the adaptationist-externalist program of the MS. The conclusion of Section 3 is that since Godfrey-Smith's book, the biological sciences have provided increasing evidence and theoretical analysis justifying the need for explanatory internalism in evolutionary biology.

The analysis carried out in sections 2 and 3 forms the basis for the main question assessed here: whether or not the SE is also committed to EE and consequently affected by the evolutionary challenges to externalism. I have argued that the SE's commitment to externalism can be seen in various authors from the birth of the SE to its contemporary adherents. The appeal to Sober's selection-for concept to characterize selected functions, the use of adaptationist explanations, the invocation of the design-like argument, or the distinction between trait function and accidents are some of the places where externalism has played an explanatory role in the SE. In particular, SE theorists inherit the explanatory logic of the MS which ascribes to selection the creative role of generating functions – that there is no function before selection processes. However, I also intend to provide a possible alternative to the SE, which is to decouple selection from externalism and understand how selection should be conceived from an internalist perspective. I have argued that the developmental turn focuses on the origin of variation as the process that gives rise to trait function, and that selection follows from the struggle of organisms for life – that selection is the result of the activities of organisms and therefore falls within the domain of EI. At the heart of this approach is the idea that the function of a trait is the cause of a trait being selected and not the other way around: instead of "no function without selection", "no selection without function".

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