Function and Selection Beyond Externalism

Addressing the impact of explanatory internalism in the selected-effect theory

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Abstract: In evolutionary theory, Explanatory Externalism—one of the pillars of the Modern Evolutionary Synthesis—holds that natural selection is the sole adaptive force driving evolution. This paper highlights several challenges to Explanatory Externalism, primarily advanced by developmental biology and its various subfields and theories. Based on this debate, I examine the implications for one of the most established accounts of biological function: the selected-effect theory. While externalist readings of selected-effect theory are common, I argue a conditional claim: *if and when* SE is interpreted within an externalist framework, two central *desiderata* remain unresolved—the *explanatory* and the *discriminatory desiderata*. Internalist explanations are indispensable in evolutionary biology for two reasons. First, in connection with the *explanatory desideratum*, internalist explanations are necessary to account for the existence of traits—not only at their origin but also in their transgenerational persistence. Second, concerning the *discriminatory desideratum*, an internalist framework shows that traits may exist in nature without being either selected or accidental, arising instead from structural properties and constraints that render them necessary conditions for the organism's existence. Due to the limits of an externalist

SE, I propose a possible alternative in which selected functions are reconceptualized from an internalist perspective. Although this framework remains underdeveloped, key ideas can be outlined through the Agential Paradigm in biology. In this view, an organism's capacity to regulate its environmental interactions generates specific trait functions, which in turn determine selection conditions across generations. Rather than treating selection as an external force imposing order on randomness, trait function itself drives selection—no selection without function. Selected functions are thus linked to the adaptive origins of traits and their persistence across phylogeny. From this agential perspective, developmental processes generate specific functions, which in turn cause the selection of traits. This article, consequently, offers an appraisal of selected-effect functions grounded in a reconceptualization of selection within the Agential Paradigm.

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

Selection, in a very real sense, just *is* development.
Denis Walsh 2015, 237, emphasis in original.

1. Introduction

In *Complexity and the Function of Mind in Nature*, Godfrey-Smith (1996) offers a systematic examination of explanatory frameworks in the life sciences, with particular attention to Explanatory Externalism (EE). Despite variations among externalist theses, they share the assumption that "the 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). While externalist approaches appear across several domains of the life sciences, my focus here is on EE within evolutionary biology.[1] The most prominent form of EE in biology, according to Godfrey-Smith, is the adaptationist program of the Modern Synthesis (MS). This is unsurprising, since "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). In

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[1] 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.

this view, natural selection—an external cause—is the sole adaptive force, with environmental conditions determining organisms' fitness and thereby shaping species' evolutionary trajectories.

This article is motivated by the systematic recognition that EE has faced sustained challenges in recent decades. The MS, once a dominant and unifying framework, has been increasingly criticized in light of conceptual and experimental advances. These critiques often draw on an internalist perspective. As Godfrey-Smith (1996, 30) defines it, "explanations of one set of organic properties in terms of other internal or intrinsic properties of the organic system will be called 'internalist.'" Within evolutionary theory, Explanatory Internalism (EI) states that organisms—and their internal properties—are a driving force of adaptive evolution.

The first aim of this article is to assess how the externalist–internalist debate in evolutionary theory bears on the selected-effect theory of functions (SE). Specifically, I ask whether critiques against MS's externalism undermine SE. My focus then is on externalist interpretations of SE, and regardless of whether there are internalist SE proposals, my main claim is *conditional*: *if and when* SE adopts an externalist stance, *then* key explanatory *desiderata* remain unaddressed. I therefore argue that SE should incorporate internalist insights to adequately explain evolved functions, and hence I sketch an account of selected functions independent of externalism. Two further contributions guide this analysis: (i) linking the externalist–internalist debate to the Newtonian and Agential Paradigms in biology, and (ii) systematizing critiques of the externalist foundations of the MS.

The analysis proceeds as follows. Section 2 outlines the SE and the core *desiderata* that any theory of function must address, with emphasis on the *explanatory* and *discriminatory desiderata*. Section 3 introduces externalism and its connection to the Newtonian Paradigm. Section 4 turns to critiques of externalism in evolutionary biology, framed through the alternative Agential Paradigm. These critiques fall into two categories: (i) not all evolved traits require functional explanation—there is existence beyond function (Section 4.1); and (ii) not all functions depend on external selection—organisms themselves play an active role in evolution (Section 4.2). Section 5 advances my conditional claim that an externalist SE would leave key *desiderata* unexplained. Finally, Section 6 argues that SE can, and should, be integrated with an internalist, agential account of evolution.

2. The SE and the desiderata for a theory of functions

The focus of this article is the SE, which warrants a brief overview. SE emerged in the 1970s through the work of scholars examining teleological and functional explanations in biology from an evolutionary perspective (Ayala 1970; Ruse 1973), with its most influential formulations appearing around 1990 by Millikan (1989) and Neander (1991). Although SE has undergone numerous refinements, all evolutionary-scale accounts converge on the principle that a trait's function is determined by the causal role it has played in natural selection processes. For example, the heart's function is to pump blood—not to make noise—because pumping blood contributed to selection, whereas making noise did not. SE is an etiological theory of function (Wright 1975). An etiological theory explains the function of an item by the effect it produces. In the SE, such an effect concerns the causal role C of a trait T in a selection process—i.e., the evolutionary effect of organisms in a population having trait T performing the causal role C.

In a recent appraisal of SE, Artiga (2020, 53–54; emphasis in original) offers the following concise definition whose generality avoids classical problems of earlier formulations—for instance, unlike Neander's (1991) account, it does not rely on genetic selection:

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 this account, hearts have the function of pumping blood because population A, with fully developed hearts, reproduced more successfully than population B, with "proto-hearts" (e.g., less efficient pumping mechanisms), due to the positive causal role that hearts played in population A's reproductive success.

Since SE is not the only biological theory of function, scholars have proposed *desiderata* that any adequate theory of function should satisfy. Drawing on Garson's (2016, 3–7) introductory analysis of biological function (see also Garson 2019; Artiga 2021; Wouters 2005; Papineau 2017), three major *desiderata* emerge as central to evaluating a biological theory of functions.

1. *The normativity desideratum:* functional explanations must allow for a normative explanatory framework in biology—traits can malfunction.
2. *The explanatory desideratum:* functional explanations must (in part) explain why a trait exists in nature.

3. *The discriminatory desideratum:* a biological theory of functions must distinguish between lucky accidents in nature and genuine biological functions.

This article focuses on the latter two *desiderata*, which warrant closer examination. The explanatory *desideratum* holds that functional explanations aim to account for the existence of a trait in nature—for example, zebras have stripes because they have the function of deterring flies (Garson 2016, 4). Importantly, as defended by Neander (1995; see also Wouters 2005; Artiga 2021), this explanatory role is typically concerned with the *persistence* rather than the *origin* of a trait function; functional explanations address why a feature continues to exist, not why it initially arose. The *discriminatory desideratum* emphasizes that not all traits' effects are genuinely functional. Some may persist merely as lucky accidents, enabling a trait to produce an effect that should not be considered its proper function. A satisfactory theory of functions must therefore distinguish between traits that exist because of their functions and those whose apparent functions are mere lucky accidents that do not contribute to the trait's existence—for instance, following another example from Garson (2019, 10), zebras do not have stripes to entertain safari guests.

This article aims to explore the externalist–internalist debate and its implications for addressing these *desiderata* in SE accounts. I begin by introducing EE and its relation to the so-called Newtonian Paradigm.

3. Explanatory Externalism and the Newtonian Paradigm

According to Godfrey-Smith, externalism is defined not merely by the presence of external forces or the denial of internal ones. In biology, EE holds that an external cause is the primary explanatory force behind a system's properties—an external cause is the *guiding* force responsible for explaining the properties of a system. What distinguishes externalism is that internal causes are considered irrelevant for explaining why a system exhibits particular traits. For example, in the classical rationalist–empiricist debate, empiricism can be seen as externalist: environmental features shape the mind, even if internal processes also play a role. The external force produces order in the mind, even if internal causes are also involved.

MS' 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.[2] 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 is not explained in adaptive terms. Variation, in the MS framework, is *not* produced by a directive force. Variation occurs randomly (that is, it is not adaptively oriented)[3]—traits vary independently of their adaptive consequences and are blind with respect to their functional value. 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—as in Newton's theory of forces. 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.[4] The system is regarded as an object

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[2] The language of "forces," or the less physically inspired notion of "causes," is common in evolutionary biology and population genetics. Among the various forces modeled to explain population change, natural selection is regarded as the principal adaptive force—the one that orients populations toward greater adaptive fit. The analysis of evolutionary causes has often proceeded through the study of difference-makers: factors that are (causally) explanatorily relevant to evolutionary change (Woodward 2005; Pearl 2009; Weber 2017; Luque 2016; Rama 2026). Within this framework, unlike other causes traditionally identified as difference-makers of *evolution*, natural selection is specifically a difference-maker of *adaptive evolution*.

[3] In this context, *random* does not imply that mutations occur purely by chance or with equal probability at all loci in the genome. Rather, it signifies that mutations do not arise because of their functional roles—that is, they are not functionally oriented products. For further discussion, see Griffiths and Stotz (2013, Chapter 8) and Pocheville and Danchin (2017).

[4] As clarified, externalism does not imply that no internal factors are relevant; rather, it holds that the guiding force is external and independent of the system itself. In Newtonian physics, for instance, weight and friction are relevant causes, yet on their own they do not explain the movement of objects, nor the very presence of the external force—gravity. I thank an anonymous reviewer for pointing this out.

that passively “waits" for an external force to act on it. The Newtonian Paradigm is adopted by “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.

Nonetheless, development is not a black box of evolution; rather, it is a dynamic process that continuously generates phenotypic variation through multiple inheritance systems, with the fitness of organisms constantly adjusted. Over the past three to four decades, the role of development in evolutionary theory has experienced a revival, as biologists increasingly recognize its complexity: “the black box is now being opened to provide a more complete picture of what really happens” (Bateson and Gluckman 2011, 17). This shift has fostered an internalist perspective in evolutionary biology, which asserts 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). Here, I use the term “developmental turn” to designate the group of theories and research fields—evo-devo, eco-devo, molecular epigenetics, extended inheritance theory, niche construction theory, among others—that challenge the MS and emphasize developing organisms as active agents in adaptive evolution, while acknowledging the plurality of perspectives within this turn (Rama 2024a).

4. Towards an Agential Paradigm: Explanatory Internalism in Evolution

In the context of the developmental turn, 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. 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 (Walsh 2015, 212).

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" (Godfrey-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, so we do not have to choose one option. 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 problematic with internalism *if* it neglects the explanatory privilege of organisms over the environment. It is important to avoid this commitment when interpreting "explanatory reciprocity" in Walsh's 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 (see Baedke et al. (2021) for a detailed 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” (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 because development is not caused only by “internal” factors (e.g., Oyama 2000; Walsh 2012, 2015). Most theories 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. This is true. 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, even recognizing the developmental role of the ecological context, I suggest that “explanatory reciprocity” should be replaced 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.

Once the core of the internalist, agential perspective is established, what critiques has this approach prompted for EE? There are many. These critiques do not arise from isolated ideas or specific points of conflict within evolutionary EE, but rather from an alternative and (relatively) systematic attempt to rethink the explanatory framework of evolutionary theory: EI. I organize the critiques around two key ideas, closely linked to the *desiderata* discussed in Section 2: (i) not all traits exist because of their function, and (ii) not all functions arise solely from selective pressures. Central to these critiques is the observation that, within the developmental turn, natural selection—understood as an external force shaping populations—is not the sole driver of adaptation; internal, agential factors also play a causal role in evolution.[5]

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[5] As an anonymous reviewer rightly noted, many scholars within the developmental turn engage primarily with the conception of natural selection inherited from the MS, potentially misrepresenting contemporary views (see Aaby 2021; Aaby & Ramsey 2022, for mid-term approaches bridging orthodox MS externalism and the Agential Paradigm). While a detailed assessment of the challenges presented here lies beyond the

4.1 Existence without selection: By-products, developmental constraints, and inherencies

The first critique advanced by the developmental turn is that the evolution of traits does not always require reference to their functional role in nature. Many traits do not arise (and/or get preserved) through ecological functions or selection, but rather through structural conditions that render them necessary components of the organism. Regardless of whether such traits confer ecological benefits (i.e., increased fitness), they may fulfill structural roles—developmental, physiological, or reproductive—that are indispensable for the organism's existence. This critique has been developed in fields such as evo-devo, molecular epigenetics, and systems biology, which highlight phenomena like evolutionary by-products, developmental constraints, and inherencies. Let's briefly describe them to reveal the structuralist foundations of internalism.

By-products

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.

Developmental Constraints

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scope of this paper, it is important to clarify the explanatory logic of my argument: While I do not discuss or evaluate these challenges, I present them to analyze their implications for the SE. The validity of this analysis depends on the robustness of the challenges posed by the developmental turn. I thank the reviewer for pointing this out.

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 the 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.

Inherencies

Various authors argue that self-organization is crucial to evolutionary theory (e.g., Kauffman 1995, Gilbert and Sarkar 2000; Newman 2022). The origin of a trait may be the product of interaction between the parts of a system at a particular level of analysis. Newman (2022) 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 Newman's (2021, 121) 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." 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.”

4.2 Functions beyond selection: autonomy, plasticity, and niche construction

The internalist and agential perspective does not rely solely on structural explanations. Functional aspects of how organisms develop, maintain, and reproduce have also shaped evolution, as highlighted by fields and theories in the developmental turn, such as eco-devo, autonomous systems theory, and niche construction theory. Contrary to the externalist view, which holds that natural selection is the sole force shaping adaptive fit, organisms themselves possess capacities to generate and preserve functions in nature. While in the MS’s externalist framework, selection is the only adaptive guide, organisms are now recognized as active causes of evolutionary change (Sultan et al. 2022; Walsh 2015). Accordingly, functional attributions in biology require an internalist perspective that does not reduce all explanations to selection (understood in terms of MS’s EE). This internalist approach is particularly relevant for key organic phenomena—autonomous self-organization, developmental plasticity, and niche construction—which I now discuss. Before, note that the constructive character of development (Lala et al. 2024) entails the capacity of organisms to rapidly adjust to environmental conditions without relying on gradual selection processes. This has prompted a body of literature on exaptations (Gould and Vrba 1982) and evolutionary mismatches (Lloyd 2021). While these phenomena should be conceived as consequences of the properties discussed in this section, they have also been a source of criticism arising directly from endorsing an internalist framework.

Autonomy

Autonomy refers to the self-organizing capacity of living systems, but unlike inherency, it requires a *functional* account of how system components contribute to maintaining the whole. Minimally, an autonomous system regulates both its environmental interactions and its internal organization to sustain life. Each component functions in relation to others to preserve, reconstruct, and reproduce the system. This regulatory capacity mediates the tension between openness and closedness: organisms are thermodynamically open, exchanging matter and energy with the environment (Bertalanffy 1969), yet operationally closed, maintaining distinct boundaries through internal organization (Maturana and Varela 1980). Such regulation enables organisms to adapt flexibly to diverse environments while preserving internal identity. The interdependence of parts, central to biological processes, underpins this capacity. The networked character of developmental factors demonstrates that regulating their interactions is crucial for adaptively directed developmental outcomes (Rama 2025a). Autonomy is thus a key organismal capacity with evolutionary significance: organisms, as autonomous agents, actively regulate environmental conditions and modify internal organization, thereby generating and shaping new functions with ecological consequences. These agential capacities align not with an externalist, Newtonian view but with an internalist framework.

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, and physiological) that affected reproductive success and spread the new variants in short periods.

But does developmental plasticity contradict EE? One interpretation allows it to fit within an externalist framework. Although biologists such as Baldwin, Waddington, and Schmalhausen recognized plasticity in the 20th century, the MS incorporated it by reducing plasticity to the genotype level: genes were posited to encode a repertoire of phenotypic outcomes across environments (Rama 2024b). On this view, natural selection explains plasticity, rendering it compatible with externalism (see Futuyma (2017) for a contemporary defense). Phenotypic plasticity is thus attributed to “plastic genes,” whose variability is itself explained by selection. This rests on a particular conception of genes in development and evolution: genes are thought to code for traits, with phenotypic outcomes specified in DNA sequences to yield a robust genotype–phenotype map. As Brigandt (2013, 84) notes, “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.” This gene-centered view, however, was later challenged as research revealed the complexity of genetic activity, regulation, and networks. A turning point was the Human Genome Project, whose major conclusion was the failure of its original aim: sequencing

DNA alone cannot explain development or evolution (Keller 2002; Lewontin 2000; Reid 2007). Development is far more complex than the Central Dogma implies (see Keller 2002; Rheinberger and Müller-Wille 2018; Griffiths and Stotz 2013; Moss 2003). Post-genomic biology situates genetic activity within molecular epigenetics, where "cells have custody of the genes," not vice versa. Gene expression is regulated by multiple organizational levels—epigenetic markers, cytoplasmic factors, and intercellular signaling—within complex systems. Explanations of development must therefore include non-genetic sources of specificity (Griffiths and Stotz 2013). In this light, "plasticity is an intrinsic property of organisms" (Sultan 2021, 6) and cannot be reduced to external forces acting on genes. Plasticity, understood epigenetically, reinforces the case for internalist factors in evolution.

Niche construction

Another field of research 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 started to be developed in the 90's and has gained popularity across this century. 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 scenarios that the organism passively deals with. The way the MS understands niches is based on the thesis of the *Autonomy of the Environment,* and is a clear sign of an Object Theory (Walsh 2018; see Section 3). 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, niche construction theory emphasizes that organisms actively participate in shaping the selective pressures they face. Rather than treating the environment as independent, organisms modify and determine the niches they inhabit. Following Chiu (2019), *material* niche construction refers to the direct alteration of the environment, such as building habitats, migrating, or invading new territories. A deeper, philosophical dimension is *experiential* niche construction (Sultan 2015), which highlights each organism's capacity to perceive and prioritize aspects of the environment (Lewontin 2000; Rama 2021, 2024c). Developmental outcomes often depend on these perceptions—for example, the perceived water availability affects amphibian metamorphosis timing (Denver 1997), and auditory input guides vocal learning in birds (Beecher & Brenowitz 2005). While other classifications of niche construction emphasize different interpretations of "niche" and "construction" (Aaby & Ramsey 2022; Stotz 2017; Trappes 2022), the central point remains: the organism's capacity to actively shape its environment constitutes a significant evolutionary factor, underscoring the need for an internalist perspective.

5. SE and Externalism

It is time now to see whether the challenges to EE affect SE. A first step now is to analyze the relationship between SE and EE. Is the SE beholden to the EE? Traditionally, in most SE approaches, SE has been closely linked to EE. Most SE theories draw on EE in one way or another. 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 primary theoretical link between SE and EE lies in the continued use of Sober's *selection for* concept to characterize functions as selected effects. Sober (1984) framed natural selection as a force driving population change—speciation, extinction, or expansion—where the relevant parameter is the causal contribution of a trait type to the differential fitness of populations. Individual-level processes are largely irrelevant; natural selection operates externally on populations. This framework exemplifies the Newtonian paradigm in biology and has been widely adopted by SE theorists, who employ Sober's terminology and conceptual apparatus (*selection of, selection for, selection against*). Classical SE proponents, such as Millikan and Neander, explicitly rely on this framework: "Only if an item or trait has been selected for reproduction…because it sometimes has a certain effect does that effect count as a function" (Millikan 1993, 35–36), and "[o]n 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). Another externalist feature of SE is its adaptationist orientation. Authors like Ruse (2003) and Neander (2017) depict natural selection as "designing" populations, aligning with the adaptationist notion of selection as a blind watchmaker that produces order from stochastic variation. As Sterelny and Griffiths (1999, 221) note, if "functions of a biological trait are those effects for which it is an adaptation," SE's reliance on selection as an external, design-like force remains central—a dependence reinforced in recent discussions by Bourrat (2021).

There are, therefore, reasons to maintain that there is a connection between SE and EE. However, rather than claiming that all SE theorists systematically endorse EE, or that no internalist SE exists, I will examine the consequences of interpreting SE within an EE framework. My claim is *conditional*: *if and when* SE is understood through EE in evolutionary biology, *then* what are the implications? In particular, can an externalist SE adequately address the *desiderata* discussed in Section 2? I will argue that the explanatory and accident *desiderata* are not satisfactorily resolved under an EE framework. This sets the stage for proposing, in the next section, an internalist perspective on SE grounded in an Agential Paradigm. I begin with the *explanatory desideratum*, drawing on the arguments from Section 4.2 (function beyond selection), and then turn to the *discriminatory desideratum*, informed by Section 4.1 (existence without selection).

The challenge outlined in Section 4.2 suggests that the *explanatory desideratum* is not adequately addressed within an externalist SE. According to this *desideratum*, functional explanations aim to account for the existence of a trait (or, in some versions, the organism bearing it) in virtue of its function (Artiga 2021). As discussed in Section 3, the MS built its EE framework on a theory of unbiased variation. Yet the developmental turn has revealed multiple ways in which the very *origin* of traits may be functionally guided, implying that functional ascriptions can apply at the moment of *origin*, not only after selection. From an internalist and agential perspective, the assumption that trait origins are purely random is untenable: autonomy, plasticity, and constructive capacities are themselves adaptive evolutionary forces.[6] This view clashes with Garson's SE account[7] which denies functional attributions to the origin of traits on the grounds that "selection hasn't yet taken place" (2019, 29).

This argument highlights that the origin of traits demands functional explanations. Yet, as noted, the *explanatory desideratum* concerns existence in a narrower sense—namely, the *persistence* of a trait in nature, rather than its initial emergence (*origin*). From this standpoint, one might argue that persistence still depends on traits being selected, regardless of whether their origin was random or functionally guided. In this way, externalist SE accounts could still be said to satisfy the *explanatory desideratum*.

I will not debate whether functional explanations in biology should be confined to persistence rather than origins (this may reflect a bias of the MS). My point is that it is mistaken to restrict the explanatory role of internalist accounts to the origin of traits. Such a view would imply that, once traits are produced, the internal and agential capacities of organisms lose explanatory

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[6] 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 not adaptively regulated. A mutation can be internally regulated so that the phenotypic variant arises for adaptive reasons (Nuño de la Rosa and Villegas 2022).

[7] Garson's view can be considered a representative of one of the most recent and elaborated externalist SE accounts. For this reason, we will discuss his work as an exemplar. Moreover, he has likely been the most active scholar conducting systematic and in-depth analyses of biological functions over the past decade (Garson, 2016, 2019).

relevance—that they matter only for origin, not for persistence. This interpretation neglects the fact that these capacities remain indispensable for the very processes of selection. Organisms must continually reconstruct selected traits in each generation, and this reconstruction cannot be explained solely through an externalist lens. Put differently, neglecting EI in persistence explanations assumes that, once a trait has originated, its preservation can be fully explained within a Newtonian Paradigm—as if external forces alone distribute traits across a population. From the perspective of the developmental turn, however, this is a misconception of what selection requires. Selected traits must be actively reconstructed in each generation, a process that cannot be explained—empirically or conceptually—within an EE framework. Even after traits have originated and been selected, their persistence depends on developmental processes that demand internalist explanations. A Newtonian framework, in which trait persistence is reduced to the external distribution of traits in a population, overlooks the developmental processes required for traits to persist. From the perspective of the developmental turn, persistence depends on developmental processes guided by internalist properties and on inheritance mechanisms adaptively modulated by organisms' regulatory capacities. Otherwise, one would have to assume that population-level gene distributions suffice to explain persistence, an assumption that both empirically and conceptually fails. Development, then, encompasses the key elements constituting the selection process, i.e., those that contribute "to the formation, maintenance or alteration of an individual organism's form, function, or its interaction with its conditions of existence [...] [Development] is the ultimate source of evolutionary novelties; it underwrites the transgenerational stability of form necessary for inheritance, and it biases evolutionary change (Walsh 2015, 233-234).

In short, EI is not only essential for explaining the origin of traits (variation and novelty) but also for their persistence across generations. This dual necessity exposes a fundamental shortcoming of an externalist SE.

Turning to the *discriminatory desideratum*, a theory of function must distinguish between traits that exist due to a mere accident and traits that exist because of the function they perform (or performed in evolutionary history). Supposedly, SE addresses this *desideratum*: "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" (Garson 2019, 28). Accordingly, if a trait is not explained by selection, it is considered a mere accident: "in the absence of selection, the activity [of that trait] should count as a lucky benefit, and not as a function" (Garson 2016, 51). I argue, however, that the considerations from Section 4.1 suggest this solution is flawed, as it fails to recognize internalist factors that can explain the existence of traits independently of selection.

The argument is straightforward. As discussed in Section 4.1, structuralist perspectives in the developmental turn suggest that traits may exist in nature not for functional reasons but due to structural constraints necessary for the organism's existence—by-products, constraints, or inherencies. Consequently, a trait can exist without being either a selected trait or a mere accident. This is not to deny the conceptual distinction between selected (selection-for) and non-selected (selection-of) traits, which remains important for assessing whether a trait causally contributed to fitness.[8] Rather, the point is that a trait can fail to enhance selection yet still cannot be considered a lucky accident; it may instead constitute a necessary structural condition for the organism and its traits to exist.

As an illustrative example, imagine that zebra stripes were not selected for—that is, that they played no causal role in selection against zebras without stripes or with alternative patterns. Evidence from other patterned tissues, such as leopard spots, suggests that such traits could eventually arise from intrinsic properties of matter, as shaped by internal conditions of developmental processes (Goodwin 1994; Newman 2022). In this case, are zebra stripes merely lucky accidents? Clearly not. Their existence cannot be attributed to haphazard events but must be understood in terms of the inherent properties of the developmental system—requiring an EI framework. Consequently, Garson's claim that standard SE can distinguish between accidents and functions relies on an externalist perspective and ignores the explanatory role of internalist factors.

This article argues that, given the rising prominence of internalism in evolutionary biology and its challenge to externalist explanations, SE—*if* dependent on an externalist framework—is likewise affected. Specifically, solutions to the *explanatory desideratum* cannot ignore the necessity of internalist explanations for the persistence of traits, and solutions to the *discriminatory desideratum*

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[8] 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 particular, 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 theories. For that reason the anti-adaptationism of Gould and Lewontin was taken seriously by many and various modifications of the SE emerged, notably Griffiths(1993) and Godfrey-Smith (1994)).

cannot disregard how internalist factors complicate the distinction between selected and accidental traits.

6. Towards an internalist SE: Rethinking Selection

The arguments from the previous section prompt two central questions: Is SE inevitably tied to externalist assumptions, or can it be reconciled with an internalist framework? Addressing these questions is crucial both for a more nuanced assessment of SE in light of the developmental turn and for evaluating whether evolutionary functions can still be meaningfully defined through selection. Although developing a full internalist account of SE lies beyond the scope of this paper, this final section highlights key considerations toward such a project.

It is important to note that internalist critiques of SE are not new. The theory has long been subject to challenges, many of them grounded in biological arguments inspired by the developmental turn. Some critiques are recent (e.g., García-Valdecasas & Deacon 2024; Balari & Lorenzo 2010, 2013; Rama 2022, 2023; Christie et al. 2021; Bourrat 2021; Bouchard 2013; Mossio et al. 2009; Rama and Trelles 2025; Fodor & Piattelli-Palmarini 2010; Kraemer 2014; Griffiths 2006), while others have been part of the debate for decades (e.g., Cummins 1975; Bedau 1991).[9] The arguments presented in the previous section, however, are distinct in that they address specific *desiderata* of SE that become controversial when assessed through a systematic internalist framework of evolution. The key point is that existing critiques of EE are closely intertwined with alternative accounts of biological function. Criticism emphasizing organisms' structural constraints is often associated with Cummins-style analyses and formal treatments of functionality (Love 2007; Amundson 2000; Balari & Lorenzo 2013). Critiques highlighting organisms' autonomous capacities have supported organizational accounts of function (Christensen & Bickhard 2002; Mossio et al. 2009), while other approaches explore functional roles in light of developmental agency (Newman 2022; Walsh 2014).[10]

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[9] These challenges have entailed pluralist views of functions, accepting multiple theories of function (e.g., Shea 2018; Neander 2017; Papineau 2017). They recognize that biological function is not limited to evolutionary functions and often endorse other accounts as well: functions that analyze single individuals life-cycles, or physiological-level processes, for instance. Being pluralist is distinct from acknowledging the role of ontogeny in shaping evolutionary functions—the focus of the developmental turn. It is one thing to assert the existence of different kinds of functions; it is another to claim that ontogenetic processes influence the emergence and persistence of selected functions.

[10] 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, which were not the most accepted ones during the twentieth century. This was definitely seen as a strength of externalism. But times have changed, and the twentieth century has brought forth a multitude of scientific theories—e.g. dynamical system theory, systems biology, cybernetics—that support internalist

Nonetheless, while an internalist SE is warranted—as argued in the previous section—it is important to acknowledge that no comprehensive alternative account of biological function currently exists. In other words, no framework systematically integrates the diversity of evolutionary phenomena outlined in Section 4 while addressing the *desiderata* discussed here. This remains a key theoretical challenge within the developmental turn. Organizational accounts often emphasize physiological regulation but are rarely extended to evolutionary functions; structuralist approaches sometimes can be in tension with agential or teleological perspectives; and agential accounts cannot ignore the constraints and inherencies inherent in evolutionary processes. Consequently, despite numerous partial advances, a robust internalist alternative to externalist SE is still lacking. Given that externalist thinking has been shaped within the MS, and the developmental turn explicitly challenges its core tenets, a unified internalist framework for biological functions is not only justified but necessary. Such a framework would provide the developmental turn with a coherent counterpart to the externalist SE.

The call for an internalist SE necessarily entails a reconceptualization of selection, even if this departs from standard interpretations. How, then, should selection be understood from an internalist standpoint? The distinction between the Newtonian and Agential Paradigms offers a useful framework. A Newtonian view on functions and selection rests on two claims: (i) *Transcendence*—selection is conceived as a force external to the domain of analysis (trait functions), exerting pressure on traits to produce their functions; and (ii) *Explanatory asymmetry*—selection is the cause of trait functions, but trait functions do not alter selection pressures; in this framework, environmental pressures act on populations, while traits themselves play no reciprocal role in shaping those pressures (as discussed in Lewontin's (2000) Autonomy of the Environment; see Section 4.2).

The Agential Paradigm outlined in Section 4 invites a rethinking of functions along two key claims. (i) *Immanence*—organisms and environments are intertwined such that traits are not passive targets of external pressures but integral to the very forces shaping selection. In this view, selection emerges from organisms' active regulation of their living conditions creating new functions. (ii) *Interactional asymmetry*—the reciprocal relation between organism and environment implies that the presence of a function can itself generate selective outcomes, rather than being merely the product of selection. Thus, while the Newtonian Paradigm depicts selection as an external cause producing trait functions, the Agential Paradigm regards trait functions as intrinsic causes that contribute to selection itself.

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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.

Following Walsh (2015), the relation between development and selection must be reconsidered in light of the developmental turn. As noted in the epigraph, if selection is conceived broadly—beyond developmental genetics to encompass the diversity of causes and interactions[11]—then the very processes that make a trait selectable are developmental. In Walsh's words:

> It [selection] is the effect on a population of the effect on individual organisms of the entire suite of 'ecological' causes of birth, survival, reproduction and death- [...] The presumed distinction between selection and development enshrined in the Modern Synthesis is a category mistake (Walsh 2015, 236).

Blurring the distinction between selection and development implies that the very processes producing functional capacities are those determining whether a trait is selected. There is no additional external force: "selection is development." Admittedly, this view may appear radical, yet it is grounded in agential thinking within the developmental turn.[12] On this account, defining functions through selection is equivalent to defining them through developmental causes of evolution, understood as the production of heritable variation in fitness. Moreover, as emphasized in the previous section, this internalist perspective is required not only to explain the origin of traits but also their persistence across generations.

Examining the debate on selected functions through the lens of the Newtonian versus Agential paradigms clarifies the divide between externalist and internalist accounts. From an externalist perspective, selection is the process that produces function, transforming chance variation into adaptive diversity. On this view, *there is no function in nature unless (and until) selection takes place*. By contrast, an internalist SE holds that it is the very construction of functional organisms that enables selection to occur. Inverting the externalist logic, *there is no selection without function*.

We can still identify the function of certain traits within the context of selection without disregarding the internalist motivations emphasized in recent decades. Darwin's "recipe" for

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[11] As emphasized in Section 4, internalism does not deny the role of external developmental factors (e.g., ecological signals). Rather, it holds that the developing agent regulates these resources to reconstruct selected traits. Internalism thus rests on the interactional asymmetry central to the Agential Paradigm.

[12] Walsh's view is also supported by the statisticalist interpretation of natural selection, particularly in how it conceives the relationship between organisms and their environment (see Rama 2025b for further analysis). However, it is important to note that statisticalism is not essential to the discussion of the internalist SE I am proposing, since Walsh's account of selection can equally be defended from certain causalist perspectives (e.g., Otsuka 2015).

natural selection—inherited variation in fitness—remains intact, as do the elements in Artiga's definition. The developmental turn, however, insists that this recipe requires an internalist explanation, emphasizing developmental processes, organism–environment coupling, self-organization, and other mechanisms that generate inherited fitness variation. If zebra stripes were selected to deter flies, this phenomenon can receive different interpretations by each paradigm. A Newtonian Paradigm would claim the stripes arose by chance and were later assigned the function of fly deterrence through cumulative selection. In contrast, an Agential Paradigm could argue that the stripes emerged via a developmental process aligned with the function of deterring flies and regulated developmental mechanisms enabled their production and persistence across phylogeny. The functional role of the stripes then shapes selection: zebras with stripes are favored. Developmental causes producing zebras with stripes cause zebras with stripes being selected—the function of deterring flies causes selection.

Of course, further work is needed to develop a fully realized internalist SE and address the *desiderata* outlined here. Nonetheless, this section offers three key insights. First, although alternative internalist theories of function exist, no comprehensive account of an internalist SE has yet been articulated. Second, adopting an Agential Paradigm requires reconceptualizing selection and development: developmental processes do not merely constrain the space of selection but actively produce traits that are subsequently selected—selection reflects the population-level effects of developmental causes. Finally, whereas an externalist SE asserts that functions exist only through selection, an internalist SE embraces the converse principle: no selection occurs without function.[13]

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[13] The analysis done here also extends to accounts of selection occurring within single ontogenetic life cycles (e.g., Garson 2017; Fresco et al. 2017; Kingsbury 2008). My focus here is evolutionary selection and space precludes a detailed discussion of these approaches. The key question is whether ontogenetic selection is driven by external or internal forces. If developmental variants are eliminated solely by environmental pressures—as in classical behaviorist models—this aligns with an externalist view. By contrast, if selection reflects the organism's adaptive regulation of variants in response to environmental conditions, an internalist perspective is warranted. For example, consider a plant that produces both small and large leaves in early ontogeny, with only small leaves retained under certain temperatures. An internalist explanation emphasizes regulatory mechanisms directing development toward small leaves to optimize thermoregulation, whereas an externalist account attributes leaf retention to environmental elimination, without invoking developmental regulation. Accordingly, from an externalist perspective, small leaves have the function of thermoregulation because they were selected; an internalist perspective reverses the causal arrow: the thermoregulatory function drives the ontogenetic selection of small leaves.

7. Conclusions

A central analytical component of this paper is the connection between internalist–externalist positions and the Newtonian and Agential paradigms. This link not only conceptually enriches both frameworks but also frames the critique that internalism poses to externalism in evolutionary biology. In this context, I have outlined two challenges that biological theories raise for externalist evolutionary theory. First, not all traits warrant adaptationist explanations based on their functional role; many traits exist for structural reasons, as in the case of biological spandrels or inheritances. Additionally, several theories emphasize processes that generate adaptive phenotypes through organisms' agentive regulatory capacities, highlighting their active role in producing trait functions as they adapt to changing environments. Almost thirty years ago, Godfrey-Smith analyzed the challenges facing the adaptationist–externalist program of the Modern Synthesis. The conclusion of Section 4 is that, since Godfrey-Smith's analysis, accumulating empirical and theoretical work increasingly supports the need for EI in evolutionary biology.

The analysis in Section 4 underpins the central question addressed here: whether SE is affected by evolutionary challenges to externalism. I identified several reasons why externalist theses are present in SE accounts, including the commitment to a neo-Darwinian Modern Synthesis, the use of design-like metaphors, and the deployment of Sober's conceptualization of "selection of." Beyond documenting these influences, I focus on a *conditional claim*: *if* an externalist view of SE is adopted, *then* at least two key *desiderata* remain unresolved within the theory, the explanatory and accidental ones. The final section advocates for an internalist reconceptualization of SE, centered on the principle that a trait's function drives its selection rather than resulting from it—shifting the motto from "no function without selection" to "no selection without function." While debates regarding the interplay between development and selection remain ongoing, particularly in the context of the Newtonian and Agential paradigms, this article has sought to situate these discussions within the SE framework for understanding biological functions.

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