

Biosemiotics at the bridge between Eco-Devo and representational theories of mind

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Abstract In this paper, we will show how Biosemiotics overlaps with both Eco-Devo and representational theories of mind. Concerning the former, Eco-Devo and Biosemiotics share the common theoretical ground in biology of taking organisms not as objects but as agents in organic processes. Their link becomes sharper once we appreciate that Eco-Devo biologists systematically appeal, albeit implicitly, to semiotic processes by speaking of the organismal regulation of development mediated by *signaling systems* and *signaling networks*. As for the latter, representations and signs could actually be enclosed under the same theory in order to think about all organic processes involving referential relationships and the flow of information. We will also argue that Biosemiotics, by calling attention to the situatedness and context-sensitive character of signs and their development, could work as an antidote to many illnesses of representationalism that post-cognitivism had brought about. We conclude that Eco-Devo and representational theories of mind must become closer. The biological underpinnings of Eco-Devo and Biosemiotics offer a fertile land to ground representations within natural sciences, while representations and signs seem to be a necessary ingredient to tackle the agentic dimension of organisms and the centrality of development in theoretical biology.

Keywords: Biosemiotics, Ecological-Developmental Biology, Representations, Signaling Systems, Agentivity

Received 31/01/2021; accepted 18/11/2021.

0. Introduction

Philosophical analysis in science is usually devoted to the meta-theoretical work of linking and contrasting different scientific disciplines to see whether they share a common ground, or whether a tension exists between them. Here we will try to promote such a kind of analysis. Particularly, we will argue that three disciplines dedicated to understanding certain kinds of organic processes share their theoretical underpinnings. They are Biosemiotics, Ecological Developmental Biology (Eco-Devo), and (post-cognitivist) representational theories of mind. This allows them to work together towards a unified picture of living systems, and to use such a union to fight against opposite (and mighty) stances. Moreover, all the disciplines involved here stand in an emergent and non-orthodox position within their respective fields (as it will be clearer

later on). So we find that philosophical labor is crucial to continue setting up their foundational tenets.

We will argue that Biosemiotics could work as a bridge between Eco-Devo and representational theories. This means, firstly, that Biosemiotics shares important insights with both disciplines, and secondly, that such common ground could help them buttress certain basic assumptions of their own. In a nutshell, Biosemiotics is an interesting land where cognitive science and Eco-Devo overlap. We plan to present the connection between Eco-Devo and Biosemiotics in section 1., while in section 2. we link Biosemiotics with representational theories of mind. Our conclusions in section 3. will make more explicit why Eco-Devo and representational theories deserve a solid bridge.

1. Biosemiotics and Eco-Devo

Biosemiotics is a relatively new discipline. Within it, many theories have been proposed in the last forty years that have differentiated as the discipline progressed, while at the same time keeping close connections in many respects. We believe that all of them have important contributions to foster Eco-Devo. Particularly, our interest will be focused on the biosemiotic approach of the Tartu-Copenhagen School, originally developed by Thomas Sebeok, rooted in Peircean semiotics and, most importantly for us, in von Uexküll's theoretical biology. Although we would refer to other frameworks in this section (such as Pattee's Physical Biosemiotics and Markoš's Biohermeneutics), our main emphasis will be on the integration of von Uexküll's tradition on Biosemiotics with Eco-Devo. Henceforth, when we talk about Biosemiotics we will refer to those proposals that put the notion of *interpretation* at the heart of semiosis. This entails that sign-object relations are always established by the capacity of the organism to sense the object and act according to the sign produced. Interpretation comes to the fore to make such sign-object interactions promoted by and relative to each organism. Semiosis, therefore, concerns the organic activity mediated by signaling systems where the organism relates to its niche in an idiosyncratic way.

This first part aims to pinpoint the connection between Biosemiotics and the understanding of development proposed by Eco-Devo. In Section 1.1. we present their shared philosophical underpinnings to show that both treat organisms as adaptive agents due to the complex, holistic, and contextualized character of developmental processes. In Section 1.2. we identify different developmental processes that are mediated by biosemiotic pathways. We also aim to underscore how Eco-Devoists systematically appeal to semiotic processes by putting "signal systems" or "signal networks" at the core of the organismal regulation of development. In Section 2.3. we connect ecological and semiotic developmental processes with the evolutionary domain, providing a sketch of the role of Biosemiotics in developmental approaches to evolution, i.e. with Evolutionary Developmental Biology (Evo-Devo). There we argue that Biosemiotics is central for a theory of variation and innovation, for understanding the adaptive dimension of evolutionary processes, and for extending inheritance systems beyond the germline. As a conclusion, we will call for an integration of Biosemiotics into Eco-Evo-Devo. In all subsections, we will follow the strategy of showing, first, that a certain phenomenon is present in Eco-Devo, and then that it is also a core ingredient in Biosemiotics.

1.1. Organisms as adaptive agents

Probably the central idea that defines both Eco-Devo and Biosemiotics, and distinguishes them from their respective antagonists, is that organisms are adaptive agents, i.e. the idea that the organism's activity is a crucial causal ingredient to explain

the complexity and diversity of life. We believe that this involves two relevant tenets: (i) the holistic and interconnected dynamics of developmental systems, and (ii) the relevance of environmental sensitivity. Let's present them separately.

1.1.1. Organismal and sub-organismal biology

As it is widely known, the discovery of the molecular gene, its form and function, secured the Weismannian picture of biological processes occurring at two different and discrete levels: the genotypic space and the phenotypic space (Lewontin 1974b, 1983a). With the consolidation of molecular genetics, the so-called genotype-phenotype map became reduced to an understanding of how genes end in protein products and build complex unicellular and pluricellular organisms from the information stored —during evolution— in the DNA. As we will see, this picture had many consequences in evolutionary thought. Regarding development, the central causal and explanatory unit was not the organism but the gene, a *sub-organismal entity*.

Eco-Devo was born from two different research areas in developmental biology: developmental genetics and phenotypic plasticity. Gilbert (2001) proposed their unification into what he baptized as Eco-Devo (see Dusheck 2002, Gilbert 2005, 2015, 2016, 2017, Gilbert, Bolker 2003, Gilbert, Epel 2015, Levins, Lewontin 1985, Lewontin 2001, Sultan 2003, 2007, 2015, 2017a, Sultan and Stearns 2005, West-Eberhard 2003, West, King, White 2003). Since then, it encompasses all ecological approaches to development. Its main purpose is to understand developmental processes as phenomena embedded in an inherited ecological system, and consequently to reject the blueprint-picture that shows development as a process of code implementation and execution (as, for instance, Rosenberg (1997) and Wolpert (1994) suggest). As Sonia Sultan defines it, «[...]ecological development, or 'Eco-Devo,' seeks to explicitly include the organism's particular environment in studying both the *signaling pathways* and the ecological and fitness consequences of phenotypic expression» (Sultan 2015: 20, emphasis added). Eco-Devo thus comes to challenge the sub-organismal viewpoint. One of its motives is the empirical and technological advances in different areas advocated to understand development (properly; cf. sect. 1.2.). A huge amount of evidence indicates that the molecular gene is far from being a developmental program. As we will see, genes are better understood as biomolecular resources of the cell. Therefore, once development has dismissed its conductor (Griffiths, Knight 1998: 258), its causal factors become democratically distributed (Oyama 2000) across a holistic and dynamic network of genetic, genomic, cellular, extracellular, and external developmental information. So, the rejection of sub-organismal biology comes from understanding development from a holistic and global viewpoint where the central unit of analysis is the whole organism and its coupling with the environment.

The reinstatement of the organism as the central explanatory unit in biology has many important theoretical consequences (Nicholson 2014, Walsh 2015), and it renews the organicist movement of the beginning of the XX century.¹ Organism-centered biology came to replace an understanding of the diversity and fitness of organisms anchored in the leading fields of the 20th century biology: population genetics (analyzing supra-organismal processes) and molecular genetics (dealing with sub-organismal processes).² Instead, organicism posits that we cannot abandon the organism in pursuit of sub-

¹ Cf. Nicholson, Gawne (2015) and Etxeberria, Umperez (2016) for the history of Organicism, from its apogee at the beginning of the 20th century, to the growth of its reputation in the last decades.

² We emphasize the rejection of sub-organismal biology, and not the supra-organismal one, because the former is directly involved in developmental processes (our target here), and not, primary, in evolutionary ones (for this, see Section 2.3.).

organismal and supra-organismal explanations, but also that organisms cannot be diluted into their environment in a way that their agentive and autonomous properties disappear. Rather, to explain organisms, we need organisms and their agentive and adaptive characters. Otherwise, biology would be reduced to take organism's development as a process controlled by molecules –not by holistic and dynamic systems– and evolution as the distribution of such molecules in a population through time –and not as the evolution of developmental systems (more on this in Section 2.3.).³ Concerning developmental issues, it has the consequence of turning organisms into the subjects of their developmental trajectories. This is so because their ontogenetic pathways are not guided by genes (sub-organismal) designed by evolution (supra-organismal). Instead, the aforementioned global and holistic view of development —the embedded organism— purports that ontogeny is a sensitive process where each pathway is taken according to what the organism needs in order to successfully stay alive. This entails that the organism is the one who takes the ontogenetic route that signifies an adaptive step according to its inner and outer conditions. The organism as an agent can regulate, stabilize, behave, metabolize, induce, promote and carry out other actions according to its possibilities and needs. Development proceeds by continuous adaptive steps that result from integrating the many informational resources at different levels of the organism. So the connection between the demise of sub-organismal biology and the emergence of agentivity is intimate. Development as a global and ecological process implies both positing the organism at the core of development and simultaneously it entails that the organism as an agent would take those adaptive pathways that the network of developmental resources allows him to take.

Moving to Biosemiotics, the rejection of sub-organismal biology is also a central principle, and most importantly, a justification for semiotic studies in the life sciences. Since the 1970s, Howard Pattee has been trying to understand the relationship between physical constraints in organic processes and the importance of a semiotic dimension to explain the cybernetic properties of organisms and their capacity to self-replicate (Pattee 2008, 2012). Similarly, biohermeneutics posits that the primary role of cells is being the active interpreters of the genetic text: «The main objective of hermeneutic biology should be to get rid of the genocentric view that takes the genome as a recipe for building the body» (Markoš 2009: 691).

But the connection between organismal biology and Biosemiotics actually goes back to von Uexküll's theoretical biology. His philosophical position lies between vitalist and mechanistic confrontations of his time, a gap that is usually filled in with organicism, which rejects the idea of a vital force flooding living beings, while at the same time accepting that not all aspects of the living can be explained within mechanicism. This position comes to vindicate certain properties of organisms (such as agentivity) that are not treated by mechanicism, but without committing to non-natural forces.⁴

The issue concerning mechanicism in science is a complex one. What is being rejected is that an organism is a collection of parts whose activity can be explained by the

³ Denis Walsh (2015) analyses the dismissal of organisms from biology in Neo-Darwinism and argues for the necessity to put them back into the life sciences. In parallel to Lee Smolin's proposal of an «agent theory of the universe» (Walsh 2015: 213), *Agent Biology* claims that what should be explained –organisms– are central to reach an explanation of themselves. Instead of positing laws and causes from outside of the *explanandum* (sub- and supra-organismal processes), and such causes applying to organisms as forces applying to objects in the Newtonian paradigm, the primary force in biology comes from within the *explanandum* itself: from adaptive, agentive organisms.

⁴ Having said so, an important school of Biosemiotics, Code Biology, developed by Marcello Barbieri (Barbieri 2015), actually departs from the non-mechanistic underpinnings of von Uexküll's Biosemiotics portrayed above (Barbieri 2014). Instead, he adopts a machine mechanism stance (cf. next footnote) and consequently takes organic *codes* to be more suitable for thinking about semiosis with machine-like models.

interaction between them, and, consequently, that all models of explanation in science must be machine-like.⁵ We can outline the organicist position against mechanicism in two steps. (i) If we look at the current state of the art of the discussion, the debates turn around the physicochemical reductionism implicit in the molecular revolution initiated by Crick and Watson and expanded in the last sixty years. As we pointed out, Eco-Evo, instead of taking the organisms' traits as resulting from the activity of a sub-organismal entity, also weights the role of the whole network of developmental resources (that constitutes, ontologically, the embedded organism) to explain ontogenesis and the organism's activity. (ii) Although the previous point goes against genetic reductionism, it does not undermine the idea that such embedded and complex whole-organism could be understood in mechanistic terms. To overcome this idea, organicism endorses that certain properties can be found only when the whole embedded organicism is analyzed *in toto*, in a way that such properties cannot be accountable by the interaction of the parts. Its slogan is "the whole is more than the sum of its parts". Agentivity is one of those properties that are attributed to the whole organism, insofar as its activity is guided, enabled, and needed by the whole organism.⁶

Such a theoretical foundation operates as a backup for the necessary study of semiosis in the life sciences. The aforementioned holistic, dynamic, and global view of development, as an extended system beyond the gene, is possible thanks to the connection between developmental resources through *signaling systems*. To overcome the physicochemical reductionism of gene-centered views, it is necessary to integrate the whole matrix of variables in development into a unified and embedded system. And this is enabled by biosemiotic pathways. So we come to Sebeok's thesis that life and semiosis are co-extensive phenomena; that «semiosis is what distinguishes all that is animate from the lifeless» (Sebeok 1986: 174). From here, it is established the «axiomatic identity of the semiosphere [the realm of Biosemiotics] with the biosphere [the realm of the living]» (Sebeok 2010: 228). That's why Hoffmeyer (2011) claims that *Biology* (read: as a purely physicochemical science) is *Immature Biosemiotics* (many would say *incomplete*, e.g. Kull, Deacon, *et al.* 2011). One would miss a central point about organic life if one ignores the

⁵ As Daniel Nicholson (2012) explains and analyses, different related doctrines are swarming around mechanism. He distinguishes three kinds of theses: (i) Mechanicism: organisms are the composition of their parts and can be explained by the interaction of such parts. (ii) Machine mechanism: life must be understood by machine-like models. (iii) Causal mechanism: a kind of explanation, based on a step-by-step causal concatenation of events and things that ends in the phenomenon to be explained. We believe that von Uexküll and Eco-Devoists would reject (ii): many properties of organisms are clearly absent in machines. Regarding (i), von Uexküll and many, but not all, Eco-Devo biologists would posit that organisms are more than the sum of their parts. Concerning (iii) and its contemporary versions in the philosophy of science (the so-called *new mechanism*; cf. for instance, Craver 2007), the situation requires more detailed argumentation. Certainly, it is not so clear that causal mechanism is incompatible with organicism; or, in other words, it may well be the case that organicism needs nothing else than causal-mechanistic explanations. The introduction of teleology suggested by many does not necessarily imply that teleological explanations cannot proceed by a causal concatenation of events through time. For instance, complex Human mental states, such as beliefs and desires, are goal-directed but, nonetheless, cognitive psychology pursues a causal, step-by-step, mechanical explanation. Be that as it may, this discussion does not challenge our central point here: that organisms as wholes play a relevant explanatory role in biology, and that such role requires that organisms be treated as adaptive agents.

⁶ Certainly, organismic biology is not free from its own problems. A first and difficult question concerns the ontology of an organism. One of the reasons that make it a difficult question concerns symbiosis. Organisms are functionally related to other organisms in their biotic environment in a way that their lives are essentially dependent on other organisms. And more interestingly, endosymbiotic processes evidence that topological differentiation of organisms is not suitable, insofar as the immune systems of many organisms, especially animals, are dependent on other organisms (bacteria). This makes it extremely difficult to trace boundaries between organisms (cf. Pradeu 2011, Gilbert, Tauber 2016 for interesting analyses; I am grateful for an anonymous reviewer for remarking on this point).

semiotic interactions of organisms. Again, this position moves beyond the sub-organismal understanding of biology and argues for the *emergence* of life from biosemiotic networks occurring at the organismic level (Emmeche 2011).⁷ Living beings cannot be exclusively considered as systems «passively subjected to universal laws of nature, but also as active systems of sign production, sign mediation and sign interpretation, that harness the physical laws in order to live and sometimes to make a more complex living» (Kull, Emmeche, *et al.* 2011: 1). These words conjure up the Eco-Devo idea that «the organism cannot be regarded as simply the passive object of autonomous internal and external forces; it is also the subject of its own evolution» (Levins, Lewontin 1985: 89).

Summing up, we have found a similar picture both in Eco-Devo and Biosemiotics. First, both see development and organism activity as complex and holistic phenomena. This involves a huge variety of developmental resources — from the genomic to the environmental ones — and a complex network of signaling systems connecting and orchestrating the complexity of organisms. This is the view that came to overcome sub- (and supra-) organismal biology. Embedded organisms are the central explanatory unit. In this sense, both disciplines were born against the reductionist understanding of organisms from gene-centered views. Agentivity enters the scene when we see the lifespan of each organism guided by itself, adjusted to what the complex web of resources allows and needs, and not by an evolved molecular code. This leads us to a particular understanding of signaling pathways: while the physiology of signaling systems is hardwired in molecular and cellular interactions, such signals, insofar as they play a central role in organismal regulation, deserve to be considered as the particular way in which each organism perceives and responds to its inner and outer conditions. In this sense, Biosemiotic pathways and Eco-Devo's signaling pathways are concerted in the role that these signals play in organismal agency.

1.1.2. Umwelt and the challenge to adaptationism

Probably, the biologist who most insistently vindicated the environmental dimension of development and its implications for theoretical biology was the late Richard Lewontin (Gould, Lewontin 1979, Lewontin 1974a, 1978, 1983b, 2001). One way to present his ideas is by contrasting them with their opposite pole, namely adaptationism. Lewontin's challenge has many implications for the understanding of development and evolution. As he remarked, a deep problem of the neo-Darwinian adaptationist thinking is the capacity to define an organism's environment independently of and pre-existing the organism. This is at the heart of what is known as Explanatory Externalism: the idea that environmental demands shape organisms by filtering random variation. The task that Darwin engaged in was to explain design without involving a designer. The complexity and order of living systems, contrary to the chaotic destiny of non-living closed systems, results from a process of selection where the environment is responsible for filtering those fitter variations that will be preserved and spread; that is, through a process of natural selection. The exterior designs the interior by gradually selecting for and against different forms and functions (Sober 1984).

Lewontin argued that this picture leads to the definition of an organism's niche as a pre-existent condition for the organism's life, as a space to be filled in; if better adapted to

⁷ Kull (2009) introduces the distinction between sigma-sciences and phi-sciences to argue that biology cannot be purely accountable by phi-sciences. Phi-sciences (as physics or chemistry) study *things* while sigma-sciences (as Biosemiotics) the *knowledge* of organisms, that is, the subjective construction of the world by each agent (cf. Hoffmeyer 2008c for a detailed exposition of the position of Biosemiotics in the natural sciences).

such niche, the organism increases in fitness, and contributes to the gradual evolution of its population. So, the external pressures that the organism confronts exist independently from it. This is the idea of being an evolutionary *adaptation*. As Lewontin illustrates, if one travels to another country, one probably will need an adaptor to charge the computer. Since the inlet to charge the battery does not fit with its plug, one would need to adapt to such pre-existent condition with a fitter adaptor. Lewontin proposed that the environment and the organism are co-defined entities. The organism also actively constructs its niche. The organism and its environment are reciprocally intervened in a way that « [t]here is no organism without an environment, but there is no environment without an organism» (Lewontin, Levins 1997: 96). This is the base of what he (and Levins) labeled as Dialectical Biology (Levins, Lewontin 1985): an understanding of biological phenomena that puts environment-organism relations at the center of biological theory. This attacks the core of adaptationist thinking: it is not the environment that establishes what the organism confronts, but the organism determines what is relevant (Lewontin 2001).

Lewontin's account also has an epistemic reading: the organism determines what is *relevant* by establishing what is *real* for him. As it will be clarified later, this means that, although not necessarily in a conscious manner, the organism must be aware of those entities to which it is related. Thus, the sensory capacities of organisms —from unicellular organisms to complex animals— construct the realm of interactions that define their niches. This is a firm bridge to Biosemiotics's town and, particularly, to Jakob von Uexküll's home.

The term *Umwelt* was coined by von Uexküll to refer to the subjective experience of the external world (the environment), while the *Innenwelt* concerns the subjective experience of the internal world (the organism itself). These notions clearly push us to understand an organism's niche not as an imposed reality to the organism (*à la* empiricism), but as an always organismically mediated relation, constrained and enabled by the perceptual capacities of each organism (and here we see the Kantian influence in von Uexküll's biology). That's why Lewontin claims that «[i]f one wants to know what the environment of an organism is, one must ask the organism» (Lewontin 2000: 54). As a result, « [t]he main methodological question for Biosemiotics is: *how to know what organisms know*» (Kull 2009: 83, emphasis in the original).

As we will see later, both the *Umwelt* and the *Innenwelt* are important to understand adaptive ontogenesis guided by organic agents. The constant adjustment of the inner and the outer conditions of life by the organism is what defines it as an agentive system capable of adapting by employing different processes of phenotypic plasticity. Thus the concepts of *Umwelt* and *Innenwelt* are central in phenotypic plasticity; any internal or external change promoted by the organism could be adaptively directed —not randomly or blindly directed — insofar as it is sensitive to the inner and outer worlds. Thus internal semiotic pathways allow regulation of organizational and dynamical interactions within the system (what is known as endosemiosis) while perceptual relations with the exterior turn behavior, or any kind of motility, into an organism's adaptively directed response (through exosemiosis). Opposing Explanatory Externalism von Uexküll stated: «Niemand ist das Produkt seines Milieus — ein jeder ist Herr seiner Umwelt [Nobody is a product of their environment- everybody is the master of one's Umwelt]» (Uexküll 1923: 266; my translation).

Previously (sec 1.1.1.), we highlighted the *agentive* dimension of organisms resulting from a holist and dynamic view of development as a process brought about by organisms-as-wholes immersed in biosemiotic pathways. Now we remark that *agentivity* comes to the fore once we see organisms as *interpreters and creators* of their own world. The idea of *interpretation* highlights the fact that the organism is needed to explain its relationship with

the environment, insofar as what is *represented* is essentially determined by the organism's sensory organs and the role played by signs in the adaptive activity it performs. Interpretation lies at the core of von Uexküll's Biosemiotic tradition and the place of Umwelten and Innenwelten in living systems. Moreover, interpretation is one of the elements of the triadic view of semiosis defended by Peirce. This leads us to consider each organism –from cells to complex animals- as interpreters of their own world; i.e. as systems whose environments are defined, in part, by their idiosyncratic semiotic relationships with the environment through signaling systems. In Eco-Devo, the agentive role of organisms as interpreters amounts to (one of) the charges against Explanatory Externalism: what is adaptive — filtered or not — cannot be defined exclusively from the exterior but from how the organism actively relates to it through semiosis.

1.2. Development with biosemiosis

In this subsection, we will explore relevant developmental processes analyzed from an Eco-Devo viewpoint. In all cases, we deal with phenomena where the agentive dimension of organisms becomes explicit, and consequently, with different ways in which an organism's phenotypes can be continuously adjusting to the struggles for life. We will show that Biosemiotics is also promoting a pretty similar landscape about ontogenesis. Indeed, the central thesis we shall defend here is that *Eco-Devoists systematically appeal to semiotic processes by putting them at the core of the organismal regulation of development*. Thus, signal networks understood as biosemiotic pathways make explicit what is the role of Biosemiotics in Eco-Devo: a central one, both in methodology and theory. In the following subsection, we will see that, in all cases, ecological mediations of development — through genomic regulation, niche construction, or scaffolding processes — are executed and controlled by biosemiotic pathways.

1.2.1. Deprogramming genes. The cell as the unit of development

Contrary to expectations and publicity, the Human Genome project located genes into a complex network of biochemical interaction within the cell rather than in a master molecule coding for the Book of Life (Lewontin 2001). As Griffiths and Stotz (2006, 2013) pointed out, we entered a post-genomic era, one where genetics must be understood in connection with other *omics* such as genomics, proteomics, metabolomics, transcriptomics, epigenomics. This new era comes to defy the picture traced by the Central Dogma in Molecular Biology and merrily embraced by neo-Darwinian biologists. According to the Central Dogma, information flows unidirectionally in the process that starts in DNA sequences and leads to protein products. Once the Central Dogma became displaced to a not so central position, protein expression became a process regulated by complex genetic regulatory networks modulated by genomic, cellular, and extracellular resources. Many epigenetic, “non-mainstream” genomic processes have been discovered involving alternative splicing, histone modifications, hormonal regulation, methylation, micro-RNA, non-coding regions, environmental signals, and other complex biochemical apparatus that picture cellular development as a result of a distributed and dynamic flow of information, instead of the linear and unidirectional one championed by the previous view (cf. Jablonka and Lamb 2014, Griffiths and Stotz 2013, Sultan 2015).

This relocation of genes within cellular development promotes new theorizing about the nature of genes (Moss 2003, Rheinberger and Muller-Wille 2018, Keller 2014). As stated by the geneticist Barbara McClintock, the genome should be pictured as «a highly

sensitive organ of the cell».⁸ Without the proper ecological niche, genes cannot play any relevant role in cell development; rather than blueprints, «the bare genes in isolation are among the most impotent and useless materials imaginable» (West-Eberhard 2003: 93). As noted earlier, this shift corresponds to a change in the unit of development, from a sub-organismal one (the gene) to an organismal one (the cell and its environment). So we find in cell development the first and indispensable footprints of adaptive agentivity. The gene does not regulate the cell but the cell regulates the gene: «Genes are things an organism can do with its genome: they are ways in which cells utilize available template resources to create biomolecules that are needed in a specific place at a specific time» (Stotz 2006: 364). The expression of genes is thus deeply sensitive to inner and external signals, so much so that ecological information cannot be put aside as a second-citizen in development. Contrary to the stance of the Central Dogma that posited the genotype as an untouchable source of information, it should be perceived «as a *repertoire of environmentally contingent possibilities* rather than a single determined outcome» (Sultan 2015: 20, emphasis in the original).

Most Biosemiotic schools share a similar view.⁹ In *Reading the Book of Life*, Markoš (2002) pursues an understanding of gene expression as a hermeneutic process carried out by the cell — the interpreter that reads the genetic code. Contrary to the idea of a predetermined developmental sequence anchored in DNA, «it is the organism itself that is the ultimate ‘reader of the book of life’ that it inherits, on the one hand, and that it must perpetually ‘read’ anew, on the other» (Markoš 2009: 659). Markoš’s insight is indeed close to the Eco-Devo idea of the gene as a highly sensitive organ of the cell pictured by McClintock. The importance of the contextualization of genes is crucial to understand how the same gene sequences can have many functions and give rise to different protein products — in the Biosemiotics jargon, genes have different *meanings* in different contexts — that allow nature — at the phylogenetic and ontogenetic scales — to promote diversity and complexity by changing the functional and semiotic place of nucleotide sequences in the dynamical network of biochemical interaction among the cell. In Markoš’s words: «Genetic information is a necessary but not sufficient condition to assign shape, localization, and function to a protein that is synthesized [...] but outside the context of their ‘maternal’ cells, many proteins collapsed into nonfunctional denatured chunks» (Markoš 2009: 667).

The post-genomic era moves beyond the molecular genes as developmental programs and re-conceptualizes the ontology and causality of genes within reactive genomes. The genome is «itself a fundamentally reactive system, a sub-system of the cell composed of DNA that has been designed over the course of evolution to *sense* and to respond to the *signals* impinging on it» (Keller 2014: 2424, emphasis added). Biosemiotics stresses this reactivated dimension of genomic activity. Genomes react to signals to produce different protein products according to their cellular context; this makes genetic activity always contextualized and dependent on the signaling network it belongs to. This entails a shift from «action to reaction» (Keller 2014: 2424), from «a collection of genes initiating causal chains leading to the formation of traits [to] an exquisitely sensitive reaction (or

⁸ Quoted in Keller (2000: 34), from McClintock’s acceptance remarks of the Noble prize in 1983; cf. also Keller (2014) and Sultan (2015).

⁹ This does not mean that the Biosemiotic understanding of genetics dovetails perfectly with most Eco-Devo readings. As expected there are many controversial points in tension. For instance, Markoš treats genes as «genuine written texts» (Markoš 2009: 675) conforming a book of life inherited and read by the cell. This could lead to the idea that genetic sequences are provided by evolution while the cell interprets it during ontogeny, which means ignoring that most of the machinery used by the cell is also somatically inherited and —following the metaphor— also part of the book of life.

response) mechanism —a device for regulating the production of specific proteins in response to the constantly changing *signals it receives from its environment*» (Keller 2014: 2428, emphasis added). The following quotation by Jesper Hoffmeyer presents the core of post-genomics in a way that an Eco-Devo biologist would probably enjoy reading:

Biosemiotics implies a major change in our conception of the role of the genetic material, the genome. Whereas the traditional view sees the developmental process and thus the phenotype as specified by the genetic setup of the organism, the genotype, Biosemiotics makes us consider the overall process as one of interpretation rather than one of specification... The process is best described as an interpretation [by the cell] with the implication that epigenetic and environmental factors must be seen as autonomous resources for ontogeny and phenotypic activity (Hoffmeyer 2008c: 59-60).

1.2.2 Constructing your niche

Niche Construction Theory is one of the principal attempts to build an evolutionary approach beyond neo-Darwinian adaptationism (Laland, Matthews, *et al.* 2016; Laland and Sterelny 2006; Scott-Phillips *et al.* 2014). Here again, ecological mediations of the organism's activity are explanatorily crucial. Contrary to the neo-Darwinian idea that the environment actively challenges the organism whose genes, blindly and eventually, will promote solutions, Niche Construction Theory highlights the active capacity of the organism (not genes) to overcome the environmental situation by acting. Therefore, such an environmental scenario is also the result of the organism's (and other species') activity. This involves the construction of the niche, its modification, migration, or invasion. In all of these cases, we are in front of an adaptive response made by the organism. As expected, these phenomena require a semiotic dimension, both in the interaction between organism and environment and the communication with the conspecifics that are usually involved in these kinds of processes; *signaling systems* are necessary to individually or collectively act on the surroundings.¹⁰

There is a more direct way to emphasize the need for a semiotic dimension by looking into a more epistemic reading of the construction of a niche. Organisms are also interpreters of the world. They construct what is *real* for them. As we already pointed out, it is the organism that determines what is relevant. This notion of relevance is linked to the specific interpretation of the world that each organism has (the aforementioned *Umwelt*). Organisms interact only with certain aspects of the world, which are not (exclusively) determined by their physical space but depend on the capacity of organisms of being interpreters. Thus, each organism has its own particular way of epistemically constructing the niche by its specific sensory system. Hoffmeyer (1997, 2008a) introduces a suitable concept for this phenomenon: the *semiotic niche*. It regards those aspects of the world to which the organism is related to (a.k.a. the organism's niche), «the outside interior» (Hoffmeyer 1998: 3), while the *Umwelt* should be understood as those subjective interpretations of the world, «the inside exterior» (*ibid.*), a.k.a. the niche's organism. Once those organism-environment relations are determined by the semiotic niche of each organism, organism and niche become a unit of interrelated and inter-defined phenomena, as Lewontin's Dialectical Biology proposed and most Eco-Devo adopts.

Karola Stotz (2010) emphasizes the difference between the *selective* niche and the *ontogenetic* niche. The former regards the place of niche variation in evolutionary

¹⁰ Heras-Escribano and Pinedo-García (2018) also emphasize the relation between Biosemiotics and Niche Construction Theory (and also with Ecological Information, a.k.a. affordances).

selection processes (Odling-Smee *et al.* 2013). However, to understand the place of the niche within the developmental time-scale, the concept of ontogenetic niche is a suitable one, whose relevance for evolution is, additionally, not constrained to natural selection processes. As Stotz explains, it regards the «internal and external ontogenetic niche [what conforms the *Innenwelt* and the *Umwelt*], understood as the set of epigenetic, social, ecological, epistemic, and symbolic legacies inherited by the organism as necessary developmental resources» (Stotz 2010: 483). Many biosemiotic pathways at different levels of the organism conform to the ontogenetic niche, but also material, energetic, geographical, or physical resources. The notion of ontogenetic niche was introduced by West and King (1987) and it seems to be one of the central missing ingredients in the gene-centered view that had pushed most biologists to embrace sub-organismal biology. In these authors's own words: «Ask not what's inside the genes you inherited, but what the genes you inherited are inside of» (West and King 1987: 552).

1.2.3 Developmental semiotic scaffolding

Scaffolding processes become a central ingredient once we look into real developmental pathways. We will see in Section 2 that it is also an important concept in cognitive science. Organisms seem to be capable of supporting further development on the basis of previous developmental stages and external information such that, once they have reached a new stage, these scaffolds may or may not be dispensed with for the organism to function properly. So while niche construction regards the capacity of organisms to change their surroundings, scaffolding processes consist of the use of external (an also internal) features to develop according to the organism's needs.¹¹ Thus, biosemiotic pathways (or what Eco-Devoists call “signaling systems”) become crucial events in the regulation of development —although not all scaffolding processes are necessarily semiotic (cf. Newman 2014). Scaffolding processes are ubiquitous in development and are crucial to understanding how complexity and functionality are achieved during ontogenesis (cf. Caporael *et al.* 2014 for a number of interesting theoretical and empirical approaches; also cf. Wimsatt, Griesemer 2007, Giorgi, Bruni 2015).

James Griesemer (2014) analyzes how external developmental scaffolding leads to the *hybridization* of developmental pathways and their phenotypic outcomes, i.e. traits which many of their present qualities map onto external information used during development. *Hybridization* thus reflects the mixture of internal and external resources involved in development. We believe that the ontology of hybridization could be a suitable frame to understand natural signs. By definition, «[a] sign is something that refers to something else» (Hoffmeyer 2010: 1; original from St. Augustine *De Doctrina Christiana*). Natural signs could be viewed as paradigmatic hybrid traits. Their development is clearly based on the interaction with the environment —such is the position, at least, of naturalist theories of intentionality (cf. Section 2). Once acquired, a sign has the main function to inform the system about its external environment where the organism habits (the *Umwelt*). Shortly, a sign is characterized by its relation with the environment (in philosophical jargon, by its reference) and the way that each organism intrinsically processes and constructs such a relation (Dretske 2004), i.e. it's a hybrid trait.¹²

¹¹ The metaphor of scaffolding has an influential and solid precursor in developmental psychobiology in the work of Ronald Oppenheim (1981) and his idea of “ontogenetic adaptation”, referring to those characters whose main operational role is to facilitate the development of other characters and allowing development to proceed on to more complex states.

¹² The phenomena of developmental scaffolding and hybridization in natural languages are analyzed by Balari and Lorenzo from an Eco-Devo viewpoint (Balari, Lorenzo 2018, Lorenzo 2018, Balari, Lorenzo, Sultan 2020). As they show in different examples, many grammatical properties of language, such as

Sultan (2015) also proposes a process for external scaffolding: “environment-cue system-response”. Its name speaks on its own. Developmental processes are deeply guided and dependent on the systematic appearance of environmental cues at certain stages of ontogenesis perceived by the organism. Instead of viewing development as the expression of a pre-determined genetic code, «[e]nvironmentally contingent development arises from a cue perception and response system, mediated by a complex signaling network» (Sultan 2007: 577). The resonance with biosemiotic processes is captured by her understanding of developmental plasticity based on environmental cues¹³:

[...] the pathways that underlie plastic expression patterns can be generally understood as *cue and response systems*: developmental, physiological, or behavioral adjustments (whether adaptive or maladaptive) that occur when an organism *perceives* some aspect of its environment as a specific piece of information and then *responds* to that cue by expressing particular phenotypic effects. [...] [T]hese systems comprise signal transduction networks that are embedded in larger regulatory networks. Phenotypic outcomes reflect the integration of these webs of environmental cues, their molecular transduction and regulatory pathways, and the feedback that occurs throughout the life cycle (Sultan 2015: 49, emphasis in the original).

This orchestra of signaling systems occurring at different stages of development echoes another insight of von Uexküll’s theoretical biology, namely its appeal to musical metaphors to understand organic activity. Although we are not going to get into this point with detail, it is relevant to call attention to the context in which von Uexküll brought this up: developmental biology itself, and in particular von Baer’s embryological studies (Kull 1999, 2001).¹⁴ As it is now widely accepted among developmental biologists, timing is crucial in ontogenesis and it can lead to several phenotypic changes (in many cases, without genetic change at all). The role of time in development is partially regulated by the external and internal semiotic pathways that intervene during ontogenesis as the instruments in an orchestra playing an elaborate and complex melody.¹⁵

Hoffmeyer introduces the notion of “semiotic scaffolding” to speak about processes «controlled by semiotic interactions between components that incessantly adjust biochemical or physiological activity to changing situations» (Hoffmeyer 2011: 60,

morphology or phonological marks, are present in a linguistic system owing to the scaffolding role they play in the acquisition of language. In these scenarios, language development requires such external scaffolds for the system to be acquired, and once these processes occur, they remain part of the system, hybridized with it.

¹³ An extremely interesting example of scaffolding that motivates a lot of theoretical reflection is the sea slug *Elysia chlorotica*. As Sultan (2015: 32) explains, it is an aquatic slug that during the first two weeks in the water eats an alga (*Vaucheria litorea*). The amazing fact is that the slug can incorporate the chloroplasts of the alga into its own cells (it really looks like a slug-alga). In this way, animal cells are capable of doing photosynthesis during their lifespan by using the organelles taken from the alga that remains active and functional in the slug’s cells. The result is a fruitful mechanism to obtain metabolic resources from the environment; that is, we are in front of an animal able of doing photosynthesis for the rest of its life thanks to a hybridization process during scaffolded development.

¹⁴ The notion of *cue* directly connects us with von Uexküll. He didn’t explicitly endorse a theory based on environmental signs but on environmental cues (that’s perhaps the reason why Sebeok named von Uexküll a *criptobiosemiotician*).

¹⁵ «Den Lebens-Prozess aber halten wir nicht für ein Resultat des organischen Baues, sondern für den Rhythmus, gleichsam die Melodie, nach welcher der organische Körper sich aufbaut und umbaut [However, we do not consider the life process to be a result of the organic structure, but rather the rhythm, as it were the melody according to which the organic body is built up and remodeled]» (Baer 1864: 280, my translation).

Hoffmeyer 2008c). From cell activity to social behavior, streams of information are flowing through semiotic pathways at different levels of organization producing signals crucial to make development move on.

1.3. Implications for Evolutionary theory

The developmental turn in evolutionary biology, while encompassing a heterogeneous collection of positions and ideas, nonetheless shares the common ground of emphasizing the role of development in evolution by positing that the processes involved in natural selection (*inheritance, variation and fitness*) cannot be understood purely in genetic (sub-organismal) terms. Evolutionary Developmental Biology (Evo-Devo) was — gradually and from the periphery — calling for an extension of evolutionary theory to include epigenetic and exogenetic causes at the developmental time-scale in adaptive evolution. In this scenario, the integration of Eco-Evo and Evo-Devo is under way (Gilbert, Bosch, et al. 2015, Sultan 2017b, Abouheif *et al.* 2014). The reasons are quite expected. Ecological mediation of developmental processes must be part of the extension of the evolutionary synthesis. Just as developmental biologists complain that without developmental studies evolution would remain misunderstood, biosemioticians claim that a «biology that wants to explain evolution cannot therefore fulfill its goal unless it integrates semiosis into its theoretical repertoire» (Hoffmeyer 2008a: 64). So, let's make explicit three points concerning Biosemiotics and evolutionary theory: (i) the importance of Biosemiotics in a theory of biological novelties and variation; (ii) its role to understand adaptivity as a cause of evolution; (iii) the inclusion of semiotic pathways within extended inheritance systems. Darwin himself was well aware that he did not propose a theory of novelty. Selection presupposes variation and novelty. Thus, paraphrasing Berry (2000: 117) and Reid (2007: 27) commenting on Eldredge (1995), one can ask: if natural selection is the filter, who's making the coffee? The neo-Darwinian answer runs at the sub-organismal level through non-adaptively directed (i.e. blind) mutations and drift at the genetic level. This view has, at least, two problems that, in part, explain much disagreement with neo-Darwinism. First, genes are not traits, so novel traits could be explained by blind changes in gene pools only if the genotype-phenotype map follows the Central Dogma's rules. We already pointed out that such rules are not the rules of development (sect. 1.1., 1.2.). Secondly, it leaves no place for developing organisms in the explanation of novelty and variation (Moczek 2008). One of the many reasons to adopt an Eco-Evo-Devo stance rests on its capacity to explain novelty at the individual level (Wagner 2014, Walsh 2015, Gould 1977, Hall 1999, Reid 2007). This is not merely a coda in mainstream evolutionary theory. On these views, as we already outlined, organisms become a *force* (Sober 1984) of adaptive evolution. Evolutionary processes can begin with the organism's modification through self-organization processes and phenotypic plasticity without getting involved in genetic-population processes. These new traits are, by definition, not blindly but adaptively directed to the organism's conditions of life.

By controlling and scaffolding development, biosemiotic pathways can promote adjustments that lead to phenotypic novelty well before genetic changes take place, in a similar vein as the Baldwin Effect, Waddington's genetic assimilation, or more generally, West-Eberhard's phenotypic assimilation where «genes are probably more often followers than leaders in evolutionary change» (West-Eberhard 2005: 6543). This is indeed what Hoffmeyer proposes:

Thus, biosemiotics holds that while genetic fixation may ultimately be the most secure mechanism for the stabilization of new traits or behaviors, such traits and

behaviors were probably often initially stabilized through semiotic loops and thus kept functional for an indefinite period of generations, allowing the time needed for the much slower mechanism of supportive genetic change to take place (Hoffmeyer 2011: 62).

Once we highlighted the connection of development and evolution, insofar as we argued that biosemiosis is a crucial ingredient in adaptive ontogenesis, it therefore also becomes a factor in adaptive evolution. To appreciate the role of semiosis in evolution, we must take into account that if developmental processes are a source of adaptive evolution, an organism's responses must be coupled with the environmental situation and its inner organizational dynamics. That is, to act adaptively, an organic system must possess a certain degree of sensitivity to the inner and outer worlds. By being sensitive to its surroundings (either other neighboring cells or the exterior world), the organism is capable to move or change them; and by being organized and semiotically interconnected complex systems, organisms are endowed with the capacity of inner modification, regulation, and adjustment. Many important evolutionary innovations arise through internal changes in the organizational structure and function of the organism that are needed to adjust inner and outer struggles for life (through endosemiosis and exosemiosis). As we pointed out, it is the capacity of organisms to respond, act, regulate, change, or preserve according to their needs what makes them adaptive agents.¹⁶

Finally, signals are also softly inherited (Jablonka 2007). This includes cultural transmission of signals involved in symbolic social interactions. But there are many other (non-symbolic) signals also belonging to the orchestra of development. They go from the somatic regulation provided by the mother cell or the epigenetic control of embryonic development, to the ecological information needed to adaptively adjust behavioral patterns during ontogeny (Jablonka, Lamb 2014). As inheritance studies are focused on the resemblance of traits between generations, an additional relevant question arises concerning the resemblance of *Umwelten*. Although subjective, *Umwelten*, as ecologically and socially scaffolded, tend to resemble among individuals of the same species (or societies) due to the sharing of inherited information, both in the genomic material and the ontogenetic niche. The subjective determinations of the Umwelt based on inter-subjective inherited materials could be the basis from where social dynamics develop and evolve.¹⁷

2. Biosemiotics and representational theories of mind

Now is the turn to see the connection between Biosemiotics and representationalist theories of mind. The introduction of (mental) representations in the ontology of science meant the birth of cognitive science. So, first, we will see the close relationship, although historically disconnected, between signs and representations. We will defend the view that *signs and representations are both determined by content, they are connected with the flow of information and are posited to promote a level-specific analysis of nature*. Despite being central,

¹⁶ Many other authors already argued for the role of organism-environment signaling relations in evolution. For instance, the notion of *affordance*, as presented by James Gibson, has been used to explain how organisms create their own *Umwelt* and adaptively act according to it (Walsh 2012, Heras-Escribano 2020, Reed 1996, Withagen, Wermeskerken 2010). In these proposals, affordances also come to supplant the adaptationist landscape with the *affordance landscape* (Walsh 2013), as opportunities for the organism to adaptively construct and change themselves and the niche according to their needs.

¹⁷ Under this analysis, the gap between subjective and public meaning that so many headaches had provoked to analytic philosophers could be filled by reliable epigenetic inheritance channels.

representational theories of cognition have been severely challenged by different authors within the so-called post-cognitivist movement. From here, many controversies were running around representationalism. Hence, secondly, in sections 2.2. and 2.3., we will argue that by rooting representations within theoretical biology underpinnings of Biosemiotics we can keep representationalism safe but at the same time deal with many of its troubles. Particularly, we will stress that *the situatedness of sign processes and the complex dynamics involved in signal development could be a key to rethinking the nature of representations.*

2.1. Representations as signals

Representations and signals have different scientific historiographies. While signals were studied within biology — for instance, in animal communication, multi-cellular interactions, or biochemical networks, representations were invoked to describe cognitive phenomena. In cognitive science, representations allow us to understand how intelligent behavior is generated by processing bearers of semantic information. The many fields that compose cognitive science systematically appeal to representational-talk, such as cognitive psychology, artificial intelligence, linguistics, cognitive neuroscience, or philosophy. However, there is a (quite explicit) connection between signals and representations. Both are defined as entities bearing information about something. Shortly, their core property is *aboutness*. As we already noted, «[a] sign is something that refers to something else» (quoted in Hoffmeyer 2010: 1). This description is indeed fairly adequate as a primary definition of representations in cognitive science as well. Such referential quality of representations has also taken to be the content of representations. So the connection is quite clear: both signals and representations are invoked in scientific analysis to speak about natural processes involving contentful relations; cf. Hoffmeyer (2012) and Kull, Deacon, *et al.* (2011: 37-38) for this idea.¹⁸

By inquiring into organic processes through referential relationships among different levels of organization, cognitive science and Biosemiotics are dedicated to understanding the same phenomenon, namely, the flow of information. At the core of cognitive science lies the idea that cognition is about processing information in neural networks. Biosemiotic pathways are also channels flooded with information, so when we see both sciences in action, we can appreciate that they deal with the same kinds of issues (one exclusively at the cognitive level, and the other in all living beings), that is, about how information is stored, transferred, transformed, modified, exchanged, generated or communicated to produce certain activities (from cellular metabolism to complex behavior).

Both representations and signals came to justify a level of analysis in nature, respectively the cognitive and the biosemiotic ones. We have already stressed (1.1.1.) the need to reject a purely physicochemical understanding of the organic world and the need to incorporate a semiotic dimension. *Representationalism* also was born as a reaction against a reductive account of behavior. The mind cannot be exclusively understood by reinforced stimulus-response events. Behaviorism was defended on the grounds that there cannot

¹⁸ Certainly, some authors that deal with problems concerning intentionality, and favor a non-representationalist position, take semiotics as the suitable theory to approach contentless intentionality like, for instance, telosemiotics (Hutto 2013) or Biosemiotic enactivism (Jesus 2016). This freedom to choose between a contentful or a contentless theory of signs is due to two facts: first, the terminology of semiotics was not historically linked to analytic philosophy (from which the notion of intentionality was introduced in cognitive science), so there is space for philosophical debate here; second, it depends mainly on what one wants to emphasize when anchoring intentionality to semiosis. Be that as it may, we believe there are enough reasons to think about signs as having content, which is quite explicit in the triadic picture drawn by Peirce.

be a science that deals with subjective, inner processes. As a response, representationalism argued that cognitive psychology (and other fields in cognitive science), by using representations as the main units of analysis, can study internal processes to tackle how intelligent behavior is generated, learned, misguided, etc. But cognitive science also denies the reduction of mental processes and mental states to brain processes and brain states. Psychology can be studied by appealing to representational content. Causal relations between such units build complex propositions that settle mental states (propositional attitudes), which will eventually bring about behavior. As we can see, these processes involve psychological categories. Clearly, the relation between the mental and the neural is one of the most difficult problems in cognitive science, and there are many positions in the field. Be that as it may, representations allowed scientists to posit causal processes at the psychological level. Similarly, Biosemiotics enabled us to explain living systems involving semiotic interactions. What makes this connection tighter is that both anti-reductionisms were intended for understanding the agential capacities of organisms. We already saw this regarding Biosemiotics, and many agential qualities of animals can also be addressed from the perspective of cognitive science.

In this section, we enumerated three common elements of representations and signals. First, both representations and signals are characterized by their content. The principal quality of signals and representations is *aboutness*. Secondly, both biosemiotic processes and cognitive processes are characteristic of the transmission, transformation, integration, and communication of referential units (signals and representations, respectively). The flow of information is not restricted to neural processes but ubiquitous in the organic world. Finally, representations and signals came to legitimate the study of phenomena at a certain level of description, not reducible to lower ones.

Should we understand mental representations within a theory of bio-signals (signs involved in natural signaling systems)? We believe that we should. A terminological variant is to understand bio-signals as representations, and then anchor mental representations (for cognitive systems) to a general theory of representations (for cognitive and non-cognitive systems). So, for us, henceforth, representations and bio-signs would be phenomena of the same kind. The reason for such (in part, terminological) unification will be clearer towards the end of the paper.

Let's end with a coda on the also so-called strong Mind-Life Continuity Thesis (cf. for instance, Thompson 2007). We just want to divorce a commitment with representationalism with a commitment with psychological-mental states. This means that our compromise with contentful representations in living systems (i.e. Sebeok's thesis) does not entail Mind-Life continuity; this would require further argumentation. The fact that intentionality goes beyond organisms with nervous systems does not imply that "cognition goes all the way down" (Dennett, Levin 2020). Similarly, the idea of organisms as interpreters should not have any cognitive connotations, insofar as it just implies that the organism-environment dialectics are relative to idiosyncratic signaling systems of each organism and its place in the world. While we argued that signs must be a necessary ingredient to explain organic processes — from unicellular organisms to complex animal behavior, this does not imply that psychological categories are explanatorily necessary too.

2.2. Situating signs

The so-called post-cognitivist movement encompasses a diverse cluster of reactions against mainstream cognitive science, particularly to its representational theory. Representations, while explanatorily useful, are difficult to explain. They were the heart of

the cognitive revolution, but at the same time they also brought about a number of apparently insurmountable problems, such as Brentano's Problem (Haldane 1989), the Hard Problem of Content (Hutto, Myin 2013), the Symbol Grounding Problem (Harnad 1990), the Frame Problem (Dennett 2005), Searle's Chinese Room (Searle 1980); Content Determination Challenges (Fodor 1990), and the Problem of Error (Dretske 1993). It is crucial to be able to disentangle these knots if one accepts (i) the role of representations in cognitive science is the central ingredient for a causal analysis of cognitive psychology, and (ii) the particular understanding of representations proposed by mainstream cognitivism as amodal, language-like symbols (cf. for foundational proposals Fodor 1975, Pylyshyn 1984, Newell, Simon 1972, Chomsky 1980, Marr 1982). Under this view, representations are understood as symbols, language-like structures bearing semantic information and being processed by their formal and syntactic properties.

This underlies the use of software/hardware distinction as a model for cognition. The identification of cognition with the software – understood as the manipulation of symbols obeying syntactic rules – to be hardwired in the brain or other functionally equivalent physical systems provides the grounds to understand the contentful and semantic dimension of cognition demarcated from the context in which behavior takes place. Classical computational cognitive science mirrors computational science as «a science of abstraction» (Aho, Ullman 1995: 1) in a way that the different levels of analysis beyond the physical substrate are understood as abstractions. This gave rise, since the beginning of cognitive science, to the use of machine metaphors and machine models to approach cognition, not only as an explanatory and predictively useful framework but to define the nature of cognition itself. In this sense, cognition can be defined in abstract terms, as the manipulation of syntactic structures bearing amodal semantic content.

This does not mean that classical representationalism posits representations as abstract entities, nor does it concern the fact that representations refer to abstract entities and not to particulars. The classical view is based on the idea that brain states — or other functionally equivalent physical systems - have semantic properties in such a way that cognition can be explained by such semantic properties. As remarked, the crucial point turns around how such semantic properties should be understood. Classical representationalism posits that semantic information is separated from the perceptual and situated context of behavior in a way that the explanation of cognition rests on the syntactic and formal properties of symbols, which, by definition do not involve the modal properties of the environment but are transduced to amodal and conceptual representations (cf. next paragraphs for the difference between symbolic and non-symbolic signs).¹⁹

Anti-representationalism dispenses representations in explaining cognition — point (i), see above-, so inevitably, it rejects (ii) as well — i.e. the representationalist theory of cognitivism, as it is the case, for instance, of enactivism (Hutto, Myin 2013) and ecological psychology (Chemero 2009). But some corners of post-cognitivism still accept (i) while trying to deal with the aforementioned problems without being committed to (ii). A pertinent question is whether such knots became Gordian only when we endorse classical views on representations, or whether they are inherent to any representationalist framework. Here we believe that Biosemiotics can come into rescue. We will discuss an important ingredient of Biosemiotics, namely the situatedness of signs, that can do justice to some of the problems present in classical representationalism

¹⁹ I am indebted to an anonymous reviewer for stressing the importance of defining the target of the critique, its associated literature, and the thesis to be discussed.

without actually giving up representations. We are not going to propose any solution to the aforementioned problems concerning representationalism, but to suggest a possible interdisciplinary path to rethink representational theories of mind.

There are a number of non-eliminativist, but yet non-classical positions about representations that emphasize the embeddedness and embodiment of mental processes (cf. Calvo, Gomila 2008, Robbins, Aydede 2008 for a comprehensive introduction to situated cognitive science). Any mental activity is situated and sensitive to its environmental and bodily situation. From this preliminary presentation, we can trace a straightforward connection with Biosemiotics by acknowledging the plurality of semiotic processes. This was present, from the beginning, in Peirce's work: beyond symbols, signs are also indexical and iconic.

What this means is that the mind is constructed, epistemically and ontogenetically, from situated signs, i.e. from signs bearing modal information about the bodily and ecological reality. Indices achieve their content by their being causally and non-arbitrary connected with the reference, that is, with what is going on in the world and the body. Icons are tied to the modal character of their reference because they are capable of representing through a kind of homomorphic relation between the sign and the object (the representation and the reference) where the properties of the latter are preserved in the former. If we think about this in ontogenetic and epistemic terms, it follows that mind-environment relations are the building blocks of further and more elaborate representational capacities, but, to understand how content is acquired and representation connected between them to construct complex webs of beliefs, we have to start with indexical and iconic relations. «Mental life is grounded in bodily intentionality as manifested in perception-action cycles, and thus ultimately in semiosis» (Hoffmeyer, Kull 2003: 261). So the embodiment and embeddedness of representations comes to the fore and demotes the abstract and machine-like picture of the mind in the foundations of cognitive science. Contentful mental states cannot be built purely abstracted and disembodied from context «since mental 'aboutness,' human intentionality, grew out of a bodily [and ecological] 'aboutness'» (Hoffmeyer, Kull 2003: 260). All in all, what we want to defend is that Biosemiotics has a repertoire of semiotic processes comprehensive enough to come to grips with the situatedness of mental processes.

Another way to express this idea concerns the dialectics of biosemiotic processes that we referred to in the last section. *Dialectical Biosemiotics* emphasizes both the construction of the world by the mind and the construction of the mind by the world (what we alluded to as the semiotic niche and the Umwelt). While "I-talk" in orthodox cognitivism supports individualism (the mind can be defined and characterized without reference to the external world), internalism (mental properties supervene on intrinsic properties of each individual), and intensionalism (content concerns the relationships, within the mind, between intentional items), Dialectical Biosemiotics would support some of the tenets of 4E cognitive science (cf. Kiverstein, Clark (2009) for an introduction to 4E cognitive science), such as embeddedness (the mind must be studied and defined according to the context where cognition occurs) and embodiment (the mind is not reduced to the brain but is also a process involving the whole body), and also beyond it, such as ecological (mind-world relations provide the foundations of cognitive capacities) and externalist (mind-world relations setup the basic intentional toolkit from where further intentionality grows) positions.

2.3. Representations in context: beyond dichotomies

In the last section, we highlighted that Biosemiotics can help search for an intermediate and non-eliminativist position between anti-representationalism and orthodox representationalism. Our emphasis was on the nature of semiosis as a situated process. Now we will focus our attention on the *bio* side of Biosemiotics to see how its theoretical underpinnings could reframe crucial issues regarding naturalism.

Everybody is well aware that the naturalization of mental representations is a difficult undertaking. We must understand how our minds came to be furnished with content, how intentionality is grounded in non-intentional footings during development, and how novel representations are acquired. As can be appreciated, a naturalistic theory of representations is intimately tied to developmental issues, that is to how referential capacities are achieved by the relation between the organism and the environment. This is quite expected when we are dealing with a trait highly dependent on experience (or what we called a “hybrid” trait). To explain the emergence of intentionality in natural terms has been labeled as the second-hardest problem in cognitive science (Pylyshyn 1984). Many solved it by abandoning representations. Others deal with it in the philosophical territory, while many proposals try to introduce a scientific framework to anchor their theories. Regarding the latter, once cognitive scientists approach these issues by looking into biology, they tend to systematically appeal to a neo-Darwinian, often gene-centered, paradigm — for instance, the Teleosemantic Project in the philosophy of mind and language (Millikan 1984, Neander 2017)²⁰, the Core Knowledge Hypothesis in cognitive psychology (Carey 2009, Spelke, Kinzler 2007), the Innate Grammar in biolinguistics (Berwick, Chomsky 2017, Chomsky 2000), or the evolved mental modules in evolutionary psychology (Barkow *et al.* 1992, Sperber 2000). Although we will not discuss these proposals in detail, we will identify two important points where Biosemiotics (and developmental biology too) can help opening new avenues to tackle representations. Firstly, the rejection of dichotomic categories in development, and secondly the role of scaffolding in the development of representations. Even though Konrad Lorenz recognized the obvious influence of his mentor, von Uexküll, the fact is that, in many relevant respects, their works have an opposing theoretical flavor. Lorenz’s theory of instinct represents a common way to think about behavior and cognition that has influenced some of the proposals mentioned in the previous paragraph; for instance, Chomsky himself has recognized the influence of Lorenz’s ethological tradition, along with the work by Tinbergen and Thorpe (cf. Chomsky 2009: 16). The core of Lorenz’s proposal (Lorenz 1986), developed after Lehrman’s critique (Lehrman 1953), is that there are two kinds of learning processes that explain how behavior develops. Instincts develop thanks to phylogenetic learning (from information obtained during evolution) and throughout a rigid process of maturation. Acquired behaviors develop due to ontogenetic learning (from information obtained during development), which is a flexible and contingent process. This distinction is grounded in the Weismannian barrier of the genotypic and phenotypic space (as Lewontin (1974b)

²⁰ Evolutionary functions — as teleosemanticists understand them — are deeply rooted in a neo-Darwinian framework. The source of teleological functions is Darwinian: evolutionary design introduces the teleological, functional, and normative ingredients in nature which are the naturalistic land on where teleosemantics is based to solve the problem of intentionality (of course, this does not deny that other aspects of teleosemantics are shared with and relevant for the proposal defended here; cf. footnote 22). Moreover, a gene-centered view of development usually plays the role of explaining how evolved type functions are instantiated in individual tokens (cf. for instance, Dretske 1988, Millikan 2000, Neander 1995, Papineau 2018). That is, to understand that inherited information is responsible for constructing the trait token according to evolutionary design (although Shea (2007, 2013) correctly shows that evolved functions rely on epigenetic inheritance systems).

presented it), and it mirrors other ubiquitous dichotomies in the cognitive sciences, such as innate-learned, inherited-environmental, cultural-biological; Kuo (1976) and Gottlieb (1997) for critical discussion.

However, we already know that the Biosemiotic tradition rooted in von Uexküll's ideas does not approve of this picture about development. Traits cannot be demarcated in such a dichotomic way insofar as ontogeny is always a contingent process dependent on endosemiotic and exosemiotic pathways. Traits cannot be separated into two groups insofar as all traits are developed thanks to information proceeding from different levels of the organism (genetic, epigenetic, and exogenetic) connected through many biosemiotic pathways. Developmental studies of cognition should abandon the idea that the kind of information that inheritance and the environment provide is different. The reasons for this are twofold. First, in the analysis of developmental causes, all resources have a qualitatively identical role. The developmental system of each organism cannot distinguish the causal role of inherited resources from non-inherited ones. The analysis of developmental outcomes concerns the interaction of many resources and processes that, at this proximate level of analysis, there are no differences between those resources that are inherited and those ones that are not. Moreover, it makes no sense to search for quantitative analysis if we take developmental causes as working together in the production of phenotypes (Keller 2010), even though this does not necessarily imply that it is impossible to analyze the robustness of the trait in relation to each resource, nor to investigate their mechanistic role in development. Secondly, we already remarked that inheritance systems are extended beyond the gene and across the epigenetic system and the ecological niche. For instance, as natural language paradigmatically exemplifies, there could be exosemiotic inheritance systems that reliably participate in the development of traits throughout generations (i.e. cross-generational stable traits strongly dependent on inherited environmental information). Similarly, endosemiotic processes within the genome also evidence that even the development of robust and pan-cultural traits is contingent and context-sensitive. Both the ancestral representational capacities and the individual-specific ones are (re)constructed during ontogenesis thanks to the epigenetic participation of biosemiotic pathways at all the levels of the organism. The moral is, therefore, that the ubiquity and centrality of biosemiotic pathways turns the dichotomic model of development into an inadequate and misguided framework to understand how situated minds really develop.

To approach the mind's ontogenesis with semiotic scaffolding gets us closer to apprehend how contentful relationships are achieved through interactions at many levels and at different stages of development.²¹ Within the many levels of semiotic scaffolding (regarding *mental* representations), for instance, we remarked the important role of body movement and proprioception (embodiment) in the ontogeny of intentionality. The semiotic pathways informing body awareness are a candidate for where further representations would be supported. Similarly, embedded sign interactions also work as building blocks to construct richer cognitive capacities. The contentful information taken from modal signs could scaffold categorization processes, build complex semantic networks, or participate in inductive learning processes (Sterelny 2010).

Beyond these, let's say primitive, cases, in social animals we find many scaffolding processes mediated by signs. Post-natal parental care and intra-familial interaction are crucial to learning the foundations of social dynamics. Here, ontogeny is not based on «the developing infant, but rather on the interactive unit, parent/child, which is

²¹ A pioneer in studying scaffolding processes at the cognitive level was Vygotsky, and different trends in post-cognitivism followed him.

examined within the context of both biological and social/environmental constraints» (Klopfer 2001: 168). These primary social interactions could also support meta-representational capacities to develop the so-called “Theory of Mind” (Sterelny 2003). These first steps in society get improved once the individual is enrolled in more complex and rich interactive dynamics, where current situations provide the building blocks to construct the following ones. These interactions are, for instance, a key in language development. Humans are experts in dealing with complex social networks. Formal education, social conventions, and institutions operate during development as scaffolds to acquire cognitive skills to deal with social — and biological — life — and troubles. As Stotz points out: «what is most distinctive about humans is their developmentally plastic brains immersed into a well-engineered, cumulatively constructed cognitive-developmental niche» (Stotz 2010: 483). Moreover, Hoffmeyer (1997) employed the term *semethic interactions* to speak about those scaffolding processes *between* different species, where «individuals of one species have acquired the capacity to interpret certain regular activity patterns (habits) characteristic for individuals of another species, which then eventually may release new kinds of regular behavioral patterns in the first species» (Hoffmeyer 2012: 108).

On the one hand, in these cases many *symbolic* signs are also introduced and scaffolded in social dynamics (à la pragmatism); semantic information, social norms, or skills could mirror the complexity of different social patterns. On the other hand, *symbolic* signs could also be rooted in prior mental indexical and iconical representations (à la cartesianism; Hutto, Satne 2015), where complex and compositional content could be based on the previous acquisition of their constituents. Generally speaking, in all these cases we have the idea that the representational repertoire acquired at a certain stage of development works as the scaffold with the help of which additional representations can be learned. Semiotic scaffolding is, therefore, (one of) the bases for the acquisition of knowledge.

3. Conclusion: building the bridge between Eco-Devo and representational theories of mind

We have tried to show that Biosemiotics could find a respectable place both in Eco-Devo and cognitive science. But, what about the relation between these other two disciplines? We believe that Biosemiotics could work as a bridge between them because its theoretical approach can provide a novel framework to deal with biological and cognitive phenomena. Thus, on the one hand, the shared biological underpinnings of Eco-Devo and Biosemiotics seem to be a fertile land to ground representations, while, on the other hand, signs and representations constitute a crucial ingredient to approach the agentive dimension of organisms posited by Eco-Devoists. Let's first consider how and why Eco-Devo can be a friendly frame for dealing with cognitive issues.

As we pointed out, the problems concerning intentionality in representations are the burden that cognitivists had to deal with to overcome the behaviorist paradigm. Most of the problems of intentionality arise when we seek a naturalist understanding of representations: to explain, without involving prior intentional talk, how brain states can have intentional properties. There are several and varied proposals to explain the origin of (contentful) intentionality in natural terms, but as we pointed out, most — if not all — explicitly or implicitly adopt a neo-Darwinian framework. Enter Eco-Devo. What we suggest is to replace the neo-Darwinian spectacles that blurred the vision of cognitive scientists with an understanding of cognitive development aligned with Eco-Devo tenets. This entails a reconceptualization of the nature of mind development, from a preformationist and disembedded stance to a constructivist and situated one; thus

promoting a conceptual shift where the adaptationist, selectionist, gene-centered, nativist, and instinct talk is replaced by the likes of scaffolding processes, niche construction, semiotic niche, developmental timing, dynamic interactions, organizational complexity, and other mechanisms drawing attention to real ecological developmental processes rather than to evolution disguised as development (Griffiths 2013).

This shift can help understand, from a well-informed biological frame, the ontology and ontogenesis of representations. Besides this, a major point to underline concerns Eco-Devo's ontological and methodological assumptions: that the central units of analysis in biology are organism-environment interactions. We are pretty lucky; we are just searching for an understanding, in naturalistic terms, of an entity that is posited by scientists to understand environmental-organism interactions: representations. So we can borrow from Eco-Devo the idea of *hybrid trait* and claim that mental representations are hybrid mental traits. Aboutness is, after all, an environmental-mental character of representations. What makes representations necessary to understand the adaptiveness of intentional behavior is that the content of what is being processed is achieved from and for a rich environmental-mental interaction during lifespan.

From the idea of hybrid representations, we can settle another issue, namely the embeddedness and embodiment of mental representations. The situatedness of minds is a corollary of the fact that their central explanatory units are paradigmatic hybrid traits. Our previous reference to West and King (1.2.2.) bears resemblance to an important aspect of situatedness that was already stressed by James Gibson, which we could take as an invitation to replace the question “what is inside your head” with “what your head is inside of” (cf. Stotz 2010). Moreover, in section 2.3. we stressed the importance of moving beyond neo-Darwinian dichotomies. Such movement is also present in Biosemiotics, although recently it was deeply analyzed and developed by developmental biology, particularly from Eco-Devo and the closely-related approach of Developmental Systems Theory (Griffiths 2002, Oyama 1985, Oyama *et al.* 2001). So, most of the connections that we identified between Biosemiotics and representational theories throughout section 2 could also be linked to Eco-Devo.

Moving on, what does cognitive science have to say in Eco-Devo? Or more appropriately, how and why a representational theory should put its hands in Eco-Devo? As we highlighted, representations, mental and non-mental (thus any organic sign), are indispensable to defend the agentic role of organisms in biology. Neo-Darwinism managed to do biology without organisms, i.e. organisms are explanatory irrelevant to understand adaptive evolution and diversity. Many authors characterized this position as black-boxing development. Evolutionary biologists can see phenotypes through genotypes, as if development were transparent (Walsh 2000). This picture sounds familiar in cognitive science. Behaviorism — for different reasons from evolutionary biology — also black-boxed a crucial ingredient: mental processes; they could see intelligent behavior through stimulus-response interactions, as if mental processes were translucent. We know that representations were the key to open the box of the mind. Maybe the same key can open the box of development.

What does this mean exactly? The vindication of the explanatory role of organisms in development and evolution implies understanding the causal role of organisms in the diversity and fitness that we find in nature (i.e. in the main target of evolutionary theories; Walsh 2007). This causal factor comes from taking ontogenesis and the organism's activity as the product of dynamic interactions at different levels of organization, “under the skin” and beyond it, and its implications for central biological processes, such as variation, inheritance and fitness. As we remarked, such dynamic interactions are mediated by signaling networks capable of informing the external and internal situation (the *Umwelt* and the *Innenwelt*) so that the organism acquires the ability

of taking an adaptive route. We considered a number of ontogenetic processes where signaling systems are crucial (1.2.). Once we assimilate signs and representations (2.1.), we can understand an organism's development as a process guided by representations, as in cognition. Certainly, insofar as we do not forget that our representational account is primarily based on the situatedness of signs, what we suggest is not so different from our conclusion of the first section, i.e. that Biosemiotics is central in Eco-Devo.

Our emphasis on representations, rather than on signs, amounts to a suggestion to mirror in Eco-Devo (some aspects of) representational theories in cognitive sciences. That is, representations could be a key to open the box of development because what was put inside it was mainly the agentic dimension of developing organisms. In cognitive science, representations were posited to understand agentic properties of minded organisms –principally of human cognition. Mental states, built from representations, are the basis for looking into the agentic capacities of animals in order to overcome both behaviorism and neuro-reductivism. Representations allowed cognitive science to treat psychological processes within the realm of scientific explanations as causal processes dealing with contentful psychological states. Eco-Devo also pursues an explanatory analysis of organisms dissociated from a purely physicochemical frame. The introduction of organisms as indispensable explanatory units in biology mirrors the introduction of minds in cognitive science. Cognitive science overcame the behaviorist dogma of neglecting any science of the mind as it was considered as the territory of subjective phenomena, hence out of the scope of science. Eco-Devo could take the same strategy and appeal to representations to tackle the agentic role of organisms, without getting into epistemological troubles with the objectivist foundations of modern science. In both cases agentic capacities are defended, referential relationships are crucial, inner and outer regulations are ubiquitous, global-dynamics founded, and an anti-reductionism is pursued. We also believe that in both cases the analysis of agentic capacities requires representations; they set the Innenwelten and Umwelten of life, from cells to plants and animals. In a nutshell, development, as minds, could also be explained by content.

There is another way to see what we are proposing here. It concerns teleology. It was a quasi-forbidden word for a long time. Neo-Darwinians, mainly thanks to Mayr's work on teleonomy (Mayr 1961, 1974) and to the etiological theories of functions in teleosemantics (Millikan 1989, Neander 1991), could accommodate it in biology.²² However, this proposal is deeply anchored in genocentrism and adaptationism. Instead, old approaches to teleology from Aristotle and Kant — let's call this *organismic teleology* (Walsh 2008) — are starting to spark a renewed scientific interest. Here, teleology lies at

²² As one anonymous reviewer remarked to me, it is important to say why my proposal is different and better than teleosemantics (so as something interesting is going in this paper). There are two key differences between the pursued integration of Eco-Devo and Biosemiotics and teleosemantics. First, there is a clear difference in their biological foundations (cf. footnote 20). Teleosemantics, at least in its mainstream views, is based on an evolutionary notion of teleological function, usually explicitly assuming a neo-Darwinian framework, while the path proposed here takes organismal agency as the locus of teleology. Secondly, both Eco-Devo and Biosemiotics try to study the meaningful processing of information in living beings in general, not exclusively in animals. Contrary to this, most (but not all) teleosemantic proposals are devoted to understanding representations in animals (such bees, frogs, or humans). In this sense, Eco-Devo and Biosemiotics represent a broader framework than most teleosemantic theories. Having said so, this does not mean that teleosemantics should be put aside but just that Biosemiotics emerges as a different biological insight to deal with the same explanatory target (naturalizing intentionality) and appealing to the same explanatory strategy (explain intentionality in terms of teleological functions) as teleosemanticists do. Although teleosemantics is not compatible with some biological insight of Eco-Devo and Biosemiotics, there are certainly many points of contact that call for a convergent and integrative view.

the level of organisms, not at the sub-organismal (Mayr's teleonomy) or supra-organismal (etiologial theories of functions). After all, teleology is intrinsic to the adaptive and agentive character of organisms. This has many consequences both for cognitive science and for theoretical biology that will not be explored here. We just want to suggest the following: the bad reputation of teleological explanations in science has to do with the fact that they seem to involve something like backwards causation, i.e. future events (the goal) causing current events (organism's action). Mayr and the etiologists solved this by saying that teleology does not come from the future but the past: the goal of a specific trait of an organism is to do whatever it was programmed or selected to do during evolution. But how does organismic teleology deal with this problem? We believe that here again representations (or signs) are crucial. Very briefly, representations of goals do have causal powers without involving any future event. We see development directed towards a goal because, as we remarked many times, ontogeny is constantly adaptively directed to the organism's worlds. This *intention* towards the current circumstance is mediated by representations. So, teleology, as agentivity, also emerges at the biosemiotic level. A note for clarification is important: we are not suggesting that the solution lies in the capacity for representing the future. In developmental terms, it would mean that development is goal-directed to an adult state. This is not our point. The capacity to represent future events is a cognitive capacity of some higher animals. An adult stage is not adaptive because ontogeny was directed to it, but because each step in development was adaptive regarding the current environment and such an environment was stable enough to maintain the adaptivity in adulthood. Development neither looks to the past nor the future, it just represents the present and adaptively develops according to it.

Acknowledgements

I thank Stephen Cowley and two anonymous reviewers for their comments and suggestions on many points of this paper. I am grateful to Sergio Balari for the discussion of the ideas presented here and for his help to make the language of this paper closer to readable English. This work has received support of the Spanish Government through grant FFI2017-87699-P, and the National Agency of Investigation and Innovation (Uruguay) through grant POS_EXT_2018_1_154759.

References

- Abouheif, Ehab, *et al.* (2014), *Eco-evo-devo: the time has come*, in *Ecological genomics*, Springer, Dordrecht, pp. 107-125.
- Aho, Alfred and Ullman, Jeffrey (1995), *Foundations of computer science. Computer Science*. W.H. Freeman & Co. Ltd.

Baer, Karl Ernst von (1864), *Reden gehalten in wissenschaftlichen Versammlungen und kleinere Aufsätze vermischten Inhalts: Reden. Erster Theil*. Vol. 1. Schmitzdorff, St. Petersburg.

Balari, Segio and Lorenzo, Guillermo (2018), «The internal, the external and the hybrid: The state of the art and a new characterization of language as a natural object», in *Glossa. A Journal of General Linguistics*, n. 1, pp. 1-33.

Balari, Segio, Lorenzo, Guillermo, and Sultan, Sonia (2020), «Language Acquisition and EcoDevo Processes: The Case of the Lexicon-Syntax Interface», in *Biological Theory*, 15, pp. 148-160.

Barbieri, Marcello (2014), «From Biosemiotics to Code Biology», in *Biological Theory*, 9, pp. 239-249.

Barbieri, Marcello (2015), *Code Biology*, Springer, Cham, Switzerland.

Barkow, Jerome, *et al.* (1992), *The Adapted mind: evolutionary psychology and the generation of culture*, Oxford University Press, New York.

Berry, Camila (2000), *Bulldogs, Watchdogs and Underdogs: Is Evolutionary Theory a Paradigm or a Kennel?*, MSc thesis, University of Victoria.

Berwick, Robert and Chomsky, Noam (2017), *Why Only Us. Language and Evolution*, The MIT Press, Cambridge-London.

Calvo, Paco and Gomila, Toni. (eds) (2008), *Handbook of cognitive science: An embodied approach*, Elsevier, San Diego-Oxford-Amsterdam.

Caporael, Linnda R., *et al.* (2014). *Developing scaffolds in evolution, culture, and cognition*. Vol. 17. MIT Press, Cambridge-London.

Carey, Susan (2009), *The origin of concepts*, Oxford University Press, Oxford-New York.

Chemero, Anthony (2009), *Radical Embodied Cognitive Science*, MIT Press, Cambridge-London.

Chomsky, Noam (1980), *Rules and Representations*, Columbia University Press, New York.

Chomsky, Noam (2000), *New horizons in the study of language and mind*, Cambridge University Press, Cambridge-New York.

Chomsky, Noam (2009), *Opening remarks*, in Piattelli-Palmarini, Massimo, Uriagereka, Juan, and Salaburu, Pello, eds, *Of Minds and Language. A Dialogue with Noam Chomsky in the Basque Country*, Oxford University Press, Oxford-New York, pp. 13-43.

Craver, Carl (2007), *Explaining the brain: Mechanisms and the mosaic unity of neuroscience*, Oxford University Press, Oxford-New York.

Dennett, Daniel (2005), «Cognitive wheels: The frame problem of AI», in *Language and Thought 3* (2005), p. 217.

Dennett, Daniel and Levin, Michael (2020), «Cognition all the way down», in <https://aeon.co/essays/how-to-understand-cells-tissues-and-organisms-as-agents-with-agendas>.

Dretske, Fred (1988), *Explaining Behaviour: Reasons in a World of Causes*, MIT Press, Cambridge-London.

Dretske, Fred (1993), *Misrepresentation*, in Goldman, Alvin I., ed., *Readings in philosophy and cognitive science*, MIT Press, Cambridge-London, pp. 297-314.

Dretske, Fred (2004), «Psychological vs. biological explanations of behaviour», in *Behavior and Philosophy*, n. 32, pp. 167-177.

Dusheck, Jennie (2002), «It's the ecology, stupid!», in *Nature*, n. 418, pp. 578-579.

Eldredge, Niles (1995), *Reinventing Darwin the Great Debate at the High Table of Evolutionary Theory*, Weidenfeld & Nicolson, London.

Emmeche, Claus (2011), *Organism and body: The semiotics of emergent levels of life*, in Emmeche, Claus, and Kull, Kalevi, eds, *Towards a Semiotic Biology. Life is the action of signs*, Imperial College Press, London, pp. 91-111.

Etxeberria, Arantza, and Umerez, Jon (2016), «Organismo y organización en la biología teórica: ¿vuelta al organicismo?», in *Ludus vitalis*, n. 14, pp. 3-38.

Fodor, Jerry (1975), *The language of thought*, Harvard University Press, Cambridge.

Fodor, Jerry (1990), *A theory of content and other essays*, MIT Press, Cambridge.

Gilbert, Scott (2001), «Ecological Developmental Biology: Developmental Biology Meets the Real World», in *Developmental Biology*, n. 1, pp. 1-12.

Gilbert, Scott (2005), «Mechanisms for the environmental regulation of gene expression: ecological aspects of animal development», in *Journal of biosciences*, n. 1, pp. 65-74.

Gilbert, Scott (2015), *Ecological developmental biology: the environmental regulation of development, health, and evolution*, Sinauer Associates, Sunderland.

Gilbert, Scott (2016), *Developmental Plasticity and Developmental Symbiosis: The Return of Eco-Devo*, in Wassarman, Paul M., eds, *Current Topics in Developmental Biology*, Elsevier, San Diego-Oxford-Amsterdam, pp. 415-433.

Gilbert, Scott (2017). «Ecological Developmental Biology», in *eLS*, John Wiley & Sons Ltd, Chichester, <http://www.els.net>.

Gilbert, Scott, and Bolker, Jessica (2003), «Ecological developmental biology: preface to the symposium 1», in *Evolution & Development*, n. 1, pp. 3-8.

Gilbert, Scott, Bosch, Thomas, and Ledón-Rettig, Cristina (2015), «Eco-Evo-Devo: developmental symbiosis and developmental plasticity as evolutionary agents», in *Nature Reviews Genetics*, n. 10, pp. 611-622.

Gilbert, Scott, and Epel, David (2015), *Ecological developmental biology: The Environmental Regulation of Development, Health, and Evolution. Second Edition*, Sinauer Associates, Sunderland.

Gilbert, Scott, and Tauber, Alfred (2016), «Rethinking individuality: the dialectics of the holobiont», in *Biology & Philosophy*, n. 6, pp. 839-853.

Giorgi, Franco, and Bruni, Luis E. (2015), «Developmental Scaffolding», in *Biosemitotics*, n. 2, pp. 173-189.

Gottlieb, Gilbert (1997), *Synthesizing Nature-nurture. Prenatal roots of instinctive behavior*, Lawrence Erlbaum Associates, Mahwah.

Gould, Stephen (1977), *Ontogeny and phylogeny*, Harvard University Press, Cambridge.

Gould, Stephen, and Lewontin Richard (1979), «The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme», in *Proceedings of the Royal Society of London. Series B. Biological Sciences*, n. 205, pp. 581-598.

Griesemer, James (2014), «Reproduction and the scaffolded development of hybrids», in *Developing scaffolds in evolution, culture, and cognition*, n. 17, p. 23-55.

Griffiths, Paul (2002), «What Is Innateness?», in *Monist*, n. 1, pp. 70-85.

Griffiths, Paul (2013), «Lehrman's dictum: Information and explanation in developmental biology», in *Developmental psychobiology*, n. 1, pp. 22-32.

Griffiths, Paul, and Knight, Robin (1998), «What Is the Developmentalist Challenge?», in *Philosophy of Science*, n. 2, pp. 253-258.

Griffiths, Paul, and Stotz, Karola (2006), «Genes in the Postgenomic Era», in *Theoretical Medicine and Bioethics*, n. 6, pp. 499-521.

Griffiths, Paul, and Stotz, Karola (2013). *Genetics and Philosophy. An Introduction*, Cambridge University Press, Cambridge-New York.

Haldane, John (1989), «Brentano's problem», in *Grazer Philosophische Studien*, n. 1, pp. 1-32.

Hall, Brian (1999), *Evolutionary Developmental Biology*, Springer, Dordrecht.

Harnad, Stevan (1990), «The symbol grounding problem», in *Physica D: Nonlinear Phenomena*, n. 1-3, pp. 335-346.

Heras-Escribano, Manuel (2020), «The evolutionary role of affordances: ecological psychology, niche construction, and natural selection», in *Biology & Philosophy*, n. 35, p. 1-27.

Heras-Escribano, Manuel, and De Pinedo-Garcia, Manuel (2018). «Affordances and Landscapes: Overcoming the Nature–Culture Dichotomy through Niche

Construction Theory», in *Frontiers in Psychology*, n. 8, <https://www.frontiersin.org/articles/10.3389/fpsyg.2017.02294/full>.

Hoffmeyer, Jesper (1997), *Signs of Meaning in the Universe*, Indiana University Press, Bloomington.

Hoffmeyer, Jesper (1998), «Surfaces inside surfaces. On the origin of agency and life». in *Cybernetics & Human Knowing*, n. 1, pp. 33-42.

Hoffmeyer, Jesper (2008a), Biology Is Immature Biosemiotics, in Sbrocchi, Leonard, ed., *Semiotics 2008*, Legas Publishing, Ottawa, pp. 927-942.

Hoffmeyer, Jesper (2008b), ed., *A Legacy for Living Systems. Gregory Bateson as Precursor to Biosemiotics. Vol. 2*, Springer, Dordrecht.

Hoffmeyer, Jesper (2008c), *Biosemiotics: An examination into the signs of life and the life of signs*, University of Chicago Press, Chicago.

Hoffmeyer, Jesper (2010), «A biosemiotic approach to the question of meaning», in *Zygon*, n. 2, pp. 367-390.

Hoffmeyer, Jesper (2011), *Biology Is Immature Biosemiotics*, in Emmeche, Claus, and Kull, Kalevi, eds, *Towards a Semiotic Biology*, Imperial College Press, London, pp. 43-65.

Hoffmeyer, Jesper (2012), «The Natural History of Intentionality. A Biosemiotic Approach», in *Biosemiotics*, n. 1, Springer, Dordrecht, pp. 97-116.

Hoffmeyer, Jesper, and Kull, Kalevi (2003), *Baldwin and biosemiotics: What intelligence is for*, in Weber, Bruce H., and Depew, David J., eds, *Evolution and learning: The Baldwin effect reconsidered*, MIT Press, Cambridge, pp. 253-272.

Hutto, Daniel, and Myin Erik (2013), *Radicalizing enactivism: basic minds without content*, MIT Press, Cambridge.

Hutto, Daniel, and Satne, Glenda (2015), «Introduction: Searching for the Natural Origins of Content», in *Philosophia*, n. 3, pp. 505-519.

Jablonka, Eva (2007), «The developmental construction of heredity», in *Developmental Psychobiology*, n. 8, pp. 808-817.

Jablonka, Eva, and Lamb, Marion J. (2014), *Evolution in Four Dimensions, Revised Edition: Genetic, Epigenetic, Behavioral, and Symbolic Variation in the History of Life*, MIT Press, Cambridge-London.

Jesus, Paulo De (2016), «From enactive phenomenology to biosemiotic enactivism», in *Adaptive Behavior*, n. 2, pp. 130-146.

Keller, Evelyn Fox (2000), *The century of the gene*, Harvard University Press, Cambridge.

Keller, Evelyn Fox (2010), *The mirage of a space between nature and nurture*, Duke University Press, Durham.

Keller, Evelyn Fox (2014), «From gene action to reactive genomes», in *The Journal of Physiology*, n. 11, pp. 2423-2429.

Kiverstein, Julian, and Clark, Andy (2009), «Introduction: Mind embodied, embedded, enacted: One church or many?», in *Topoi*, n. 1, pp. 1-7.

Klopfer, Peter H (2001), *Parental care and development*, in Russell, Grey D., Griffiths, Paul E., and Oyama, Susan, eds, *Cycles of Contingency: Developmental Systems and Evolution*, MIT Press, Cambridge, pp. 167-173.

Kull, Kalevi (1999), «Biosemiotics in the twentieth century: A view from biology», in *Semiotica*, n. 1-4, pp. 385-414.

Kull, Kalevi (2001), «Jakob von Uexküll: an introduction», in *Semiotica*, n. 134, pp. 1-59.

Kull, Kalevi (2009), «Biosemiotics: To know, what life knows», in *Cybernetics and Human Knowing*, n. 3-4, pp. 81-88.

Kull, Kalevi, Deacon, Terrence, *et al.* (2011), *Theses on Biosemiotics: Prolegomena to a Theoretical Biology*, in Emmeche, Claus, and Kull, Kalevi, eds, *Towards a Semiotic Biology. Life is the Action of Signs*, Imperial College Press, London, pp. 25-41.

Kull, Kalevi, Emmeche, Claus, *et al.* (2011), *Why biosemiotics? An introduction to our view on the biology of life itself*, in Emmeche, Claus, and Kull, Kalevi, eds, *Towards a semiotic biology. Life is the action of signs*, Imperial College Press, London, pp. 1-21.

Kuo, Zing Yang (1976), *The dynamics of behavior development: an epigenetic view*, Random House, New York.

Laland, Kevin, Matthews, Blake, *et al.* (2016), «An introduction to niche construction theory», in *Evolutionary Ecology*, n. 2, pp. 191-202.

Laland, Kevin, and Sterelny, Kim (2006), «Perspective: seven reasons (not) to neglect niche construction», in *Evolution*, n. 9, pp. 1751-1762.

Lehrman, Daniel (1953), «A Critique of Konrad Lorenz's Theory of Instinctive Behavior», in *The Quarterly Review of Biology*, n. 4, pp. 337-363.

Levins, Richard, and Lewontin, Richard (1985), *The dialectical biologist*, Harvard University Press, Cambridge.

Lewontin, Richard (1974a), «Annotation: the analysis of variance and the analysis of causes», in *American Journal of Human Genetics*, n. 3, pp. 400-411.

Lewontin, Richard (1974b), *The genetic basis of evolutionary change*, Columbia University Press, New York.

Lewontin, Richard (1978), «Adaptation», in *Scientific American*, n. 3, pp. 212-230.

Lewontin, Richard (1983a), *Gene, organism and environment*, in Bendall, Derek S., ed., *Evolution from molecules to men*, Cambridge University Press, Cambridge, p. 273-286.

Lewontin, Richard (1983b), «The Organism as the Subject and Object of Evolution», in *Scientia*, n. 1-8, pp. 65–95.

Lewontin, Richard (2000), *The triple helix: Gene, organism, and environment*, Harvard University Press, Cambridge.

Lewontin, Richard (2001), *It Ain't Necessarily So: The Dream of the Human Genome and Other Illusions*, New York Review of Books, New York.

Lewontin, Richard, and Levins, Richard (1997), «Organism and environment», in *Capitalism Nature Socialism*, n. 2, pp. 95-98.

Lorenz, Konrad (1986), *Evolution and modification of behavior*, University of Chicago Press, Chicago.

Lorenzo, Guillermo (2018), «Long-distance paradox and the hybrid nature of language». in *Biosemiotics*, n. 3, pp. 387-404.

Markoš, Anton (2002), *Readers of the book of life. Conceptualizing evolutionary developmental biology*, Oxford University Press, New York.

Markoš, Anton (2009), *Excerpts from Readers of the Book of Life*, in Favareau, D., ed., *Essential Readings in Biosemiotics*, Springer, pp. 657–696.

Marr, David (1982), *Vision*, W.H. Freeman, New York.

Mayr, Ernst (1961), «Cause and Effect in Biology: Kinds of causes, predictability, and teleology are viewed by a practicing biologist», in *Science*, n. 134, pp. 1501-1506.

Mayr, Ernst (1974), *Teleological and Teleonomic, a New Analysis*, in Cohen, Robert S., and Wartofsky, Marx W., eds, *Methodological and Historical Essays in the Natural and Social Sciences*, Springer, Dordrecht, pp. 91-117.

Millikan, Ruth (1984), *Language, thought, and other biological categories. New foundations for realism*, MIT press, Cambridge.

Millikan, Ruth (1989), «In defense of proper functions», in *Philosophy of science*, n. 2, pp. 288-302.

Millikan, Ruth (2000), *Biofunctions: Two Paradigms*, in Ariew, Andrew, Cummins, Robert, and Perlman, Mark, eds, *Functions. New Essays in the Philosophy of Psychology and Biology*, Oxford University Press, New York, pp. 113-143.

Moczek, Armin P. (2008), «On the origins of novelty in development and evolution», in *BioEssays*, n. 30, pp. 432-447.

Moss, Lenny (2003), *What genes can't do*, MIT Press, Cambridge.

Neander, Karen (1991), «Functions as Selected Effects. The Conceptual Analyst's Defense», in *Philosophy of Science*, n. 2, pp. 168-184.

Neander, Karen (1995), «Misrepresenting & malfunctioning», in *Philosophical Studies*, n. 2, 109-141.

Neander, Karen (2007), *Biological approaches to mental representation*, in Matthen, Mohan, and Stephens, Christopher, eds, *Philosophy of biology*, Elsevier, Amsterdam, pp. 549-565.

Neander, Karen (2017), *A Mark of the Mental*, MIT Press, Cambridge.

Newell, Allen, and Herbert, Simon (1972), *Human Problem Solving*, Prentice Hall, Englewood Cliffs.

Newman, Stuart A. (2014), *Excitable media in medias res: How physics scaffolds metazoan development and evolution*, in Caporael, Linnda R., Griesemer, James R., and Wimmsatt, William C., eds, *Developing scaffolds in evolution, culture and cognition*, MIT Press, Cambridge, pp. 109-123.

Nicholson, Daniel J (2012), «The concept of mechanism in biology», in *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, n. 1, pp. 152-163.

Nicholson, Daniel J (2014), «The return of the organism as a fundamental explanatory concept in biology», in *Philosophy Compass*, n. 5, pp. 347-359.

Nicholson, Daniel, and Gawne, Richard (2015), «Neither logical empiricism nor vitalism, but organicism: what the philosophy of biology was», in *History and Philosophy of the Life Sciences*, n. 4, pp. 345-381.

Odling-Smee, John, *et al.* (2013), *Niche construction: the neglected process in evolution (MPB-37)*, Vol. 37, Princeton University Press, Princeton.

Oppenheim, R. W. (1981), *Ontogenetic adaptations and retrogressive processes in the development of the nervous system and behavior: A neuroembryological perspective*, in Connolly, Kevin J., ed., *Maturation and development: Biological and psychological perspectives*, Cambridge University Press, Cambridge, pp. 73-109.

Oyama, Susan (1985), *The Ontogeny of Information*, Duke University Press, Durham.

Oyama, Susan (2000), «Causal democracy and causal contributions in developmental systems theory», in *Philosophy of Science*, n. 67, pp. 332-347.

Oyama, Susan, *et al.* (2001), *Cycles of contingency: developmental systems and evolution*, MIT Press, Cambridge.

Papineau, David (2018), *Teleosemantics*, in Smith, David Livingstone, ed., *How Biology Shapes Philosophy. New Foundations for Naturalism*, Cambridge University Press, Cambridge, pp. 95-120.

Pattee, Howard (2008), *The necessity of biosemiotics. Matter-symbol complementarity*, in Barbieri, Marcello, ed., *Introduction to biosemiotics*, Springer, Dordrecht, pp. 115-132.

Pattee, Howard (2012), *Cell psychology: an evolutionary approach to the symbol-matter problem*, in Pattee, Howard, and Rączaszek-Leonardi, Joanna, *Laws, Language and Life*, Springer, Dordrecht, pp. 165-179.

Pradeu, Thomas (2011), *The limits of the self: immunology and biological identity*, Oxford University Press, New York.

Pylyshyn, Zenon (1984), *Computation and cognition: Towards a foundation for cognitive science*, MIT Press, Cambridge.

Reed, Edward S. (1996), *Encountering the world: Toward an ecological psychology*, Oxford University Press, New York.

Reid, Robert (2007), *Biological emergences: evolution by natural experiment*, MIT Press, Cambridge.

Rheinberger, Hans-Jorg, and Muller-Wille, Staffan (2018), *The Gene: from Genetics to Postgenomics*, The University of Chicago Press, Chicago.

Robbins, Philip, and Aydede, Murat (2008), ed., *The Cambridge Handbook of Situated Cognition (Cambridge Handbooks in Psychology)*, Cambridge University Press, Cambridge.

Rosenberg, Alex (1997), «Reductionism redux: computing the embryo», in *Biology and Philosophy*, n. 4, pp. 445-470.

Searle, John (1980), «Minds, Brains and Programs», in *Behavioral and Brain Sciences*, n. 3, pp. 417-457.

Scott-Phillips, Thomas C., et al. (2014), «The Niche Construction Perspective: A critical appraisal», in *Evolution*, n. 5, pp. 1231-1243.

Sebeok, Thomas (1986), «The problem of the origin of language in an evolutionary frame», in *Language Sciences*, n. 2, pp. 169-176.

Sebeok, Thomas (2010), *Biosemiotics: Its roots, proliferation and prospect*, in Favareau, D., ed., *Essential Readings in Biosemiotics*, Springer, Dordrecht, pp. 217-236.

Shea, Nicholas (2007), «Representation in the genome and in other inheritance systems», in *Biology & Philosophy*, n. 3, pp. 313-331.

Shea, Nicholas (2013), «Inherited representations are read in development», in *The British journal for the philosophy of science*, n. 1, pp. 1-31.

Sober, Elliott (1984), *The nature of selection: evolutionary theory in philosophical focus*, University of Chicago Press, Chicago.

Spelke, Elizabeth S., and Kinzler, Katherine D. (2007), «Core knowledge», in *Developmental Science*, n. 1, pp. 89-96.

Sperber, Dan (2000), *Metarepresentations in an evolutionary perspective*, in Sperber, Dan, *Metarepresentations: A multidisciplinary perspective*, Oxford University Press, New York, pp. 117-137.

Sterelny, Kim (2003), *Thought in a hostile world: the evolution of human cognition*, Blackwell, Oxford.

Sterelny, Kim (2010), «Minds: extended or scaffolded?» in *Phenomenology and the Cognitive Sciences*, n. 4, pp. 465-481.

Stotz, Karola (2006), «With ‘Genes’ Like That, Who Needs an Environment? Postgenomics’s Argument for the ‘Ontogeny of Information’», in *Philosophy of Science*, n. 5, pp. 905-917.

Stotz, Karola (2010), «Human nature and cognitive–developmental niche construction», in *Phenomenology and the Cognitive Sciences*, n. 4, pp. 483-501.

Sultan, Sonia (2003), «Commentary: the promise of ecological developmental biology», in *Journal of Experimental Zoology Part B: Molecular and Developmental Evolution*, n. 1, pp. 1-7.

Sultan, Sonia (2007), «Development in context: the timely emergence of eco-devo», in *Trends in Ecology & Evolution*, n. 11, pp. 575-582.

Sultan, Sonia (2015), *Organism and environment : ecological development, niche construction, and adaptation*, Oxford University Press, New York.

Sultan, Sonia (2017a), «Developmental plasticity: re-conceiving the genotype», in *Interface Focus*, n. 7, <https://royalsocietypublishing.org/doi/pdf/10.1098/rsfs.2017.0009>.

Sultan, Sonia (2017b), *Eco-Evo-Devo*, in Nuno de la Rosa, Laura, and Müller, Gerd, eds, *Evolutionary Developmental Biology*, Springer, Dordrecht, pp. 1-13.

Sultan, Sonia, and Stearns, Stephen (2005), *Environmentally contingent variation: phenotypic plasticity and norms of reaction*, in Hallgrímsson, Benedikt, and Hall, Brian, eds, *Variation. A Central Concept in Biology*, Elsevier, Amsterdam, pp. 303-332.

Thompson, Evan (2007), *Mind in life: biology, phenomenology, and the sciences of mind*, Harvard University Press, Cambridge.

Uexküll, Jakob J. von (1923), «Weltanschauung und Gewissen», in *Deutsche Rundschau*, n. 197, pp. 253-266.

Wagner, Gunter (2014), *Homology, Genes, and Evolutionary Innovation*, Princeton University Press, Princeton.

Walsh, Denis (2000), «Chasing shadows: natural selection and adaptation», in *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, n. 1, pp. 135-153.

Walsh, Denis (2007), *Development. Three grades of ontogenetic involvement*, in Matthen, Mohan, and Stephens, Christopher, eds, *Philosophy of biology*, Elsevier, Amsterdam, pp. 179-199.

Walsh, Denis (2008), *Teleology*, in Ruse, Michael, ed., *The Oxford Handbook of Philosophy of Biology*, Oxford University Press, New York, pp. 113-137.

Walsh, Denis (2012), *Situated adaptationism*, in Kabasenche, William P., O'Rourke, Michael, and Slater, Matthew H., eds, *The environment: Philosophy, science, and ethics*, MIT Press, Cambridge, pp. 89-116.

Walsh, Denis (2013), *The Affordance Landscape: The Spatial Metaphors of Evolution*, in Wolfe, Charles T., Huneman, Philippe, and Reydon, Thomas A. C., eds, *History, Philosophy and Theory of the Life Sciences*. Springer Netherlands, pp. 213-236.

Walsh, Denis (2015), *Organisms, Agency, and Evolution*, Cambridge University Press, Cambridge.

West-Eberhard, Mary Jane (2003), *Developmental plasticity and evolution*, Oxford University Press, New York.

West-Eberhard, Mary Jane (2005), «Developmental plasticity and the origin of species differences», in *Proceedings of the National Academy of Sciences*, n. 102. suppl. 1, pp. 6543-6549.

West, Meredith J., and King, Andrew P. (1987), «Settling nature and nurture into an ontogenetic niche», in *Developmental Psychobiology*, n. 5, pp. 549-562.

West, Meredith J., King, Andrew P., and White, David J. (2003), «The case for developmental ecology», in *Animal Behaviour*, n. 4, pp. 617-622.

Wimsatt, William C., and Griesemer, James R. (2007), *Reproducing entrenchments to scaffold culture: The central role of development in cultural evolution*, in Sansom, Roger, and Brandon, Robert N., eds, *Integrating evolution and development. From theory to practice*, MIT Press, Cambridge, pp. 227-323.

Withagen, Rob, and Wermeskerken, Margot van (2010), «The role of affordances in the evolutionary process reconsidered: A niche construction perspective», in *Theory & Psychology*, n. 4, pp. 489-510.

Wolpert, Lewis (1994), «Do we understand development?», in *Science*, n. 266, pp. 571-573.