

Chapter 10

Organization and Inheritance in Twenty-First-Century Evolutionary Biology



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Abstract During the last few years, various authors have called for the elaboration of a theoretical framework that would better take into account the role of organisms in evolutionary dynamics. In this paper, I argue that an organism-centered evolutionary theory, which implies the rehabilitation of an organizational thinking in evolutionary biology and should be associated with what I will call a heuristic of collaboration, may be completed by an organizational perspective of biological inheritance. I sketch this organizational perspective – which allows going beyond gene-centrism –, show how it grounds a systemic concept of heritable variation suited to the new evolutionary framework, and highlight some of its explanatory value and theoretical implications for evolutionary thinking.

10.1 Introduction

The gene-centered theory of evolution is sometimes presented as obsolete. Associated with twentieth century's modern synthesis, it is accused to overlook the role of organisms and of their properties in evolutionary dynamics (Walsh, 2006; Nicholson, 2014). Many authors have therefore recently called for the elaboration of a more organism-centered evolutionary biology (Walsh, 2010; Laland et al., 2015), notably in the context of an extended evolutionary synthesis (Pigliucci & Müller, 2010). Such biology is notably expected to integrate non-genetic channels of inheritance in its models but also to make some room to the concept of agency (Walsh, 2015) and biological organization (Müller, 2017) insofar as organisms – at the center of its preoccupations – are generally considered as paragons of organized and purposive biological systems. The objective of this paper is to argue that an organism-centered evolutionary biology may be enriched by a not only extended but also organizational perspective of biological inheritance, to sketch this perspective and to highlight its theoretical implications for evolutionary thinking.

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The argument is structured as follows. In Sect. 10.2, I briefly present the contemporary literature which invites departing from a gene-centered evolutionary theory and embracing a more organism-centered framework. I further suggest that an organizational perspective of biological inheritance appears as a missing ingredient in this theoretical movement that not only involves the return of an organizational thinking in evolutionary biology but that also follows a more global perspective shift, from a heuristic of replication – in which evolution is thought as a competition among self-replicating objects endowed with their own adaptive value – toward a heuristic of collaboration – in which biological objects are necessarily considered as parts of integrated wholes and cannot replicate independently. In Sect. 10.3, I rest on earlier studies (Pontarotti, 2015; Mossio & Pontarotti, 2019) to sketch an organizational perspective of biological inheritance suited to an organism-centered evolutionary biology, and I notably highlight that this perspective grounds a systemic concept of heritable variation appropriate to the new evolutionary biology’s framework. In Sect. 10.4, I evoke some theoretical implications of an organizational account of inheritance for evolutionary thinking. I show how this account allows making sense of the evolution of “non-standard” biological systems¹ and how it induces a change of perspective, in the wake of earlier contributions, as far as lineages, fitness, selection, and evolution are concerned.

10.2 Toward a More Organization-Centered Framework for Twenty-First-Century Evolutionary Biology

In this Section, I briefly present the literature announcing a perspective shift, from gene-centrism toward organism-centrism, in evolutionary biology. I then highlight that an organism-centered evolutionary biology is expected to make important room for the concept of organization in its explanations. Consequently, I argue that it may be completed by an organizational perspective of biological inheritance.

10.2.1 An Extended Evolutionary Synthesis to Fill in the Explanatory Gaps of the Gene-Centered Framework

The theoretical framework of evolutionary biology has been seriously challenged for the last few years. Many authors have indeed advocated the necessity to adopt an extended evolutionary synthesis (EES) in order to overcome some of the theoretical and explanatory limitations of modern synthesis (MS) (Pigliucci & Müller, 2010).

¹The concept of non-standard biological systems usually refers to symbiotic associations or to insect colonies including abiotic parts (mounds). Here, it will designate all biological systems whose parts cannot simply be accounted by classical interactionist accounts (gene/environment). For more details, see Sect. 10.4.

EES is described as a movement of conceptual and disciplinary extension (Pigliucci & Müller, 2010) but also as an alternative ecological-developmental perspective to evolution (Laland et al., 2015). In this respect, EES is not just an extension of MS but rather a “distinctively different framework for understanding evolution” (Laland et al., 2015). EES is meant to be more inclusive than MS. Indeed, while the latter makes sense of evolutionary phenomena through the articulation of Neo-Darwinism, Mendelism, and population genetics,² the former is willing to include new elements in evolutionary thinking, notably concepts of evolutionary-developmental biology (e.g., plasticity), an extended vision of inheritance, as well as ideas about evolvability (Pigliucci, 2009, p. 218).

Let us go into more details. While MS ignores developmental processes, EES intends to shed light on the developmental origin of organismal variations. It stresses on the role of developmental constraints regarding the diversification of forms³ (Müller, 2017) and that of plasticity – “the capacity of organisms to develop altered phenotypes in reaction to different environmental conditions” (Müller, 2017, p. 5) – on evolutionary dynamics. Besides, while MS is based on a genetic account of inheritance according to which the trans-generational reoccurrence of features is exclusively underpinned by the replication of genes, EES integrates data about so-called non-genetic inheritance, for example, epigenetic and behavioral transmission. The framework also takes into account niche construction (Laland et al., 2015), namely, the fact that organisms modify their surroundings in such a way that they alter the selection pressure exerted on their offspring (Odling-Smee et al., 2003). This inclusion stresses on the “reciprocal causality” (Müller, 2017) at play in evolution, which means that organisms are not only submitted to independent selective forces but that they also define the selective pressures exerted on them and their offspring.

More generally, EES is meant to go beyond some “basic restrictions and methodological commitments” of MS (Pigliucci & Müller, 2010, p. 13). According to MS, evolution is a gradual process mainly driven by the selection of small and random genetic variations correlated with phenotypic differences (Mayr, 1998). ESS, as for it, intends to overcome gradualism (Pigliucci & Müller, 2010; Laland et al., 2015; Müller, 2017) in highlighting that evolutionary change can follow various paths (Pigliucci & Müller, 2010). As mentioned above, EES also aims at going beyond externalism, the hypothesis according to which independent selection

²Beyond the articulation of Mendelian genetics and Neo-Darwinian evolutionary theory through the mediation of population genetics, MS refers to the agreement of various disciplines – systematics, zoology, botany, paleontology, and natural history – on a set of core hypothesis (e.g., gradualism, creativity of natural selection, etc.).

³It is important to make a clear distinction between the hypothesis of organismal origin of variation, according to which variation is originated and constrained by organisms themselves (and their developmental processes), and trade-off adaptationism, which states that organisms are trade-offs of adapted traits (e.g., trades between traits enhancing survival and traits enhancing reproduction). In the first case, organisms (and developmental processes) impose constraints on variation and have a key explanatory value in evolutionary theory. In the second case, natural selection is still the main explanans of organismal characteristics (for a detailed analysis, see Huneman, 2017).

pressures are the main drivers of evolutionary change (Pigliucci & Müller, 2010; Müller, 2017). Finally, while MS is based on statistical analysis, EES appears as a causal-mechanistic framework (Pigliucci & Müller, 2010). In this perspective, evolution is not primarily portrayed as a change in gene frequencies mainly caused by natural selection (Dobzhansky, 1937) but as a change in phenotypes partly driven by developmental processes (Helanterä & Uller, 2010). These processes are thought to “share responsibility” with natural selection in the determination of evolutionary trajectories (direction and rate of evolution, origin of variation, etc.) (Laland et al., 2015). Genes, as for them, are sometimes described as followers (West-Eberhard, 2003; Pigliucci, 2009).

10.2.2 Focus on Organisms and Introduction of an Organizational Thinking

In this context, the focus of evolutionary biology changes radically. Evolution is not anymore thought as a matter of genetic dynamics but rather of organismal changes. Organisms – which are often described as developmental systems – appear as key causal agents in evolution. As summarized by Laland and colleagues (2015), EES is “characterized by the central role of the organism in the evolutionary process and by the view that the direction of evolution does not depend on selection alone and need not start with mutation.” While MS explains biological evolution by focusing on the scale of genes, ESS is grounded on the assumption that “the organisms themselves represent the determinants of selectable variation and innovation” (Pigliucci & Müller, 2010, p. 13). In brief, EES represents a “different way of thinking about evolution, historically rooted in the organicist tradition” (Müller, 2017). As a result, it is meant to better take into account the role of organisms’ properties in the determination evolutionary trajectories.

On this specific point, the literature about EES meets other studies dedicated to the return of organisms in evolutionary biology (Bateson, 2005; Walsh, 2006, 2015).⁴ For example, Walsh (2006) analyzes that contemporary evolutionary biology has forgotten organisms in asking how supra-organismal entities (populations) change under the effect of sub-organismal entities (genes, replicators). He calls for the development of a Kantian-flavored biology which would take into account organismal properties in its explanations. Inspired by West-Eberhard’s contribution (2003), Walsh also suggests that phenotypic accommodation can sometimes precede genotypic one, and that genes can thus be followers in evolution (Walsh, 2006, p. 778). In a way, all these contributions follow considerations early on made by Mayr (1963, p. 184), who claimed that changes in gene frequencies is an effect and not a cause of evolution. To him, describing evolution as a change in gene

⁴For a general appraisal regarding the return of organisms in evolutionary biology, see Huneman (2010) and Nicholson (2014).

frequencies amounts to neglect the mechanisms that cause organisms and populations' transformations.

To sum up, “the emerging view of evolution” presents organisms as “the primary agents of evolutionary change” (Nicholson, 2014). In this perspective, organisms are thought as a major *explanans* – and not only *explanandum* – of evolutionary processes (Huneman, 2010); organismal properties do not only appear as elements that should be explained, but they are also – and crucially – conceived as elements which contribute to the explanation of evolutionary phenomena. Now, if one considers, in line with an old tradition usually thought of as tracing back to Kant (1790), that the most fundamental and distinctive property of organisms is to be (self)organized, the emerging view of evolution should involve the rehabilitation of the concept of organization and the introduction of an organizational thinking in evolutionary biologists' toolkit.

10.2.3 *From a Heuristic of Replication to a Heuristic of Collaboration*

These elements, I argue, are part of a more global perspective shift that is more or less implicitly announced in the literature. Such shift takes its distance with what I will hereinafter call a *heuristic⁵ of replication* (atomistic, gene-eye view) and embraces what I will name a *heuristic of collaboration* (systemic view).

The *heuristic of replication*, embodied by Dawkins's work on the selfish gene (1976, 1982), states that evolution can be conceived as a process mainly driven by the selection of virtually⁶ atomized units endowed with intrinsic capacities of self-replication and with their own adaptive value. It corresponds to what Walsh (2015) calls the Replicator biology. The *heuristic of collaboration*, as for it, rests on the hypothesis that biological objects cannot be considered otherwise than as parts of integrated wholes: they cannot replicate, evolve, and have any adaptive value independently from these wholes. In other words, this heuristic implies that heritable variations cannot be considered as virtually atomized traits correlated to virtually atomized genes (or replicators) but rather as parts of systems including interdependent elements.

The push toward the heuristic of collaboration subtly emerged in various contributions. It notably appeared in Gould and Lewontin's (1979) critique of the adaptationist program which considers organisms as aggregates of virtually atomized

⁵A heuristic is not a faithful account of reality but rather a theoretical tool that is supposed to help scientists grasping something from the objects that they study.

⁶The adverb “virtually” should be understood in the context of a given heuristic. It denotes the fact that even if biologists have always been aware that evolution takes place among organisms and that heritable variations are necessarily located in integrated biological systems, these elements were overlooked in theoretical models (see, e.g., Dobzhansky, 1970, p. 65, who recognizes the limits of considering traits as independent entities).

traits. It was also expressed in Lewontin's argument according to which the only biological entities able to self-replicate are not genes but organisms as complex systems (1993) or in developmental systems theory, which states that full developmental systems, and not genes alone, can replicate (Griffiths & Gray, 1994). More recently and in a similar vein, Fox Keller noted that DNA is neither stable nor able to replicate independently from a full cellular machinery (2000, pp. 26–27). Turner (2000, 2004), as for him, proposed a physiological interpretation of Dawkins' extended phenotype (1982). He argued that selection does not target replicators but rather whole systems able to self-maintain through the collaboration of various internal and external physiological parts which specify how flows of matter and energy are channeled. Finally, one can mention Walsh's (2010) elaboration of an alternative Neo-Darwinism that would not focus on replicators but on organisms and the various calls that are made for a "shift toward a network thinking" in evolutionary biology (Baptiste & Huneman, 2018). Even if all these approaches should not be conflated, they all reflect some endeavor toward the elaboration of an evolutionary biology focusing on integrated wholes and on networks and not on atomized objects, be they genes, or traits associated with these genes.

10.2.4 A Missing Organizational Perspective of Biological Inheritance?

Finally, the integration of an organizational thinking in evolutionary biology cannot be limited to the inclusion of organismal properties (and developmental timescales) in theoretical models. It might also require the integration of organizational concerns at the level of inheritance, which is traditionally thought as a key element for evolution (Lewontin, 1970; Sterelny, 2001).

It is generally asserted that EES notably relies on an extended vision of inheritance (Pigliucci & Müller, 2010; Laland et al., 2015). This means that the framework takes into account, in addition to genetic replication and transmission, various channels involved in the reoccurrence of traits across generations (Jablonka & Lamb, 2005; Danchin et al., 2011). Epigenetic inheritance (through the maintenance of epigenetic marks such as DNA methylation) can underpin the return of phenotypic outcomes such as defense against predators and pathogens (Holeski et al., 2012) and floral symmetry (Cubas et al., 1999). Behavioral inheritance takes place when social interactions mediate the reoccurrence of behavioral traits (Galef & Laland, 2005), notably those involved in the determination of the feeding niche (Slagsvold & Wiebe, 2007). Symbiotic transmission, which can be considered as a second mode of genetic inheritance (Gilbert et al., 2012), is linked, in many insects, to the trans-generational maintenance of metabolic capacities (Douglas, 2009).

The integration, in the evolutionary framework, of multifarious channels of inheritance and therefore of multifarious heritable variations⁷ could have major theoretical consequences. It could notably weaken the statement that heritable variation is always small and random (Jablonka & Lamb, 2005). In this respect, it would damage the MS's core hypothesis which states that natural selection of small and random heritable variation is the main determinant of evolutionary change.⁸ However, the inclusion of extended inheritance into evolutionary theory comes with some requirements. First, it demands the *elaboration of a consistent theoretical framework* regarding inheritance. This framework should include more than genetic mechanisms, but it should not result from a mere cumulative approach (Merlin, 2017) which would basically consist in integrating, into biological legacies, anything that appears as a “good” transmitted across generations (developmental resources, developmental factor, source of information). Such approach would make sense from a metaphorical point of view,⁹ but it would be theoretically unsatisfactory insofar as it would turn inheritance into a vague, ill-defined concept (Mossio & Pontarotti, 2019). Some of the accounts of extended inheritance outlined during the last few years have intended to establish this consistent framework (Griesemer, 2000; Jablonka, 2002; Pontarotti 2015; Mossio & Pontarotti, 2019).

Second, one could also consider that a framework suited to an evolutionary biology characterized by an organizational thinking should make some room to the concept of organization. While different extended perspectives of inheritance could be compatible with the emerging view of evolution, an organizational approach, beyond overcoming genocentrism, would be fully consistent with an organization-minded evolutionary biology. Besides, it would notably present the advantage of implying a theoretically fecund *systemic* concept of heritable variation, as explained in Sect. 10.3. In this respect, it would unambiguously participate in the perspective shift from a *heuristic of replication* (atomistic, gene-eye view) to a *heuristic of collaboration* (systemic view).

⁷Inheritance usually refers to the transmission of traits – eye color and liver metabolic capacities – across generations of organisms. When compared with other instances in the population, these traits can be considered as heritable *variations*. For example, we can say that inheritance is responsible for the recurrence of a *trait* like a specific eye color in a lineage but also that it is responsible for the recurrence of variation in eye color when the whole population is taken into account. This variation can be linked to differential adaptive value. On this topic, Mameli (2005, p. 367) makes a distinction between inheritance of features and inheritance of differences (“‘trait’ can be used to refer to a particular value (being 176 cm tall) as well as to sets of possible values (height)”.)

⁸This consequence is made obvious by a famous historical episode: that of the temporary eclipse of Darwinism at the dawn of the twentieth century, caused by the mutationist vision of heritable variation adopted by the first Mendelians (Huxley, 2010 [1942], p. 22; Gayon, 1992a, p. 14).

⁹It is useful to remind that, according to historians, biological inheritance was initially a metaphorical concept (López-Beltrán, 1994; van der Lugt & de Miramon, 2008). It was indeed imported from the legal sphere into the medical vocabulary to refer to diseases that appeared to be transmitted like goods from parents to offspring.

10.3 An Organizational Perspective of Biological Inheritance

In this section, I present an organizational account of inheritance that has been elaborated in earlier studies (Pontarotti, 2015; Pontarotti 2017; Mossio & Pontarotti, 2019). I show that, beyond overcoming genocentrism, opening a way to explain organisms' stability and bounding the phenomenon of biological (extended) inheritance, this account appears as a key ingredient for an organism- and organization-centered evolutionary biology grounded on a heuristic of collaboration.

10.3.1 *Principles of an Organizational Perspective of Biological Inheritance*

The organizational account of biological inheritance is grounded on recent theoretical studies dedicated to biological autonomy and putting emphasis on the concept of biological organization (Mossio & Moreno, 2010; Montévil & Mossio, 2015; Moreno & Mossio, 2015). These studies place themselves in the wake of earlier contributions which conceive of biological systems as organized beings (Kant, 1790; Bichat, 1801; Bernard, 1885; Bertalanffy, 1968; Kauffman, 1995).¹⁰ According to them, biological systems include differentiated parts (cells, tissues, organs) that collaborate in order to maintain the system to which they belong.

In this view, biological systems are more precisely conceptualized as far from equilibrium open thermodynamical systems which maintain themselves through exchanges of matter and energy with their environment. They display differentiated parts that are interdependent¹¹ for their maintenance and that collectively channel flows of matter and energy so as to maintain themselves and the system to which they belong. These parts are called functional constraints insofar as they are said to perform biological function (Mossio et al., 2009). They notably display stability with respect to the process they harness in a given system (Montévil & Mossio, 2015). For example, the cardiovascular system can be depicted as an organized (or functional) constraint given that (1) it contributes to channel flows of matter and energy in the organism, (2) it is dependent on the organisms' other parts (e.g., the digestive system, the respiratory system, etc.) to maintain the organism (and, thereby, itself) as a whole, and (3) it exhibits stability with respect to the process that it harnesses, namely, blood circulation.

¹⁰It is important to specify that these contributions are not equivalent even if they all conceive of living beings as organized ones. To Kant, for example, purposiveness and "self-organization" are regulative concepts necessary to make sense of the movement observed in some natural objects. This transcendental consideration is not endorsed by the other authors. In addition, while Bichat considers that living beings are animated by vital forces, Bernard rejects this concept. Bertalanffy's approach, as for it, is characterized by thermodynamics considerations.

¹¹ See Sect. 10.4 for an analysis of the concept of "interdependence".

The constraints that constitute an organized system are involved in a Kantian-flavored circular causality: they produce each other in the system that they contribute to maintain and which reciprocally contributes to their maintenance. The loop of interdependencies among a set of constraints is referred to as “organizational closure”. Organization, in this context, is defined as closure of constraints and is associated with intrinsic teleology (Mossio & Bich, 2014).

Organization as closure of constraints is a theoretical principle that allows explaining how a biological system maintains itself in an environment with which it exchanges flows of matter and energy. In this respect, it plays the role of *explanans* for the stability of biological systems and their constitutive parts. The theoretical principle of organization as closure of constraints can therefore be used to conceive of biological inheritance, which traditionally refers to the like-begets-like phenomenon (Darwin, 1859) and more globally to the idea of trans-generational stability.

From an organizational point of view, biological inheritance refers to the continuity, across generation breaks, of organizational patterns displayed by biological systems (Mossio & Pontarotti, 2019). It does not primarily designate the reoccurrence of – virtually atomized – traits underpinned by the replication of, virtually atomized, genetic factors but rather the trans-generational *conservation of functional networks*.¹² Because organized constraints collectively channel flows of matter and energy in such a way that they maintain themselves and the system to which they belong, inheritance can also be described, in this context, as the cross-generation conservation of specific regimes of flow of matter and energy channeling (Pontarotti, 2017).

10.3.2 *Inheritance and Organization: Toward the Conception of Multifarious Heritable Variations*

The organizational perspective of inheritance is compatible with the hypothesis according to which inherited objects can be multifarious: traditional organs such as hearts but also epigenetics marks, external artifacts produced by organisms or symbionts. As argued elsewhere (Pontarotti, 2016; Mossio & Pontarotti, 2019), the concept of (inherited) organized constraints is abstract enough to be applied to objects

¹²One may object that the concept of constraints is too narrow to include, in biological legacies, elements that appear as not functional but that are traditionally thought as heritable (e.g., short-sightedness). The question of inheritance of *prima facie* nonfunctional or dysfunctional traits has been addressed in another paper (Mossio & Pontarotti, 2019). To sum up, from an organizational point of view, heritable dysfunctional objects are still falling under the definition of constraint when they contribute to the maintenance of a given organizational regime, even if it is in a poorer way (e.g., short-sightedness refers to a poorer way of perceiving the environment). Besides, non-functional traits (e.g., eye color) are considered as “subordinary hereditary characteristic” when they are one aspect of an object (e.g., the eye) which is itself functional.

which are not traditional organs; similarly, the concept of biological organization as closure of constraints applies to natural systems which depart from traditional organisms. It more precisely permits going beyond the common and simplified vision, reminded by Dupré & O'Malley (2007, p. 834), according to which biological systems are free-living cells or coordinated groups of cells containing the same genome.

In other words, an organizational perspective of biological inheritance allows conceiving of non-standard biological systems exhibiting multifarious heritable variations. Non-standard biological systems usually refer to symbiotic associations or to insect colonies including abiotic parts. In this paper, it designates all biological systems whose parts cannot simply be accounted by classical interactionist accounts (gene/environment). In other words, it refers to biological systems – such as human beings – that are more than groups of coordinated cells containing the same genome and that possibly include symbiotic and/or behavioral parts (involving or not the use of artifacts).

For pragmatic reason, it can be argued that non-standard biological system can undergo two kinds of variation: *genetic mutations* (changes in a DNA sequences) and *non-genetic acquisitions* (development of a new behavior, recruitment of new microorganisms, etc.) The first are conserved through *genetic inheritance* and the second through *non-genetic inheritance*. In this view, a functional variation appearing in a biological lineage is not necessarily due to a genetic mutation and can be conserved through non-genetic channels. For example, a heritable metabolic change in the capacity to degrade cellulose can be due to a mutation in some DNA sequences, to the acquisition of a cooking technique, to the acquisition of some microorganisms, etc. It can be conserved through various genetic and non-genetic mechanisms.

10.3.3 Inheritance and Organization: An Approach Suited to the Heuristic of Collaboration

When compared to other accounts that widen the scope of inheritance beyond gene-centrism (Jablonka, 2002; Bonduriansky, 2012; Griffiths & Stotz, 2013), the organizational perspective presents some important and specific characteristics that make it more suited to the emerging organisms-centered view of evolution.

- *Extension without dilution*. First, it extends inheritance beyond genetics while keeping it clearly bounded and thereby avoids its dilution into the vague concept of biological stability.¹³ Indeed, it offers tools to distinguish inheritance – conservation

¹³ While the concept of extended inheritance first appears as theoretically and explanatorily fecund (insofar as it promises to overcome the limitations of gene-centrism), it can lead to consider as inherited any elements being stable across generations and having some causal influence on the reoccurrence of traits. In other words, it can lead to think about inheritance as a concept synonymous with stability (Mossio & Pontarotti, 2019). As a result, the extension of inheritance can

of functional patterns across generations – from stability of environment, stability of ecosystems, etc. The organizational perspective only grants the status of heritable objects to those elements which can fall under the definition of functional constraints (e.g., hearts, nests, etc.) at a given scale. It regards stable flows of matter and energy (e.g., nutrients) and stable functional elements whose (physical) persistence is not primarily explained by their being part of a networks of interdependent constraints (e.g., persisting caves used as shelters), as part of stable environments (Mossio & Pontarotti, 2019). In this respect, the organizational account specifically defines inheritance and environmental stability as two different phenomena. It clarifies that stable biological (or biologically relevant) objects are either part of a *heritable* organization or part of a *stable* environment but not both at the same time (Pontarotti, 2022).

- *Collective stability*. Second, the organizational perspective invites to invalidate the classical distinction between hereditary factors (genes), understood as the causes of heredity, and hereditary traits (observable features), conceived as effects of the former. This distinction has been expressed through the opposition between the genotype and the phenotype since Johannsen's (1911) seminal contribution and has been a structuring one in the twentieth century. However, it appears as irrelevant in the presented theoretical framework, where genes and other biological constraints belong to a network of interdependent objects involved in a circular causality (Pontarotti et al., 2022). In an organizational view, distinguishing supposedly causal factors from supposedly epiphenomenal traits makes no sense. Inheritance is not a matter of (selfish) replication but rather of systemic, and therefore collective, stability.

While the genetic theory explains the stability of organismal traits by that of DNA sequences¹⁴ supposedly endowed with self-replicative and causal properties (Dawkins, 1976), an organizational perspective distributes the explanation for traits stability to various interdependent parts conceived as functional constraints: DNA sequences involved in the production of proteins, cells, socially learned behaviors, microorganisms performing some metabolic work in the system they constitute with their hosts, etc. On this point, the organizational perspective appears in line with the previously mentioned heuristic of collaboration. It also somehow echoes older “dynamical” or “energetist” conceptions of inheritance rejecting atomistic approach (Gayon, 1992b, pp. 432–433). Among them, Thompson's vision (1942) is critical about the fact of attributing to individual particles something that is due to the “energy of their collocation”, while Nanney's conception (1957) suggests that inheritance can refer to the behavior of a full system.

conceal the fact that the concept initially designates a specific phenomenon – the stability of organismal traits – which is explained by the presence of some specific causal factors (López-Beltrán, 1994). When thinking about extended inheritance, the challenge is therefore to include more than genes in inheritance while avoiding to turn it into an all-inclusive concept.

¹⁴Mendelian genes are theoretical units but genes have been conceived of as DNA sequences since the middle of the twentieth century.

Other extended accounts of inheritance evoke the replication of elements belonging to organized biological systems (Jablonka, 2002) and state that replication is a collective matter (Griffiths & Gray, 2004). However, these accounts do not rest on a clear concept of biological organization and/or do not put the concept of organization at their core. This prevents them from clearly bounding extended inheritance and from proposing a theoretically informed explanation of biological trans-generational stability.

- *Systemic heritable variation.* The organizational perspective further and more importantly has the specificity of implying a *systemic* concept of heritable variation, which is also consistent with a heuristic of collaboration. Conceiving of inheritance as the conservation of functional patterns indeed implies that heritable variations cannot be considered per se but should first and foremost be conceptualized as changes affecting complete biological networks. Insofar as parts of biological systems are thought as constraints which are interdependent for their maintenance within and across generations, new heritable variations should be considered as events that modify organizational regimes and that ground new organizational deals (Pontarotti, 2017).

This implies that a new heritable variation theoretically limits or enables further variations in the considered organizational pattern, within and across generations, following whether it turns out to increase or reduce the cost of a function. For example, the acquisition of a new metabolic capacity to degrade cellulose could be energetically costly for a system and therefore limit the possibility for further variations, but it could on the contrary reduce the energetic cost of the function and therefore leave some room for further changes. The termites that come to rely on fungi to digest cellulose become free from constraints on the digestion rates faced by the termites that rely only on intestinal digestion (Turner, 2004, p. 335). They can mobilize energy at much higher rates than their competitors (Turner, 2004, p. 339). The fact of counting on symbionts to perform part of the digestive process – a phenomena that some authors call functional “outsourcing” (Turner, 2004, p. 335; Bouchard, 2013, p. 261) – can enable or limit further modifications in the considered systems. If the acquisition of the symbionts reduces the cost of nutrition or if it provides the system with more energy, this system may undergo other costly variations.

These considerations notably require admitting, in accordance with the life-history theory, that there is a trade-off for the allocation of resources among the parts of biological systems involved in survival and reproduction (Stearns, 1992, Fabian & Flatt, 2012). They also somehow appear in line with the thesis according to which biological systems are integrated wholes in which parts cannot be individually optimized (Gould & Lewontin, 1979), even if Gould and Lewontin’s conception should not be conflated with the trade-off adaptationism endorsed by the life-history theory (see footnote 3).

10.4 Explanatory Value and Theoretical Implications of an Organizational Perspective on Biological Inheritance for Evolutionary Thinking

In this last section, I show that an organizational account of biological inheritance, beyond being a key ingredient for the elaboration of an organization-centered evolutionary biology, can modify perspectives and shed new light on various evolutionary phenomena.

10.4.1 *Stabilization of Non-genetic Acquisitions and Evolution of Non-standard Biological Systems*

It has been argued that non-genetic inheritance could have an impact on evolutionary trajectories (Jablonka & Lamb, 2005; Bonduriansky & Day, 2018). It has also been said that it is “crucial to make sense of the evolution of complex biological individuals” such as symbiotic associations or insects colonies including mounds and fungi (Bouchard, 2013, p. 259). However, non-genetic elements are generally thought as relatively labile when compared with genes (see Richards et al., 2010 for epigenetic marks), and non-genetic inheritance is sometimes referred to as trans-generational plasticity (Mesoudi et al., 2013). This seems to prevent non-genetic *acquisitions* from having any impact on evolutionary dynamics. Actually, such conclusion relies on a theoretical commitment toward a gene-centered evolutionary biology, based on a heuristic of replication where biological stability is thought as a property of virtually atomized objects able to make faithful copies of their structure and thought on the model of Dawkins’s replicators (1976). Endorsing this view, Sterelny (2001) argues that, to have an effect on cumulative evolution mainly driven by natural selection, non-genetic inheritance should present the same properties as genetic inheritance and should notably ensure the reconstruction of highly variable replicators exhibiting stability and having a common evolutionary fate.

An organization-centered biology, based on a heuristic of collaboration where heritable variations are not conceived as virtually atomized and self-replicating elements, leads to a very different conclusion. More precisely, an organizational perspective of biological inheritance, grounded on the idea of collective stability, opens a way to make sense of the stabilization of *prima facie* labile non-genetic *acquisitions* in the course of evolution and, thereby, of the evolution of non-standard biological systems (as defined in Sect. 10.3). As explained above, an organizational account of biological inheritance implies that heritable variation – be it a genetic mutation or a (plastic) non-genetic acquisition – grounds a new organizational deal and can have systemic consequences. In modifying a system’s access to flows of matter and energy (access to new resources, increased or decreased cost of a

function, functional redundancy¹⁵), it determines the possibility for further variations in this system. When these further variations occur, the other original parts of the system may not be able to survive without the earlier changes, even if these changes are non-genetic acquisitions (e.g., epigenetic marks, socially acquired behaviors). More generally, a systemic vision of heritable variation allows outlining three conditions favoring the stabilization of non-genetic inherited elements and the consequent evolution of non-standard biological systems. These conditions are those which increase the *interdependence* of parts, namely, environmental changes, random functional losses, and appearance of other costly functional variations.

For example, an insect can acquire microorganisms that perform cellulose degradation via so-called facultative symbiosis, where both host and symbionts can reproduce independently (Moran et al., 2008). But the host-symbiont association can become irreversible in the case of an environmental change (food shortage that would favor the systems that are more performant for digestion), in the case of a functional loss (if the insect loses the capacity to digest cellulose) or if a costly variation arises in the system.¹⁶ Another speculative example is the acquisition of sewing techniques and of clothing traditions in humans. Under some climates, these heritable acquisitions can be considered as a functional innovation regarding thermoregulation. In some circumstances (loss of genetic capacity to perform thermoregulation, costly variation, environmental change), this acquisition can become more crucial for the maintenance of other parts of the systems, such as hearts. Finally, one can imagine a situation where the decreased cost of the digestive function, related to the acquisition of cooking techniques destroying toxins, leaves some rooms for costly mutations linked to the development of brain. This is what is suggested by the tenants of the expensive tissue hypothesis (Aiello & Wheeler, 1995).

Before concluding, it is important to make some clarifications regarding the concept of *interdependence*. According to the recent literature dedicated to biological autonomy and biological organization, the constitutive constraints of biological systems are, by definition, interdependent. However interdependence can take different forms and meanings. According to a first meaning, two objects are interdependent when they are conserved by producing each other (*reciprocal production and symmetrical dependence involving joined conservation*). For example, the liver of an organism cannot be conserved without the activity of the heart within and across generations, and vice versa: the liver and the heart are therefore produced by each other, and if the former is destroyed, the latter is also destroyed. However, reciprocal production can also come with asymmetrical dependence. For example, the

¹⁵Note that methylation marks seem to be involved in the silencing of redundant genetic elements (Rapp & Wendel, 2005, p. 82).

¹⁶More generally, the case of symbiosis, which is a paradigmatic example to think about organizational inheritance (Pontarotti, 2016), provides many examples of conditions leading to the increased interdependence of parts. For example, the loss of genes in vertically transmitted symbionts is said to be at the origin of plastids and mitochondria (Sachs, 2013, p. 632). Besides, a host can come to tolerate a parasite if even more dangerous parasites are present in the environment (van Baalen & Jansen, 2001).

conservation of hunting tools participating in the food channeling process, in a human lineage, can depend on the conservation of hearts, and vice versa, but in some conditions (food abundance), hearts can be maintained without these manufactured tools. According to a second meaning, two objects are interdependent when they are maintained in a joint way, notably at the trans-generational timescale, even if they do not necessarily produce each other (*mere joined conservation*). For example, in an organism, the kidneys can be conserved if eyes are destroyed during the life cycle, but the kidneys and eyes can be jointly maintained at the trans-generational timescale: if the former reoccurs, the latter will in principle also reoccur. In this case, the kidneys are not directly dependent on the eye for their production and conservation,¹⁷ but the elements needed to rebuild the kidneys and to rebuild the eyes (notably DNA sequences) are conserved together.¹⁸ According to a third meaning, two objects are interdependent when they need to interact for the maintenance of a given organizational regime (and therefore for their maintenance as organizational constraints in this given regime) even if they can otherwise be maintained without one another. For example, the heart of an organism involved in a facultative symbiosis can be dependent on some microorganisms for the maintenance of a given pattern of matter and energy channeling, but not for its maintenance within and across generations (*joined action for the maintenance of a given organizational regime*).

These distinctions are important if one wants to apply the organizational framework to think about biological inheritance and the evolution of non-standard biological systems. They contribute to clarify that parts of biological systems exhibiting multifarious variations are minimally interdependent according to the third meaning (*joined action for the maintenance of a given organizational regime*) but that they can become interdependent in the first and strongest meaning (*reciprocal production and symmetrical dependence involving joined conservation*) in the circumstances mentioned above (environmental changes; random functional losses; appearance of other costly functional variations). This strongest kind of interdependence involves the common fate of parts (not mediated by bottleneck), a property which is one of the main hallmarks of biological individuals (Bouchard, 2013; Godfrey-Smith, 2009).

¹⁷However, the kidneys are fully dependent on sensitive organs more globally. One can therefore consider that there is interdependence in the strong sense (*reciprocal production*) between kidneys and sensitive organs.

¹⁸This is what happens when objects that do not have any function (which do not comply with the definition of constraints) are conserved. These objects are conserved jointly with others which have, as for them, a clear function (e.g., DNA sequences used to build eye color are jointly conserved with sequences used to build pupil). They can be considered as “subordinate hereditary characteristics” (Mossio & Pontarotti, 2019).

10.4.2 *Perspectives on Fitness, Natural Selection, and Evolution*

As explained above, the organizational perspective on biological inheritance appears as a major ingredient for an evolutionary biology based on a heuristic of collaboration. Below, I sketch how its integration into evolutionary thinking could induce, in the wake of earlier contributions, a change of perspective with regards to lineages, fitness, selection, and evolution.

First and foremost, assuming that inheritance is a matter of conservation of functional patterns – regardless of the parts being involved – and not of replication of genetic elements, implies that evolutionary biology should track *functional lineages* and not genetic ones. In this view, specialists should more precisely track the fate of integrated networks, not of virtually atomized alleles correlated with phenotypic variations. The key units of the living world are not elements heuristically depicted as selfish individuals eager to self-replicate but rather as parts collaborating with others in the context of organized networks. The stability of these parts is not linked to their intrinsic capacity of making faithful copies of themselves: it is related to their being integrated in networks channeling flows of matter and energy.

In this context, *fitness* cannot be thought of as the property of atomized objects but must be attributed to full organized systems whose spatial boundaries are outlined by interdependent constraints. It cannot be conceptualized, like in twentieth-century evolutionary biology, as a matter of differential replication (of genes) or as a matter of differential reproduction (of genetically homogenous organisms), but it should rather be thought as the differential capacity of integrated networks to channel flows of matter and energy in order to maintain themselves within and across generations.¹⁹ In accordance with earlier studies (van Valen, 1975, p. 267), fitness can therefore be said to rest on the differential quantity of energy controlled by a biological system. Put another way, it can refer to differential management of resources (Pontarotti, 2017). Finally, it can globally be envisioned as a matter of differential expansion (van Valen, 1989, p. 7), some systems being more capable than others to make more of themselves in space and time (through reproduction, growth, etc.), depending on their performance in resources channeling.

From this point of view, *natural selection* does not target genes but networks with differential performances as far as resources management – and therefore spatiotemporal maintenance and expansion – is concerned. It selects among networks exhibiting differential efficiency regarding the control of material and energetic flows. This line of argument is consistent with the idea according to which natural selection targets effects and not structures as such, in a given environment (Rosenberg, 1994). It also somehow meets the hypothesis of physiological selection advanced by Turner (2004) when thinking about the evolution of “extended organisms” such as termite-fungi-mound systems. It is important to note, here, that

¹⁹For details about intergeneration breaks and therefore about temporal limits of organized systems involved in evolution, see Mossio & Pontarotti, 2019.

according to Turner, genes should not be primarily considered as replicators but rather as specifiers²⁰ of future functions, as elements, among others, specifying how flows of matter and energy are channeled (Turner, 2004).

The *evolution* of non-standard biological systems, as for it, can be thought on the model of the evolution which took place before the appearance of DNA. In a world inhabited by autocatalytic sets of molecules, what matters, for evolution, is not the differential replication of discrete entities but the variations impacting network's efficiency regarding maintenance (Kauffman, 1995). The point can be summarized as follows: "if the result (of a variation in an autocatalytic set of molecules) were a more efficient network – one better able to sustain itself amid a harsh environment – then these mutations would be rewarded, the altered web crowding out its weaker competitors" (Kauffman, 1995, p. 73). In this view, evolution can no more be defined as a change in gene frequencies (Dobzhansky, 1937) or as a change in developmental programs during phylogeny (Oster & Alberch, 1982, p. 444). It must rather be viewed as a process leading to changes in regimes of canalization of flows of matter and energy through time (Pontarotti, 2017), as a change in organizational regimes.

It should also be noted that an organizational account of biological inheritance makes it possible to articulate three elements that were conceived separately in modern synthesis but that an organism-centered evolutionary biology is willing to link again: development, inheritance, and evolution (Walsh, 2010; Nicholson, 2014). Indeed, such an account makes no theoretical distinction between hereditary factors (genotype) and developed traits (phenotype), considering all of them as inherited organized constraints. It also acknowledges a continuity regarding the processes involved in the conservation of biological systems within and across generations (Mossio & Pontarotti, 2019).

Finally, let us go back to the role of natural selection in this theoretical context. This role would be limited by theoretical models, based on a heuristic of collaboration, in which the dynamics of interdependence between parts of biological systems would be more important than multi-level selection of selfish elements in the determination of biological evolution. These models would, for example, take their distance with Szathmáry and Maynard Smith (1995) work on evolutionary transitions. The latter indeed clearly relies on a heuristic of replication and insists on the role of multilevel selection in the appearance of new kinds of individuals, an event in which elements which could initially replicate independently become interdependent for their own replication. The collaborative point of view associated with the integration of an organizational thinking in evolutionary biology would rather be in line with the literature about constructive neutral evolution (Lukes et al., 2011). The latter indeed offers a perspective in which evolution principally rests on games of interdependence: "In this conception, mutation is not a source of raw materials, but

²⁰"Specifiers are the catalytic surfaces that specify particular types of chemical reactions. These can be affected both by translated information in replicators (genes) and by environmental conditions" (Turner, 2004, p. 342).

an agent that introduces novelty, while selection is not an agent that shapes features, but a stochastic sieve” (Stoltzfus, 2012). This reduced role for natural selection would be consistent with the main statements of EES which gives an important explanatory role to the internal dynamics of organized systems.

10.5 Conclusion

In this paper, I have argued that the emerging organism-centered evolutionary biology, which theoretically makes some important room to the concept of organization, is missing some organizational perspective of inheritance, the latter being known as a key ingredient for evolutionary processes. I have outlined an organizational account of biological inheritance, and I have detailed the systemic concept of heritable variation (genetic mutation and non-genetic acquisition) that it contributes to ground. Finally, I have sketched some implications of an organizational perspective of biological inheritance for an evolutionary theory which would be based on a heuristic of collaboration rather than on a heuristic of replication. The big picture set in this article deserves being developed in future contributions. For instance, it will be important to further analyze the link between organization and developmental mechanisms, the latter being at the center of extended evolutionary synthesis. Organization, as presented in this paper, makes abstraction of mechanistic and temporal details. But these details could be of great relevance for the elaboration of a theoretical framework which would better take into account the causal role of organized biological systems in evolutionary dynamics.

References

- Aiello, L. C., & Wheeler, P. (1995). The Expensive-Tissue Hypothesis: The Brain and the Digestive System in Human and Primate Evolution. *Current Anthropology*, 36(2), 199–221.
- Baptiste, E., & Huneman, P. (2018). Towards a dynamic interaction network of life to unify and expand the evolutionary theory. *BMC Biology*, 16, 56. <https://doi.org/10.1186/s12915-018-0531-6>
- Bateson, P. (2005). The return of the whole organism. *Journal of Biosciences*, 30(1), 31–39.
- Bernard, C. (1885 [1878]). *Leçons Sur les phénomènes de la vie communs aux animaux et aux végétaux*. Librairie J.-B. Baillière et Fils (source : Gallica.fr).
- Bertalanffy, L. (1973 [1968]). *Théorie générale des systèmes*. Traduction par J.-B. Chabrol. Bordas.
- Bichat, F.-X. (1801). *Anatomie générale appliquée à la physiologie et à la médecine*. Brosson, Gabon et C^{ie} (source : Gallica.fr).
- Bonduriansky, R. (2012). Rethinking heredity, again. *Trends in Ecology & Evolution*, 27(6), 330–336.
- Bonduriansky, R., & Day, T. (2018). *Extended inheritance: A new understanding of inheritance and evolution*. Princeton University Press.

- Bouchard, F. (2013). What is a symbiotic superindividual and how do you measure its fitness? In F. Bouchard & P. Huneman (Eds.), *From groups to individuals: Evolution and emerging individuality* (Vienna series in theoretical biology) (pp. 243–264). MIT Press.
- Cubas, P., Vincent, C., & Coen, E. (1999). An epigenetic mutation responsible for natural variation in floral symmetry. *Nature*, *401*(6749), 157–161.
- Danchin, E., Charmantier, A., Champagne, F., Mesoudi, A., Pujol, B., & Blanchet, S. (2011). Beyond DNA: Integrating inclusive inheritance into an extended theory of evolution. *Nature Reviews Genetics*, *12*(7), 475–486.
- Darwin, C. (1859 [2008]). *L'origine des espèces au moyen de la sélection naturelle ou la préservation des races favorisées dans la lutte pour la vie*. Flammarion.
- Dawkins, R. (1976). *The Selfish Gene*. Oxford University Press.
- Dawkins, R. (2008 [1982]). *The extended phenotype*. Oxford University Press.
- Dobzhansky, T. (1937). *Genetics and the origin of species*. Columbia University Press.
- Dobzhansky, T. (1970). *Genetics of the evolutionary process*. Columbia University Press.
- Douglas, A. E. (2009). The microbial dimension in insect nutritional ecology. *Functional Ecology*, *23*(1), 38–47.
- Dupré, J., & O'Malley, M. (2007). Metagenomics and biological ontology. *Studies in History and Philosophy of Biological and Biomedical Sciences.*, *38*(4), 834–846.
- Fabian, D., & Flatt, T. (2012). Life history evolution. *Nature Education Knowledge*, *3*(10), 24.
- Fox Keller, E. (2000). *The century of the gene*. Harvard University Press.
- Galef, B. G., Jr., & Laland, K. N. (2005). Social learning in animals: Empirical studies and theoretical models. *Bioscience*, *55*(6), 489–499.
- Gayon, J. (1992a). *Darwin et l'après-Darwin : Une histoire de l'hypothèse de sélection dans la théorie de l'évolution*. Kimé.
- Gayon, J. (1992b). Animalité et végétalité dans les représentations de l'hérédité. *Revue de Synthèse, Springer Verlag/Lavoisier*, *4*(3), 49–61.
- Gilbert, S., Sapp, J., & Tauber, A. (2012). A symbiotic view of life: We have never been individuals. *The Quarterly Review of Biology*, *87*(4), 325–341.
- Godfrey-Smith, P. (2009). *Darwinian populations and natural selection*. Oxford University Press.
- Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptationist programme. *Proceedings of the Royal Society of London. Series B, Biological Sciences.*, *205*(1161), 581–598.
- Griesemer, J. (2000). Development, culture, and the units of inheritance. *Philosophy of Science*, *67*, S348–S368.
- Griffiths, P. E., & Gray, R. D. (1994). Developmental systems and evolutionary explanation. *The Journal of Philosophy*, *91*(6), 277–304.
- Griffiths, P., & Gray, R. (2004). The developmental systems perspective: Organism-environment systems as units of evolution. In K. Preston & M. Pigliucci (Eds.), *Phenotypic integration: Studying the ecology and evolution of complex phenotypes* (pp. 409–431). Oxford University Press.
- Griffiths, P. E., & Stotz, K. (2013). *Genetics and philosophy: An introduction*. Cambridge: Cambridge University Press.
- Helanterä, H., & Uller, T. (2010). The Price equation and extended inheritance. *Philosophy & Theory in Biology*, *2*(201306), 1–17.
- Holeski, L. M., Jander, G., & Agrawal, A. A. (2012). Transgenerational defense induction and epigenetic inheritance in plants. *Trends in Ecology & Evolution*, *27*(11), 618–626.
- Huneman, P. (2010). Assessing the prospects for a return of organisms in evolutionary biology. *History and Philosophy of the Life Sciences*, *32*(2–3), 341–371.
- Huneman, P. (2017). Why would we call for a new evolutionary synthesis? The variation issue and the explanatory alternatives. In P. Huneman & D. Walsh (Eds.), *Challenging the modern synthesis: Adaptation, development, and inheritance*. Oxford University Press.
- Huxley, J. (2010 [1942]). *Evolution, the modern synthesis*. MIT Press.

- Jablonka, E. (2002). Information: Its interpretation, its inheritance and its sharing. *Philosophy of Science*, 69(4), 578–605.
- Jablonka, E., & Lamb, M. (2005). *Evolution in four dimensions*. MIT Press.
- Johannsen, W. (1911). The genotype conception of inheritance. *The American Naturalist*, 45(531), 129–159.
- Kant, E. (2000 [1790]). *Critique de la faculté de juger*. Vrin.
- Kauffman, S. (1995). *At home in the universe. The search for the laws of self-organization and complexity*. Oxford University Press.
- Laland, K. N., Uller, T., Feldman, M. W., Sterelny, K., Müller, G. B., Moczek, M., Jablonka, E., & Odling-Smee, J. (2015). The extended evolutionary synthesis: Its structure, assumptions and predictions. *Proceedings of the Royal Society B*, 282(1813), 1019.
- Lewontin, R. C. (1970). The units of selection. *Annual Review of Ecology and Systematics*, 1, 1–18.
- Lewontin, R. C. (1993). *Biology as ideology: The doctrine of DNA*. Harper Collins.
- López-Beltrán, C. (1994). Forging inheritance: From metaphor to cause, a reification story. *Studies in History and Philosophy of Science Part A*, 25(2), 221–235.
- Lukes, J., Archibald, J. M., Keeling, P. J., Doolittle, W. F., & Gray, M. W. (2011). How a neutral evolutionary ratchet can build cellular complexity. *International Union of Biochemistry and Molecular Biology Life*, 63(7), 528–537.
- Mameli, M. (2005). The inheritance of features. *Biology and Philosophy*, 20(2), 365–399.
- Mayr, E. (1963). *Animal species and evolution*. Harvard University Press.
- Mayr, E. (1998). Prologue: Some thoughts on the history of the evolutionary synthesis. In E. Mayr & W. B. Provine (Eds.), *The evolutionary synthesis: Perspectives on the unification of biology* (pp. 1–48). Harvard University Press.
- Merlin, F. (2017). Limited extended inheritance. In D. Walsh & P. Huneman (Eds.), *Challenging the modern synthesis* (pp. 263–279). Oxford University Press.
- Mesoudi, A., Blanchet, S., Charmantier, A., Danchin, E., Fogarty, L., Jablonka, E., Laland, K. N., Morgan, T. J. H., Müller, G. B., Odling-Smee, J., & Pujol, B. (2013). Is non-genetic inheritance just a proximate mechanism? A corroboration of the extended evolutionary synthesis. *Biological Theory*, 7(3), 189–195.
- Moran, N. A., McCutcheon, J. P., & Nakabashi, A. (2008). Genomics and Evolution of Heritable Bacterial Symbionts. *Annual Review of Genetics*, 42, 165–190.
- Montévil, M., & Mossio, M. (2015). Biological organisation as closure of constraints. *Journal of Theoretical Biology*, 372, 179–191.
- Moreno, A., & Mossio, M. (2015). *Biological autonomy. A philosophical and theoretical enquiry*. Springer.
- Mossio, M., & Bich, L. (2014). What makes biological organisation teleological? *Synthese*, Springer. <http://link.springer.com/article/10.1007/s11229-014-0594-z>
- Mossio, M., & Moreno, A. (2010). Organisational closure in biological organisms. *History and Philosophy of the Life Sciences*, 32(2–3), 269–288.
- Mossio, M., & Pontarotti, G. (2019, 2020). Conserving functions across generations: Inheritance in light of biological organization. *British Journal for the Philosophy of Science*, 1–33.
- Mossio, M., Saborido, C., & Moreno, A. (2009). An organizational account of biological functions. *The British Journal for the Philosophy of Science*, 60(4), 813–841.
- Müller, G. B. (2017). Why an extended evolutionary synthesis is necessary. *Interface Focus*, 7, 20170015.
- Nanney, D. (1957). The role of cytoplasm in heredity. In W. D. McElroy & B. Glass (Eds.), *A symposium on the chemical basis of heredity, 1956* (pp. 134–135). The Johns Hopkins Press.
- Nicholson, D. (2014). The return of the organism as a fundamental explanatory concept in biology. *Philosophy Compass*, 9(5), 347–359.
- Odling-Smee, J., Laland, K. N., & Feldman, M. W. (2003). *Niche construction: The neglected process in evolution*. Princeton University Press.
- Oster, G., & Alberch, P. (1982). Evolution and bifurcation of developmental programs. *Evolution*, 36(3), 444–459.

- Pigliucci, M. (2009). “An extended synthesis for evolutionary biology”, the year in evolutionary biology 2009. *Annals of the New York Academy of Sciences*, 1168, 218–228.
- Pigliucci, M., & Muller, G. B. (2010). Elements of an extended evolutionary synthesis. In *Evolution – The extended synthesis*. MIT Press.
- Pontarotti, G. (2015). Extended inheritance from an organizational point of view. *History and Philosophy of the Life Sciences*, 37, 430–448.
- Pontarotti, G. (2016). Extended inheritance as reconstruction of extended organization: The paradigmatic case of symbiosis. *Lato sensu*, 3(1), 93–102.
- Pontarotti, G. (2017). *Au delà du tout génétique: une perspective organisationnelle sur l'hérédité biologique et ses implications en biologie de l'évolution*. PhD dissertation. Université Paris 1 Panthéon-Sorbonne.
- Pontarotti, G. (2022). Environmental inheritance: Conceptual ambiguities and theoretical issues. *Biological Theory*, 17(1), 36–51.
- Pontarotti, G., Mossio, M., & Pocheville, A. (2022). The genotype–phenotype distinction: From Mendelian genetics to 21st century biology. *Genetica*, 150(3–4), 223–234.
- Rapp, R. A., & Wendel, J. F. (2005). Epigenetics and plant evolution. *New Phytologist*, 168(1), 81–91.
- Richards, C., Bossdorf, O., & Pigliucci, M. (2010). What role does heritable epigenetic variation play in phenotypic evolution? *Bioscience*, 60(3), 232–237.
- Rosenberg, A. (1994). *Instrumental biology or the disunity of science*. University of Chicago Press.
- Sachs, J. L. (2013). Origins, evolution, and breakdown of bacterial Symbiosis. In S. A. Levin (Ed.), *Encyclopedia of biodiversity* (Vol. 5, 2nd ed., pp. 637–644). Academic.
- Slagsvold, T., & Wiebe, K. (2007). Learning the ecological niche. *Proceedings of the Royal Society B*, 274, 19–23.
- Stearns, S. C. (1992). *The evolution of life histories*. Oxford University Press.
- Sterelny, K. (2001). Niche construction, developmental systems and the extended replicator. In S. Oyama, P. E. Griffiths, & R. Gray (Eds.), *Cycles of contingency: Developmental systems and evolution* (pp. 333–349). MIT Press.
- Stoltzfus, A. (2012). Constructive neutral evolution: exploring evolutionary theory’s curious disconnect. *Biology Direct*, 7(1), 35.
- Szathmáry, E., & Maynard Smith, J. (1995). The major evolutionary transitions. *Nature*, 374, 227–232.
- Thompson, D. A. W. (1942). *On growth and form* (nouv. ed.). Cambridge University Press.
- Turner, J. S. (2000). *The extended organism, the physiology of animal-built structures*. Harvard University Press.
- Turner, J. S. (2004). Extended phenotypes and extended organisms. *Biology and Philosophy*, 19(3), 327–352.
- Van Baalen, M., & Jansen, V. A. A. (2001). Dangerous liaisons: The ecology of private interest and common good. *Oikos*, 95(2), 211–224.
- Van der Lugt, M., & De Miramon, C. (2008). Penser l’hérédité au Moyen Âge : une introduction. In M. van der Lugt & C. de Miramon (Eds.), *L’hérédité entre Moyen Âge et Époque moderne. Perspectives historiques* (pp. 3–37). Edizioni del Galluzzo.
- Van Valen, L. M. (1975). Life, death, and energy of a tree. *Biotropica*, 7(4), 259–269.
- Van Valen, L. M. (1989). Three paradigms of evolution. *Evolutionary Theory*, 9, 1–17.
- Walsh, D. M. (2006). Organisms as natural purposes: The contemporary evolutionary perspective. *Studies in History and Philosophy of Biological and Biomedical Sciences*, 37(4), 771–791.
- Walsh, D. M. (2010). Two Neo-Darwinisms. *History and Philosophy of the Life Sciences*, 32(2–3), 317–339.
- Walsh, D. (2015). *Organisms, agency, and evolution*. Cambridge University Press.
- West-Eberhard, M. J. (2003). *Developmental plasticity and evolution*. Oxford University Press.

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