

**The Organism in Evolutionary Explanation:
From Early 20th Century to the Extended Evolutionary Synthesis**

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Abstract: In recent years there have been a number of calls for integrating developmental and organismal phenomena into evolutionary theory. This so-called Extended Evolutionary Synthesis (EES) argues that evolutionary theory should not primarily explain certain evolutionary phenomena by highlighting genes and populations but organisms instead, in particular how their development and behavior biases and drives evolutionary change. Here, we offer a new historiography that focuses less on the differences between the EES and the Modern Synthesis, but seeks to provide a better understanding about which theoretical and explanatory traditions the organism-centered framework of the EES draws on. This concerns especially three currently resurfacing explanatory roles granted to organisms in evolution: organisms should allow (1) contextualizing parts in development, especially genes, (2) focusing on reciprocal organism-environment relations (in contrast to, e.g., gene-environment interactions), and (3) understand the role of agency in evolution. Through this analysis, we show that the EES advances a revival of older explanatory roles granted to the organism in evolutionary research, which became marginalized in the second half of the 20th century. This new perspective helps to re-center contemporary theoretical debates towards relevant questions of explanatory standards in evolutionary biology.

Keywords: Organism; Modern Synthesis; Organicism; EES; Explanation; Explanatory standards

1 Introduction

What does the proposal to extend the evolutionary synthesis mean? *Prima facie*, the answer to this question seems to be straightforward. “Extending” suggests that there exists older or accepted consensus practices and standards of theorization in evolutionary biology that should

be augmented or widened.¹ The label of *Extended Synthesis*, introduced by some evolutionary biologists (Pigliucci 2007; Müller 2007; Pigliucci and Müller 2010b; Laland et al. 2014, 2015; Müller 2017d), seems to clarify this historical reference point even more. It suggests a relation to the *Modern Synthesis* (MS). In short, if the name is taken at face value, the Extended Synthesis tries to broaden some features of the MS. In this chapter we argue that this historiography is limited and currently hinders fruitful theoretical debates about what is epistemologically entailed by the framework of the Extended Evolutionary Synthesis (EES; *sensu* Laland et al. 2015).

Discussion about the historical status of the EES usually adopt a contrastive approach that separates it from the MS. This holds for both its advocates (Laland et al. 2014, 2015; Pigliucci 2017; Müller 2017d; Jablonka and Lamb 2020) as well as its critics (Wray et al. 2014; Futuyma 2017; Gupta et al. 2017; Lu and Bourratt 2017; Charlesworth et al. 2017; Svensson, this volume). In this common contrastive framework, the innovative potential and novelty of the EES for evolutionary biology is emphasized or downgraded, respectively, depending on how liberal the MS was considered to be with respect to integrating developmental phenomena, such as developmental bias, plasticity-led evolution, and niche construction. The results of these historical assessments are then taken to be sufficient by most authors to embrace or reject the project of an EES altogether. However, this bundle of historiographic problems (e.g., how plural or gene-centered the MS was with respect to developmental causes of evolution or channels of inheritance, how novel the ideas stemming from the EES really are, etc.) should not be conflated with the theoretical and philosophical problem of what EES-type explanations (if anything) could bring to evolutionary biology (see, for instance, Baedke et al. 2020).

In other words, the EES debate has so far been overtly fixated on the labels that surround it. This focus on the *name* prevents drawing sufficient attention to the ideas and explanatory roles central concepts play inside the framework elaborated by Laland et al. (2015). Here, we contend that two central concepts reintroduced by the EES are that of the *developing organism* as a causally efficacious unit in evolution and the *organism-environment relationship* as a fundamental frame to study reciprocal, protracted evolutionary interactions. The so-called “organism-centered perspective” of the EES (Laland et al. 2015) captures the idea that organism-centered – rather than gene- or population-centered – explanations of evolution provide a perspective, often neglected since the mid-20th century, that would broaden our

¹ Such widening could be understood, for example, in terms of its models, the domain of application of theories, or what experimental practices can be derived from it (see Grisemer 2019).

understanding of evolution (see also Uller et al. 2020; Uller and Laland 2019). Adding explanations of developmental and organismal causes, studied in fields and research areas such as evolutionary developmental biology (Evo-Devo), epigenetics, and niche construction theory, to the causal picture of evolutionary theory should lead to “more complete explanations” (Laland et al. 2015) and a “significantly expanded explanatory capacity” (Pigliucci and Müller 2010a: 12). Interestingly, while there is often agreement in evolutionary biology over the existence of these phenomena, at the same time, their explanatory relevance is questioned (Wray et al. 2014; Futuyma 2017; Dickins 2019; Svensson 2020).

Against the background of the stalemate the EES debate has seemingly reached at this point with many evolutionary biologists talking past each other, in this chapter we seek to shift the focus of the discussion away from debating names towards more thorough and theoretically more fruitful historical analyses. Therefore, we concentrate on the explanatory roles the organism plays in the EES, and on how these roles have been defended and criticized in the history of evolutionary biology. We take a historical approach that asks: Where does the idea of the organism as a central explanatory unit in evolutionary theory come from and what is the focus and structure of organism-centered evolutionary explanations in the EES? What roles should we grant to the organism and to organism-environment relations in evolutionary explanations? Should it matter to emphasize the organism to build a richer evolutionary science?

We will show that, when directing the attention to organism-centered explanations, it becomes possible to see that the EES unwittingly reintroduced certain roles granted to the organism in early 20th century organicist biology, but which later became lost or marginalized in evolutionary biology. We identify three currently resurfacing explanatory roles organisms are thought to play in evolutionary biology: organisms should allow (1) contextualizing parts, especially genes, in development; (2) focusing on reciprocal organism-environment relations (in contrast to, e.g., gene-environment interactions); and (3) understanding the role of agency in evolution.

In what follows, we, first, discuss the conceptualization of organisms in early 20th century biological debates (in organicism, dialectical materialism and holism; section 2), and identify the three above epistemic roles ascribed to organisms in evolutionary explanations (section 3). Second, we show how each of these roles was marginalized by evolutionary biologists in the second half of the 20th century (section 4), before being recently reintroduced by research conducted under the umbrella term of the EES (section 5). We close with an outlook

on how this history could stir fruitful debates about the conceptual and theoretical framework underlying the EES and about the explanatory standards evolutionary biologists want their evolutionary explanations to hold (section 6).

2 The organism before the Modern Synthesis

At the dawn of the 20th century, intense discussions revolving around the conceptual, epistemic and ontological foundations of biology arose in several Anglo-Saxon and German-speaking scientific communities. According to Laubichler (2017: 95-96) this debate focused on (a) the divergence between a rapidly increasing number of new empirical findings and experimental results on the one side, and a lack of conceptual and theoretical frameworks on the other, which resulted in a data crisis around 1900; (b) the attempt to establish the foundations of biology based on these new findings; and (c) the evaluation of the epistemological and methodological preconditions of biological research.

Embryologist Julius Schaxel, for instance, mulled over the state of biology at his time and asserted that “[a] general biology, a science of life as such, exists in name only” (Schaxel 1919: 2; German original). In response to this widespread sense of crisis (see also Baedke 2019), scholars reflected upon the basic concepts that underpin biology. One of such was (and still is) the *organism concept*.²

In the first decades of the 20th century, especially in the interwar period, manifold biological perspectives centered on the organism emerged in different local contexts of the globe (Haraway 2004 [1976]; Esposito 2017; Baedke 2019). In recent years, historians have begun to study them in depth mainly in three geographical and geopolitical contexts: in Great Britain (Nicholson and Gawne 2014, 2015; Peterson 2016), the United States of America (Esposito 2014, 2016), and in Germany and Austria (the tradition of German holism; Amidon 2008; Rieppel 2016; Müller 2017c; Baedke 2019; Fábregas-Tejeda et al. 2021). Different stances within the organicist movement (on this notion, see Nicholson and Gawne 2015) represented a break in the dichotomous opposition between mechanism and vitalism (see Allen 2005), and, by integrating elements from both positions, were presented as alternatives that allowed to settle this fierce, long-lasting debate in history of biology (Beyler 1996: 252; Haraway 2004 [1976]: 2).³ For example, in embryological investigations, the organicist movement tried to reconcile ontological materialism with observations of biological

² For a history of the organism concept from 17th to the 19th century, see Cheung (2006, 2014).

³ On whether the vitalism-mechanism was ever fully settled, see Peterson and Hall (2020); see also Hein (1972).

emergence, and, in that sense, it paved the way between unassailable vitalism and reductionist mechanism (Gilbert and Sarkar 2000: 3).

As historian Herbert J. Muller asserted, scholars from the organicist movement, in contrast to abstract vitalists and staunch mechanists, wanted to re-center biological explanations on the living organism: “The vitalists insisted that some altogether new principle—an entelechy, an *élan vital*—was necessary to explain life; the mechanists insisted that the principles of physics were not only adequate but essential. Both tended to lose sight of the living organism in their logical dispute over explanation” (Muller 1943:106). For organicists, “(...) the fundamental fact in biology, *the necessary point of departure is the organism. (...) Although parts and processes may be isolated for analytic purposes, they cannot be understood without reference to the dynamic, unified whole that is more than their sum*” (Muller 1943:107; emphasis added).

Similar to today’s organism-centered perspective of the EES, members of the organicist movement defined “the living individual [as] the fundamental unity of biology” (Russell 1930: 166), and “organism” as a special way of thinking or a *proto concept* (Urbegriff; Bertalanffy 1928: 74).⁴ The physiologist John Scott Haldane (1917:3) christened this new biology *organicism*, zoologist William Emerson Ritter (1919: I 28) *organismalism*, and theoretical biologist Ludwig von Bertalanffy (1932: 80) “organismische Biologie” (*organismic biology*). Similarly, the embryologist and theoretical biologist Julius Schaxel called for an *organismic basic conception* (organismische Grundauffassung; Schaxel 1919: 125) of biology.

At least three different theoretical strands can be identified inside the organicist movement (see Baedke 2019): *organicism* (e.g., Ludwig von Bertalanffy, Lawrence J. Henderson, William Emerson Ritter, Edward Stuart Russell, Conrad Hal Waddington, Paul Alfred Weiss, Joseph Henry Woodger), *dialectical materialism* (e.g., John Desmond Bernal, Joseph Needham, Marcel Prenant, Julius Schaxel), and different versions of *holistic biology* (including German Ganzheitsbiologie; e.g., Friedrich Alverdes, Bernhard Dürken, Kurt Goldstein, Adolf Meyer-Abich, Hans Böker, John Scott Haldane, Jakob von Uexküll, Emil Ungerer, Jan C. Smuts, William Morton Wheeler).

Members of this heterogeneous movement agreed on the following two viewpoints (Nicholson and Gawne 2015; see also Beckner 1969), albeit with different nuances: First, the

⁴ For historians such as Peterson (2016: 249), British organicism was a ‘meta-theoretical commitment’ about how to conceive organisms and living phenomena. Hein (1969) acknowledges that what distinguished the organicist movement from mechanism or vitalism were different meta-theoretical commitments that lead to disparate standards for understanding (and evaluating) biological evidence and provided different heuristic frameworks.

organism is the most central ontological unit in biology. It transcends the properties of its parts (e.g., genes, cells), influences the part's organization in coordination with environmental cues, and actively constructs its environment. Second, the organism should be fundamental to frame scientific explanations in diverse biological subdisciplines. In particular, organismic organization, emerging in development and in constant interaction with the environment, should be the explanatory and methodological starting point of biology. Accordingly, many (if not all) biological processes – including evolutionary ones – can only be investigated effectively when the unit of the organism is considered.

Members of the organicist movement argued that the right theoretical framework of biology is neither reductionist mechanism nor vitalism, but a *third way* that builds on the above two premises. Against this background, in the next section we focus on three central explanatory roles granted by organicist movement scholars to the organism in biological explanations. As we will see below, these discussions are thematically similar to those held within the EES debate (see section 5).

3 Three explanatory roles of the organism in the organicist movement

Thinkers in the organicist movement built their explanations of biological phenomena by ascribing chief epistemic roles to organisms. Here, we outline three central ones: (1) contextualizing parts (e.g., genes, cells) in development; (2) framing organism-environment causal reciprocity; and (3) understanding the role of agential processes in evolution.

(1) *Contextualizing genes and cells in development*: Organicists thought that the parts of organisms are molded and constituted in a dynamic interaction that involves the entire organism and its environment (Esposito 2017). Organisms, as dynamic wholes, have to be conceived as active entities that build themselves, capable of adapting and changing their forms and behaviors according to external circumstances. In a representative example of organicist rationale, E.S. Russell (1930:149) asserted: “The life of an organism is essentially a unitary functional or dynamical process, in which *whole* and *parts* are inextricably interconnected. Both whole and parts are together the expression of the life of the individual.”

The discussion about the relationship between organismic wholes and parts was important for early 20th century biologists, especially in how they should conceptualize the phenomena of development and heredity. For instance, in his 1930 book *The Interpretation of Development and Heredity*, E.S. Russell asked:

Is development to be treated as essentially an activity of the organism as a whole, or can its full explanation be found by analysing the process into its constituent elements? Is heredity essentially the reappearance and realization of the functional potentialities of the whole, or are the separate characters of the organism transmitted piecemeal, being represented separately in material form in the germ? Are development and heredity functions of the organism as a whole, or functions of its cells, or of still smaller constituent units? In general, is the organism a real unity or individual, not completely reducible to its constituents, or is it a mere composite, built up as a hierarchy of independent units? Can the whole be fully explained in terms of its parts, or must the parts ultimately be explained in terms of the whole? (Russell 1930: 2-3).

For some authors of the organicist movement, the organismic whole should always be explanatorily salient. In that same vein, Russell (1930: 240) maintained that “the organism is from the beginning a whole, from which by self-differentiation the parts are derived”; taking an idea from an epistolary exchange with philosopher of history R. G. Collingwood, he claimed that “(t)he parts are the way in which the whole organizes itself” (Russell 1930a: 240 fn1). Developmental biologist Bernhard Dürken contended that “[i]t should not be said that the organism as a whole is built up of parts, but that the organism, which is characterized through a consistent wholeness, develops parts and then, subsequently, has parts” (Dürken 1936: 17; German original). In other words, the whole temporally precedes the differentiation of the parts or, even more, for some authors it is ontologically prior compared to the parts (Meyer 1935: 88). Thus, scholars of the organicist movement argued that organismic wholes always have to be investigated first in the study of development (see also Ungerer 1965: 80-82).

Leveraging this organicist framework of wholeness, organicist authors argued that heredity should be framed as the re-constitution of ontogenetic resources and causal interactions that bring about the constancy (or deviations) of form from one generation to the next.⁵ Against the burgeoning views of geneticists of his time, Russell (1930:16) argued that “the real cause of resemblance is the same factor that creates this organic architecture. *Hereditary resemblance is [...] a byproduct of development*, and will be explained only when we succeed in explaining development” (emphasis added). Heredity and development, Russell believed, should be jointly studied as they constitute two-sides of the same organic phenomenon.

⁵ Russell (1930) strongly disagreed with the adjudication of a special causal status to lower-level hereditary units such as genes or Weismann’s biophors. He even argued that it is misguided “to ascribe to these units the powers and capabilities which we know only as belonging to the organism as a whole” (Russell 1930:49).

(2) *Organism-environment reciprocity*: The organicist movement not only rested on philosophical reflections and scientific theorizations, but was driven by multiple experiments that were carried out on the plasticity, robustness and inextricable embeddedness of plants and animals in their environments (see Müller 2017a, c; Nickelsen 2017; Nicoglou 2018; Baedke 2019). Also noteworthy were studies on the environmental responsiveness of developing organisms, including their transgenerational effects, which were undertaken in the first half of the 20th century (for example, the work conducted in Vienna at the *Biologische Versuchsanstalt*, directed by the Austrian zoologist Hans Leo Przibram; see e.g., Müller 2017a, b; Nickelsen 2017: 170-175; Nicoglou 2018:107-111).

In particular, the idea of reciprocity between organism and environment was a fundamental principle for multiple organicist positions. For example, J.S. Haldane (1884:32-33) highlighted: “The organism is thus no more determined by the surrounding than it at the same time determines them. The two stand to one another, not in the relation of cause and effect, but in that of reciprocity.” Organism-environment reciprocity was mainly construed as a relationship of *ontological co-constitution* or one of *reciprocal causation* (for a detailed analysis, see Baedke et al. 2021). According to the view of ontological co-constitution, organism and environment are commingled and form a single interacting system that cannot be disentangled. In turn, reciprocal causation is usually defined as a feedback loop between two interacting, yet separate entities or processes (in this case, an organism and its particular environment). The notion of organism-environment reciprocity had different origins in organicism, dialectical materialism, and (German) holistic biology. For holistic thinkers, such as Haldane or the theoretical biologist Jakob von Uexküll, this idea was inspired by readings of Immanuel Kant (see Brentari 2015; see also, e.g., Ungerer 1919; Haldane 1931). In his 3rd critique (*Kritik der Urteilskraft*), Kant described reciprocity as the distinctive organizational pattern of organisms. The organism is generated and maintained as a whole by the reciprocal interaction of its parts. This Kantian view of reciprocity between the organismal whole and its parts was expanded and applied to different levels, such as the relation between organisms and their environment (see Canguilhem 2008 [1965]).

For British organicists like embryologist Conrad Hal Waddington and theoretical biologist Joseph Henry Woodger,⁶ the perspective of A.N. Whitehead on the organism-environment relationship was highly influential. Whitehead argues that there are “two sides to

⁶ In general, British organicists were deeply inspired by Alfred North Whitehead’s (1925) “philosophy of organism” – a systemic view of the organism that emphasizes the complex interrelatedness of its developing parts with each other and the environment (see Peterson 2011, 2016; Nicholson and Gawne 2014).

the machinery” of evolution (Whitehead 1925:163). One side includes natural selection in which the externalist “givenness of the environment dominates everything.” But there is another side which scholars had paid less attention to: “The other side of the evolutionary machinery, the neglected side, is expressed by the word creativeness. The organisms can *create their own environment*” (emphasis added).

Waddington picked up Whitehead’s proto-niche construction idea (see Waddington 1929: 66, 1953, 1957: 104-108; Waddington et al. 1954). He argued that evolution involves not only changes in the genetic system, the epigenetic system, and the system of natural selection, but also in the “exploitive system”. The last system refers to the influence exerted by the organism on its environment, which creates a feedback loop between organismal activities and environmental selection pressures: “Animals [...] live in a highly heterogeneous ‘ambience’, from which they themselves select the particular habitat in which their life will be passed. Thus the animal by its behaviour contributes in a most important way to determining the nature and intensity of the selective pressures which will be exerted on it” (Waddington 1959: 1635-1636). Waddington highlighted that, in order to develop a theory of evolution that includes the exploitive system, biologists should replace views of unidirectional causality with reciprocal causation: “we have to think in terms of circular and not merely unidirectional causal sequences“ (Waddington 1960: 400; see also Baedke et al. 2021).

Another group of the organicist movement, dialectical materialists, came to similar views on reciprocity, although, compared to organicists and holists, through quite different philosophical sources. They were influenced by Hegel’s and Schelling’s romantic philosophies of nature and by the writings of Karl Marx and especially Friedrich Engels’ *Dialectics of Nature*. Dialectical materialists like Julius Schaxel (1931), biochemist Joseph Needham (1937) or zoologist Marcel Prenant (1935) argued that all processes in nature comprise reciprocal influences between antagonists that lead to qualitatively different and novel forms (or levels) of organization (see, e.g., Hopwood 1997). They argued that these formations (from quantitative reciprocal interactions to qualitative novel forms) could only be captured by a *dialectical biology* (Schaxel 1931: 492), a conceptual framework focusing exclusively on the mutual interactions between organisms or the organism and its environment. This dialectical framework formed the theoretical background of Levins and Lewontin (1985)’s book, although these influential evolutionary biologists did not acknowledge this older and rich theoretical tradition.

(3) *Organismal agency*: The observations that organisms have the ability to actively react to environmental changes, autonomously construct and maintain their organization and identity despite changes in material composition and form, regenerate, self-reproduce, etc., have long puzzled philosophers and scientists. How do we explain the apparent purposiveness of organismal development and actions? Are organisms agents of their own development and evolution? To put it simply, we could say, following philosopher of biology Robert Wilson (2005: 6-7), that “an agent is an individual entity that is a locus of causation or action. It is a source of differential action, a thing from which and through which causes operate.”

Many authors that belonged to the organicist movement defended the general view that organisms “differ from machines [...] by virtue of the fact that their purposiveness is internal or immanent, and also because their form and activities are regulable” (Russell 1924a: 267; see also Nicholson 2013). The intrinsic purposiveness of organisms (in contrast to the extrinsic purposiveness of machines, always set by an external designer) means that organisms, through their activities (that are usually responsive to environmental inputs and contingencies), pursue goals of their own, such as surviving, reproducing, overcoming challenges throughout life cycles, or simply maintaining their organization in manifold developmental contexts.⁷ For example, Russell devoted entire books to review the empirical manifestations of organismal agency in developmental phenomena like regeneration and in animal behavior (Russell 1934, 1945; see also Rignano 1930 for a similar case).

In general, theories of organismic agency and/or the constructive potential of organisms were widely discussed by members of the organicist movement. These authors tried to develop a middle position between, on the one hand, attempts to outlaw the concept of purposefulness from the study of organisms (or to restrict it to intentional behaviors; see, e.g., Roux et al. 1912: 460) and replace them altogether with mechanistic explanations that rest on physiochemical reduction, and, on the other, vitalist endeavors to frame organismic purposiveness in terms of non-physical influences, such as Driesch’s (1908) postulation of the *entelechy*. By drawing on rich philosophical sources, like older Aristotelian and neo-Kantian debates, as well as on phenomena such as self-organization and the explorative processes of development and

⁷ This should not be confused with the idea that there is an underlying teleology in all of Nature (what Okasha 2018 would call “agential thinking type 1”). Authors in the organicist movement embraced type 2 of “agential thinking” (*sensu* Okasha 2018), i.e., they conceptualized organisms as evolved agents, as difference-makers in the world, but that did not lead them to embrace speculative views about the underlying purposes of Nature (for example, seeing natural selection as picking out phenotypes in accordance to a preordained goal). The teleological explanations of the organicist movement were mainly concerned with the agentic character of organisms and not with a guiding *telos* in life or evolution.

behavior, they tried to better understand the goal-directedness of organisms (e.g., Haldane 1917; Schaxel 1919; Russell 1924b; Bertalanffy 1928). According to their views, the organism molds itself and its environment in development and evolution, like “clay modeling itself” (Russell 1924b: 61). In particular, the organism was conceived as an “active environment-related subject” (Meyer-Abich 1948: 39; German original).

The active role that organisms play in evolution was pointed out in myriad scientific works of the organicist movement (for an analysis, see Esposito 2017; see also Nicoglou 2018: 111-116). John Scott Haldane, for example, emphatically rejected conceptions of organisms as passive subjects in evolution (see Haldane 1935). The German botanist Emil Ungerer parted ways with the regulative ideal of the Kantian view of teleology (assumed only as a heuristic principle to guide scientific research) and, instead, investigated agency as a constitutive property of organisms in his studies of plant regulation (see Ungerer 1919). In that same line, the Dutch eco-morphologist Cornelis van der Klaauw argued that the heuristic view of agency was not enough for biology, and that organisms exhibited constitutive purposiveness during development. In his eco-morphological approach, van der Klaauw (1948) developed frameworks to study animal morphology that took several elements into account, such as the ecological setting of the organism and its environment, the functions performed, as well as the relationships between the organism and its conspecifics, and those established with other species.

The theory of *Umkonstruktion* by the German eco-morphologist Hans Böker, fueled through various field excursions and empirical research in several vertebrate species, can be interpreted as another example of investigation around some facets of organismal agency and evolution. According to Böker (1935), the organism should be understood as a historical whole that is in harmony with its parts and with the environment in which it thrives; whenever this bio-morphological equilibrium is disturbed by changes originating in the environment, the organism must strive to regain it, otherwise it is at risk of dying. The morphological perturbations prompted by environmental change can subsequently bias variation in the interrelated parts of the organism in a long series of changes that dovetail to restore the bio-morphological equilibrium. For Böker, this did not happen through a *bona fide* Lamarckian process, but rather, by a multigenerational selection process similar to what would later be called *genetic assimilation* (for an analysis of Böker’s stance, see Fábregas-Tejeda et al. 2021).

Even Conrad Hal Waddington would assign some important evolutionary role to organismal agency in his later works. His basic idea was that “before an organism’s

environment can exert natural selection on it, the organism must select the environment to live in” (Waddington 1961a:89). For instance, he subverted the textbook exemplar of adaptation and directional selection of the peppered moth in the industrially darkened forests of Great Britain through his view of the exploitive system. Waddington (1961a) highlighted that, in the industrial melanism case, before natural selection can sort out variants according to their fitness differential, organisms first have to select the environment in which they will live. And this act that occurs during the ontogeny of peppered moths is not devoid of evolutionary significance: “The effective environment in which they are subjected to natural selection is, in fact, the darkened bark which *they themselves choose*; it is not something completely external, but is a combination of the outside world and the moth’s own behavior” (Waddington 1961a:90; emphasis added).

As a final example of agential thinking in the organicist movement and its heirs (of many more that could be cited), British ethologist William Homan Thorpe argued that the behaviors of organisms not only affect their development, but have downstream causal effects in the speciation patterns of populations. For example, he studied how genetic changes could follow and make an acquired behavioral preference hereditary (e.g., Thorpe and Jones 1937; Thorpe 1940), a phenomenon akin to what was later called the *Baldwin effect* by Julian Huxley and George Gaylord Simpson. In fact, historian of science Gregory Radick (2017) contended that Thorpe’s thinking actually infiltrated into the Modern Synthesis. Thorpe’s empirical work, as publicized by Julian Huxley in his 1942 book *Evolution: The Modern Synthesis*, served to popularize and revitalize “the fortunes of what became one of the mainstays of agential science [in evolutionary research], the Baldwin effect.” In that sense, Radick claims, the Modern Synthesis was not completely inimical to animal agency, a point that we will revisit in the next section.

As we saw, authors in the organicist movement granted to organisms three central explanatory roles: (1) contextualizing genes and cells in development; (2) underscoring organism-environment reciprocity; and (3) incorporating the role of agency in evolutionary processes. But what happened to these organism-centered frameworks after their heyday during the interwar period? Why do only few evolutionary biologists know about them today? To that we turn our attention now.

4 Streamlining the organism after the Modern Synthesis

Recently, historians of biology have investigated some of the reasons that explain the (almost complete) disappearance of organicism from discourses, theorizations about the phenomena of the living and biological practices in the second half of the 20th century. Donna Haraway (2004 [1976]) argued that, in the case of the Theoretical Biology Club, the organicist stance was diluted because it did not have the correct institutional (and disciplinary) support to keep it afloat (see also Peterson 2016):

Needham tried to construct an institute around the new paradigm commitments but was unable to obtain needed financing. Beginning in 1934 he corresponded with Dr. Tisdale of the Rockefeller Foundation, which was then interested in fostering study on the borderlines of traditional disciplines. [...] Needham submitted a long memorandum outlining a plan for an Institute for Physico-chemical Morphology [...]. By 1938 the idea was dead [...]. The reasons are controversial and complex, but the success of Needham's institute certainly would have altered the course of biological investigation in England after the 1930s. Instead, factors combined to break up the collaboration of members of the paradigm community, and World War II finally sealed the issue (Haraway 2004:134).

For example, in his original plan for an organicist research institute (see also Abir-Am 1987), Needham had nominated Waddington to lead the area of experimental embryology, Joseph Henry Woodger would head the section of theoretical embryology, and, as head of the division of genetic embryology, Needham designated Theodosius Dobzhansky (Peterson 2016: 118), who later joined the buoyant Californian group of Thomas Hunt Morgan and eventually became one of the chief architects of the Modern Synthesis.

As Abir-Am (1982: 341) argues, in the history of 20th century biology, decisions in funding policies determined the course of nascent disciplines (or, at least, were central in their directions). Just as the Rockefeller Foundation turned its back on Needham, they began to push for research in what would later be called "molecular biology" (see Kay 1993). Post-war life sciences funding policies would favor research in reductionist fields such as molecular biology (see de Chadarevian 2002), rather than holistic research like that pursued by organicists. "The molecular view of life," as historian Lily Kay (1993) would call it, prevailed over what we would call the "organicist view of life" (see also Nicholson 2014). Brooks (2019: 24) says on this point: "It was, as the story goes, the politics of research funding that seemed to doom

organicism: With the molecular revolution just around the corner, it seemed simply the wrong place and time for the movement to take root”.

The German holists, in a similar case to the British organicists, also planned the establishment of a center to anchor organism-centered research: in 1942 Adolf Meyer-Abich and the particle physicist Pascual Jordan founded the journal *Physis: Beiträge zur naturwissenschaftlichen Synthese* in which they announced the creation of a research institute to explore organicist themes from multiple scientific disciplines (Beyler 1996: 268-269). However, the idea would not come to fruition and the journal *Physis* would not get very far (see Dahn 2019). The project to discipline German holism (with research institutes, journals, and specialized communities) would also not take root (see Beyler 1996). In general, German holistic biology would be discredited after the events of World War II: because of its affiliation with Nazi ideology, biologists from other latitudes would judge these theorizations as anathema and deliberately avoided citing German-speaking organicist authors (Wise 1994: 244; for analyses, see Harrington 1996; Rieppel 2016).

Moreover, around those years many older members of the international organicist movement had died (J. S. Haldane in 1936; Wheeler in 1937; Henderson in 1942; Schaxel in 1943; Ritter, Dürken, and Uexküll in 1944; Alverdes in 1952).⁸ Others turned their research interests to new topics – e.g., Woodger to logic, Needham to the history of China, Bertalanffy to systems rather than organisms (see Nicholson and Gawe 2015; Peterson 2016), or to politics and/or popular science writing (Schaxel and Bernal). For many of the German-speaking advocates of holistic ideas, the end of the Second World War was a *caesura*, a break with the past. In the 1940s and 50s the (relative) number of monographs discussing organisms significantly dropped (see Figure 1).

⁸ What’s more, during the Nazi upsurge in Austria, organicist scientists based at the *Biologische Versuchsanstalt* were expelled from their workplace, barred from entering and some, such as its director Hans Przibram, were transported to (and later executed in) concentration camps (Taschwer 2014; Müller 2017c).

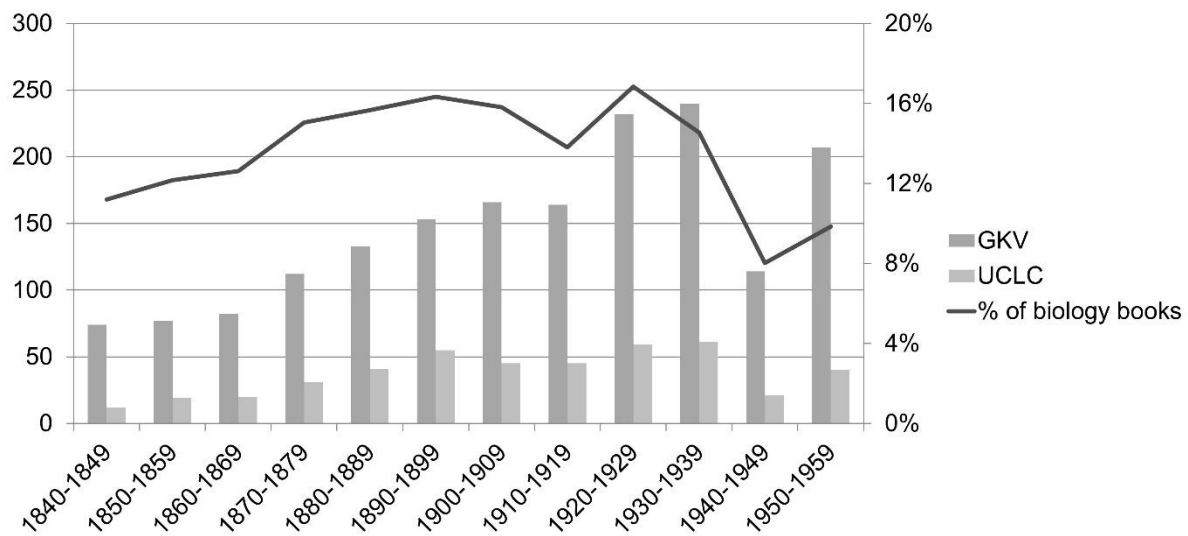


Figure 1: The use of the concept of the organism between 1840 and 1959. Depicted is the number of monographs containing *organism*, *organisms*, *Organismus*, or *Organismen* in their titles. Entries are taken from two bibliographic databases: University of Cambridge Libraries Collection, UCLC (light grey bars) and German Union Catalogue, GVK (dark grey bars). Only biological books are considered. Single monographs may appear more than one time in each database. The black line shows the percentage of all “organism books” (in GVK and UCLC) compared with all biological books published per year (i.e., entries in both databases matching keyword or substance for “biology” or “Biologie”) (see Baedke 2019).

The Theoretical Biology Club disbanded and received strong criticisms from scholars like the immunologist Peter Medawar, who, although was originally trained under the guidance of Woodger and Waddington, would not hesitate to publicly criticize organicism as a form of antiquated, speculative and useless way to do biology once he landed positions of power (Peterson 2016: 156-158). In addition to that, Ernst Mayr on several occasions discredited the work of organicists by wrongly cataloging it as “Lamarckian” (and, in the case of Conrad Hal Waddington, even as “Lysenkoist”; see Robinson 2018: 179, 184, 187, 190),⁹ a label of mistrust that, however, served to dismiss the organicist *corpus* in the second half of the 20th century and to justify that evolutionary biologists overlooked it (see Peterson 2016: ch. 11).

In this post-war scenario, the organicist movement left the international arena to dwell in obliviousness; in parallel, the Modern Synthesis, which should be understood as both a

⁹ Waddington always considered himself a *bona fide* Darwinian and contended that genetic assimilation was not an alternative to explanations that appealed to gradual, random genetic mutations and natural selection, but supplementary to them (see, e.g., Waddington 1961b). Through his views on developmental canalization, Waddington considered genetic assimilation to be a genuine Darwinian mechanism underpinning the inheritance of acquired characters, not related whatsoever to Lamarckian soft inheritance but depending upon the genetic capability of organisms to respond plastically to environmental changes via non-directed, preexisting cryptic genetic variation (for a detailed analysis, see Baedke 2018: 27-29; Loison 2019)

movement that sought theoretical unification and a discipline-building effort (see Smocovitis 1994), held sway. Furthermore, molecular biology and evolutionary biology (which would become increasingly gene-centered with the passing of decades) would dominate the landscape of the second half of the 20th century. These two movements had a significant impact on the explanatory standards of evolutionary research, especially on those three epistemic roles granted to the organism by the organicist movement that subsequently were underestimated, ignored or merely abstracted away.

First, genes became strongly decoupled from their organismic context and came to be regarded as the primary determinants of phenotypic characters. As Gawne et al. (2018) have showed, the vast majority of evolutionary biologists from the second half of the 20th century onwards construed a simplified view of the genotype-phenotype map and lost sight of the fact that the origin of phenotypes can only be properly understood by integrating findings from all levels of organization of an organism (see #Ågren in this volume#). While molecular approaches offered a (to some extent successful) reductionist research program that abstracted from the context of the whole organism, population geneticists focused on the transmission of alleles and their dynamics in populations,¹⁰ rather than on the developing organism (which was later held to be merely an epiphenomenon or a vessel of genetic programs) with all its material, concrete interactions with the environment or other conspecifics (see Walsh 2019). Although there were some good scientific reasons for taking this approach (Ågren 2021) and even some architects of the Modern Synthesis did not entirely forgo an ontogenetic perspective (see Depew 2017), an important consequence was that the organism was no longer understood as a major ontological and theoretical challenge that had to be addressed by evolutionary theory (see also Walsh 2015).¹¹

Second, the explanatory roles of organism-environment reciprocity in the organicist movement changed significantly after the institutionalization of the Modern Synthesis and especially through later developments in evolutionary biology. In the course of the second half of the 20th century, views of organism-environment reciprocity were increasingly marginalized (for a detailed discussion, see Baedke et al. 2021). This trend was driven by the attempt to

¹⁰ One might even qualify this statement further. Medawar (1981) claimed that “The most important single innovation in the modern synthesis was [...] the new conception that a population that was deemed to undergo evolution could be best thought of as a population of fundamental replicating units—of genes—rather than as a population of individual animals [or organisms in general]”.

¹¹ An important exception, although not very influential in the last years of his career, was Sewall Wright, who still vouched for the importance of the organism in evolution against far-reaching gene-centered currents (see Wright 1980; see also Steffes 2007; Ågren 2021).

establish clear boundaries between organisms and environments as a methodological stipulation for fruitful research – as Haldane (1936:349) put it, this separation is “a practically and theoretically valuable abstraction” for population genetics. In this view, the environment is seen as an external causal factor, that, apart from generating selection pressures on organisms, is a “source of error that reduces precision in genetically studies”, and thus one has “to reduce it as much as possible” (Falconer 1960: 140). Waddington (1957: 189) denounced this shortcoming: “Any further influence which the environment might have was degraded to the status of mere ‘noise’ in the system of genetic determination.”

As another example of an impoverished view of the causal roles that the environment plays in evolution, Mayr (1970:2) claimed: “the *true role* of the environment in evolution could not be understood until the nature of small mutations and of selection was fully comprehended” (emphasis added). Moreover, the persuasive split between proximate and ultimate causes advanced by Mayr (1961) resulted in a move away from the study of organism-environment reciprocity: through the lens of this dichotomy, the organism is only a developmental unit, wherein proximate causes are instantiated through the decoding of a genetic program; in contrast, the environment becomes evolutionary relevant as the reservoir and source of selective pressures, which are ultimate causes of evolution that shape the make-up of genetic programs. In line with these views, mainstream evolutionary biology increasingly adopted an asymmetric, unidirectional view of the organism-environment relationship (e.g., Williams 1992: 484).

In addition, evolutionary studies on reciprocity focused on other *relata*. Instead of organism-environment reciprocity, gene-environment reciprocity was increasingly studied in population genetics (Haldane 1946; Lerner 1950; Falconer 1952), for example, through path analysis (Wright 1960). New models of reciprocal relations between genes and populations as well as genes and environments (Fisher 1930; Kirkpatrick 1982) addressed population regulation by genetic feedbacks (e.g., Pimentel 1968), positive and negative frequency-dependent selection (Fisher 1930; Wright 1969; Charlesworth 1971), and eco-evolutionary dynamics (Thompson 1998). The importance of these evolutionary models notwithstanding, and despite what some scientists claim (Brodie III 2005; Svensson 2018), the vast majority of these models did not encompass organism-environment reciprocal causation, but focused on other *relata*. As a consequence of these developments, the organism lost its previous explanatory function as a causal agent that constructs its environment, and thus its own development and evolution.

Third, and as an expansion of the previous marginalization, the view of the organism as an agent of development, and especially evolution, disappeared within the dominant framework of evolutionary biology. There, genes were construed as the sole agents of evolution, most of the times in ways that turned out to be empirically and conceptually unwarranted (see Okasha 2018: ch. 2; for criticisms of the cognate idea that genes are the main agents of development, see, e.g., Moss 2003; Griffiths and Stotz 2013). According to the gene-centric rationale, “[t]he production of whole organisms, and their differential survival and reproduction, are causally necessary consequences of the activities of [genetic] replicators” (Walsh 2017:243). For instance, in a highly influential book, Monod (1971) contended that organismic purposiveness could be completely reduced and accounted for by citing invariant molecular mechanisms that get transmitted intergenerationally (for an analysis, see Walsh 2017).

While it is true that Modern Synthesis-inspired work integrated the import of some organismal factors into their evolutionary theorizations, such as the evolutionary role of behavior in particular cases of Baldwin effect (although considering it rather marginal and not challenging central tenets of the synthetic theory, see Simpson 1953; see also Depew and Weber 2003 and chapters therein), most of the phenomena associated with organismal agency discussed inside the organicist movement became unheeded. One of the reasons for this development was that teleology “transmogrified” into teleonomy, as philosopher Krieger (1998) would say.

Colin Pittendrigh (1958) proposed the term “teleonomy” to encompass the study of purported end-directed processes (such as adaptation) in the hope of ridding biology from the encumbrances of the loaded term of teleology. In the hands of Mayr (1961:1504), however, teleonomy became restricted to “systems operating on the basis of a program, a code of information”. For Mayr (1974:140), this meant that a “*teleonomic process or behavior is one which owes its goal-directedness to the operation of a program*” (emphasis in original). In particular, this implied that all the seemingly goal-directed processes unfolding in ontogeny (including agential behaviors) are under the controlling action of a genetic program inscribed in the sequence of DNA (for a distinction between closed and open programs, see also Mayr 1964).¹² Mayr’s understanding of teleonomy was backed up by a widespread adoption among biologists of concepts from cybernetics and information theory (see Mayr 1985 [1974]: 134, 142, 144), which collected criticisms from some authors that used to belong to the organicist movement (see Bertalanffy 1951), but ultimately to no avail.

¹² For a different reading of the concept of genetic program in Mayr’s work, see Dickins (2021).

Moreover, other influential evolutionary biologists, such as Simpson (1958: 520-521) and Williams (1966: 258-269), advocated for the epistemic legitimacy of shoehorning all agential processes under the heading of *teleonomy*. Although a scientific and philosophical debate ensued on the proper status of teleological (and teleonomic) explanations in late 20th century evolutionary biology, the genetic program understanding of intrinsic purposiveness (shaped by bouts of natural selection) prevailed in the field (for an analysis, see Krieger 1998). If organisms *seem* to be agents to us is merely because genetic programs that encode purposive-like traits were selected for in evolutionary time: “Each particular program is the result of natural selection, constantly adjusted by the selective value of the achieved endpoint” (Mayr 1974:141). If not vitalism, the only conceivable alternative for many evolutionary biologists was “to regard internal [organismic] teleology as a product of evolution by natural selection” (Dobzhansky et al. 1977: 96). Organismal agency, then, was rendered a mere evolutionary *product*, but not a *cause* that has some bearing on the process of evolution.

An additional problem was that many evolutionary biologists collapsed discussions concerning finality in evolution (e.g., divine design, orthogenetic trends) with the problem of organismal purposiveness and specifically of agential, goal-directed processes. This contributed to making most evolutionists think that, using Okasha (2018) useful terminology, “agential thinking 1” (the problem of teleology in nature) and “agential thinking 2” (the treatment of evolved entities, such as organisms, *qua* agents that pursue intrinsic goals) is one and the same problem. Uncareful conceptual treatments of the subject of teleology made any discussion of organismal agency equivalent to teleology in its broadest sense.¹³ Accordingly, it is no surprise that a fair number of evolutionary biologists are still today reticent to entertain the idea that organisms are causal difference-makers in the world and that some evolutionary consequences must obtain from this fact, a view which is usually scorned at.

In sum, many trends in evolutionary biology lead to an explanatory framework that focused on the transmission of genes and its effect on populations, rather than on the developing organism and its reciprocal interactions with the environment and agential activities. Evolutionary thinkers established a narrower conception of the organism, both internally (organisms are primarily the product of genetic programs) and externally (organisms are not agents that co-construct their environment and thus modulate their selection pressures).

¹³ Mayr (1974) did draw a distinction between different senses of teleology in biology: (a) Unidirectional evolutionary sequences; (b) goal-directed processes; and (c) teleological systems. As organismal agency mostly pertains to (b), it is unfortunate that most biologists did not follow Mayr’s pedagogical taxonomy.

However, this “eclipse of the organism” in evolutionary theory (see Walsh 2015) has been increasingly challenged since the 1980s and especially in recent years.

5 Rediscovering explanatory roles of the organism in the EES

Since the 1980s, many of the calls to extend, expand or replace the Modern Synthesis (see Depew and Weber 2013 for an overview) channeled discourses that called for the reconstitution of the organism as a central unit in evolutionary biology. Stephen J. Gould, for example, judged the decline of the concept of organism as a setback to be remedied by the emergence of a reformed theory of evolution that, among other things, would return “to biology a concept of organism” (Gould 1980: 129). David Rollo, in the preface of his book *Phenotypes: Their Epigenetics, Ecology and Evolution*, stated that the purpose of his work was to return the organism to its rightful place as the center of selection and evolution (Rollo 1994: xi). Susan Oyama, putting forward her vision of the place of developmental systems theory (DST) in evolutionism, explained that her goal was to “put organisms back” into evolution or, in other words, to “restore the organism” (Oyama 2000: 30–31).¹⁴ In a similar vein; Brian Goodwin stated in 1999:

Organisms have *disappeared as fundamental entities*, as basic unities, from contemporary biology because they have no real status as *centres of causal agency*. Organisms are now considered to be generated by the genes they contain. [...] Thus organisms are arbitrary aggregates of characters, generated by genes, which collectively pass the survival test in a particular environment. [...] [T]here is *no causally efficacious unit* that transcends the properties of the interacting parts. This is the sense in which organisms have disappeared from biology (Goodwin 1999: 230; emphases added).

This situation, however, has changed in recent years. Especially advocates of the EES try to reestablish the organism as a central explanatory unit in evolutionary biology. This new “organism-centered perspective” (Laland et al. 2015) stresses the idea that organisms are the central explanatory units to not only understand evolutionary relevant dynamics in (gene-) regulatory processes during embryo- and morphogenesis, but also to study developmental plasticity, non-genetic channels of inheritance, and constructive behaviors that shape organisms’ niches and selection pressures (West-Eberhard 2003; Jablonka and Lamb 2005, 2017; Laland et al. 2014, 2015; Walsh 2015; Sultan 2015; Müller 2017a; Uller et al. 2018,

¹⁴ For a different reading of the role of the organism in DST, or the lack thereof, see Pradeu (2010).

2020). This new framework of the EES unwittingly ties in with the central three cornerstones of organism-centered evolution once defended by the organicist movement in the early 20th century. This includes, (1) the conceptualization of genes as parts in extracellular, organismal and developmental contexts, and the consideration of these contextual wholes in shaping evolutionary trajectories; (2) the idea that evolution is the result of organism-environment reciprocal interaction (rather than of external environmental factors causing changes in allele frequencies and population dynamics); and (3) that organismal agency is a key explanatory component for understanding how organisms co-construct their evolution. Let us briefly discuss these three revived dimensions of the organism.

First, the organism is granted an explanatory role inside the EES and related Evo-Devo views of evolution that allows properly contextualizing parts and their causal contributions in development. For Laland et al. (2015: 6), lower levels (e.g., genes) do not prevail over higher levels of organismal organization as causation runs reciprocally between them: “causation not only flows from the lower levels of biological organization, such as DNA, ‘upwards’ to cells, tissues and organisms, but also from the higher level ‘downwards’, such as through environmental- or tissue-induced gene regulation” (Müller 2017a). In particular, the view of constructive development defended inside the EES “does not assume a bijective function (i.e., a one-to-one correspondence) between genotype and phenotype, nor grants causal privilege and programmatic jurisdiction to genes driving individual development; instead, the developmental system is viewed as responding flexibly and creatively to internal and external inputs, through condition-dependent gene expression, and through physical properties of cells and tissues and ‘exploratory behaviors’ of several systems” (Fábregas-Tejeda and Vergara-Silva 2018a: 179; see also Gawne et al. 2018 on the de-idealization of the genotype-phenotype map).

A recurring theme in Laland et al. (2015) is the fact that phenotypic variation can be biased by the processes and organizational dynamics of development, which channel the evolution (i.e., increasing the probability of occurrence) of certain functional phenotypes and restricting the possible space of realized forms. Developmental bias, an Evo-Devo notion, has been mobilized as an important epistemic cornerstone of the discussion of the structure and assumptions of the EES. Another important key theme for Evo-Devo, facilitated variation (*sensu* Kirschner and Gerhart 2005), is used as a conceptual scaffold by EES proponents to explain the presence of developmental biases: the core processes of development concurrently exhibit high robustness and exploratory behaviors that allow them to stabilize and select certain

states over others (Laland et al. 2015; see also Uller et al. 2018).¹⁵ Additional key themes of Evo-Devo (e.g., evolvability, modularity) are also mobilized in EES explanations (for an analysis, see Fábregas-Tejeda and Vergara-Silva 2018a). Moreover, EES defenders embrace a view of development in which the organism co-constructs its own developmental trajectories by means of plastically responding to, integrating and shaping environmental cues.

Second, in recent years, evolutionary biology in general and advocates of the EES in particular tied in with the older idea of organism-environment reciprocity (see Baedke et al 2021). This especially concerns research on phenotypic plasticity and niche construction (Laland et al. 2013, 2015; Mesoudi et al. 2013; for discussion, see Fábregas-Tejeda and Vergara-Silva 2018a, b; Svensson 2018; Buskell 2019; Baedke 2019). Here, organisms' plasticity and niche construction behaviors are studied as feedback circles that modify the natural selection pressures working on the constructor and other organisms (Lewontin 1983; Sterelny 2001; Odling-Smee et al. 2003; Chiu and Gilbert 2020).¹⁶ This process is said to have a co-directive effect on adaptive evolution “by imposing a consistent statistical bias on selection” (Laland et al. 2017). Examples include the building of artifacts by animals, like nests, mounds, burrows, and mounds, the creation of shade and change of nutrient cycling by plants, and the modification of physical and chemical conditions. By focusing on such examples, for instance, Clark et al. (2020) collected evidence that niche construction affects the variability and strength of natural selection in a way that is possible to distinguish between constructed and non-constructed environmental sources of selection.

In order to explain the feedback between constructing organisms and environments as well as the developmental effects on evolutionary trajectories (and vice versa), advocates of the EES argue that the traditional dichotomy between ultimate and proximate causes (Mayr 1961) should be replaced by a concept of *reciprocal causation* (Mesoudi et al. 2013, Laland et al. 2011, 2013, 2015, 2017).¹⁷ This view holds that developing organisms are not only products but also causes of evolution and starting points of evolutionary trajectories. Thus, the proximate causes of developmental processes should not be strictly isolated from ultimate causes of evolutionary processes. Instead, proximate causes feed back to affect the direction and rate of

¹⁵ For a counterposition on facilitated variation and its compatibility with traditional evolutionary thinking, see Dickins (2021: 142-144).

¹⁶ For conceptual frameworks that distinguish diverse kinds of feedback processes in niche construction, see Aaby and Ramsey (2020) and Chiu (2019).

¹⁷ For an overview of criticisms against Laland et al.'s concept of reciprocal causation, see Baedke and Gilbert (2020). For conceptual challenges that go along with adopting views of organism-environment reciprocity, see Buskell (2019) and Baedke et al. (2021).

adaptive evolution. As a consequence, investigating developmental mechanisms, from mechanisms of gene expression or cell and tissue development to organisms' constructive actions in their local environments, offer explanatory relevant information on how organisms evolve.

Some authors involved in the EES debate trace back this idea of causal reciprocity between organism and environment to Levins and Lewontin's (1985) book *The Dialectical Biologist* (see Svensson 2018) or cite Waddington (1969) to highlight proto-niche construction views (see Laland et al. 2016; see also Odling-Smee et al. 2003) – albeit without being aware of the fact that these authors are actually late examples of an older and much richer movement that took organism-environment reciprocity as a theoretical starting point to reason about evolution, independent of (and not as a reaction to) the MS.¹⁸

Third and finally, this renewed interest in organisms' constructive roles in shaping their selective environment in the EES reintroduced the concept of organismal agency to evolutionary theory in recent years. EES advocates commonly use agential terms like “active phenotypes” (Watson and Thies 2019), “active agents” and “purposive organisms” (Laland et al. 2019; see also Sultan 2015; Sultan et al. 2022). Rather than embracing a spurious vitalist notion of agency and non-material purposiveness, these authors seek to highlight behavioral drivers of evolution or the general idea that organisms (and their phenotypes) are leaders in evolution (West-Eberhard 2003, 2005). Genes merely follow agential changes in evolution. In other words, organisms introduce (in a biased manner) new phenotypes into populations, which are subsequently stabilized by genes.

While, so far, no consensus has been reached on which kind of theory of agential causation should be adopted to strengthen especially the status of niche construction as a theory, several frameworks have been put forward. Laland et al. (2019) draw on classical understandings of the purposiveness of organisms through thermodynamics and self-organization (see Schrödinger 1944; see also Nicholson 2018; Baedke 2019). Others have highlighted that any theory of evolutionary-relevant purposive behavior of organisms should include the experiential side of niche construction (Sultan 2015; Chiu 2019).¹⁹ It should be able

¹⁸ There are scarce references to organicist authors within the EES literature and not a single comprehensive discussion on the historical pedigree of EES-type reasoning about the active role of organisms in evolution. Some exceptions of succinct mentions are Müller (2017d: 8) and Jablonka and Lamb (2020: 1, 71).

¹⁹ An experienced environment refers to the mediating interface between organism and the physical environment. What counts as an environmental cue (e.g., temperature, pressure, location, etc.) depends on the organism's sensory system and the active modulations performed by the organism (see Sultan 2015). Experienced cues are transduced into chemical and cellular processes (which regulate, e.g., gene expression patterns or microbiome composition), and lead to metabolic, morphological or behavioral changes. A difference in experienced

to distinguish, but also integrate, the different causal and explanatory roles the organismal agent is performing by changing its environment (i.e. modifying its physical properties) and by changing its relation to it (i.e. by experiencing it differently), as both cases can have very different evolutionary effects (see Baedke et al. 2021). Another distinction has been made between agential and contributory forms of niche construction (Aaby and Desmond 2021). In the first case, organisms act as agents if niche constructing effects result from goal-directed behavior under the control of the organism (e.g., plants alter leaf-morphology to optimize light exposure). In the second case, organisms act as contributors if the effects of niche construction do not arise from a goal to perform the constructive activity (e.g., bacteria create novel niches through energy-rich detritus that different strains can metabolize).

Yet other approaches of organismal agency draw on the concept of affordances (i.e. what an organism can do is based on its traits and its environment together). For example, Denis Walsh argues that organisms are not objects of evolutionary forces but agents that co-constitute the affordances that shape evolution. Organisms enact evolution as they pursue their goals, negotiate their “affordance landscapes”, and construct their conditions of existence (Walsh 2015: 241). He states:

Since its inception in the early 20th century, the modern synthesis theory of evolution has been guided by a methodology that explicitly prohibits explanations of phenomena in the natural world that appeal to the fulfillment of goals and purposes [...]. Increasingly, it is becoming apparent that the purposiveness of organisms, as manifest in the robust, reactive plasticity of their various systems, from gene networks to entire organisms, is pivotal to the process of evolution. (Walsh 2017: 257).

Recently, these emerging debates around an agency-focused extension of evolutionary biology have gained substantial funding support. An example of this is the research network “Agency, Directionality, and Function: Foundations for a Science of Purpose”, which includes 24 different projects that should address the role of organismal purposiveness for evolutionary biology, ranging from theoretical models to empirical tests.

6 Conclusions

environments between two organisms living in the same physical surroundings means that the environment is experienced differently by each organism (e.g., as favorable or unfavorable, as stressful or non-stressful). For discussion on experiential niche construction, see Baedke et al. (2021).

In recent years, many scientists and philosophers of science have called for a return of the organism in the biosciences. They have especially argued for expanding the standard population genetic framework of evolutionary biology by a more organism-centered account. This EES should focus less on genes and more on developing organisms and their active, reciprocal interactions with their environments. Unfortunately, this development lacks a clear historical understanding on which theoretical traditions it draws on. Almost exclusively, the EES debate has focused on contrasting the current attempts to highlight organisms' roles in evolution by juxtaposing this approach with that of the MS (construed in many different ways). We showed that taking this historical lens is rather limited, as the core epistemic claims of the organism-centered perspective of the EES actually did not emerge in the history of biology as a reaction to the MS. Instead, its most central ideas about organisms and the organism-environment relationship were developed independently from the MS and were widely debated in early 20th century biology. This concerns especially three currently resurfacing explanatory roles that organisms should play in the evolutionary process: organisms should allow (1) contextualizing parts (especially genes) in development; (2) focusing on reciprocal organism-environment relations (in contrast to, e.g., gene-environment relations); and (3) understanding the role of agency in evolution.

This new historiography, which links evolutionary debates in early 20th century organicism, dialectical materialism and holism with contemporary discussions, allows to better understand the conceptual and theoretical framework underlying the EES. However, understanding the origin and theoretical presumptions of this explanatory framework does not necessarily mean that, *ipso facto*, this approach is feasible or desirable. In fact, it faces the challenge of how to integrate the newly highlighted explanatory role of the organism with the quite different explanatory standards of mainstream evolutionary theory, which largely focuses on genes and populations, but not organisms as causally efficacious units. In short, we need to answer: when organism-centered explanations have more explanatory power and should be chosen over gene-centered explanations, and vice versa?

When we seek to add explanations of developmental and organismal causes, like developmental bias, phenotypic plasticity, niche construction, to the explanatory framework of evolutionary theory we need to know due to which epistemic virtues organism-centered explanations are better and which tradeoffs between explanatory standards (like precision, sensitivity, proportionality, and idealization) we face when trying to integrate organismal and

genetic accounts of evolution.²⁰ If organism-centered explanations do not meet criteria of explanatory power entrenched in the field (like a specific degree of precision, sensitivity or proportionality) scientists will remain skeptical on whether they carry explanatory power and increase our understanding of evolution. Then, these critics might reject the integration of organismal and populationist views within a more pluralist framework of evolutionary causation. In addition, this perspective stresses that evolutionary biologists need to start reflecting not only on the evidence that supports genetic or organismal causes of evolutionary change, but on which explanatory standards they want their evolutionary explanations and models to hold. In other words, they need to decide whether they give the explanatory standards of early 20th century organism-centered accounts of evolution another chance or not.

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²⁰ For a detailed discussion of this challenge and how to solve it, see Baedke et al. (2020).

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