Evolutionary pluralism and the ideal of a unified biology

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Abstract

Biological evolution is often regarded as a central and unifying axis of biology. This article discusses historical aspects of this ideal of unification, as well as signs of its disintegration from the 1960s to 1980s. We argue that despite new proposals for the synthesis of biological knowledge, contemporary evolutionary biology is characterized by pluralism. The main points in favor of evolutionary pluralism are discussed and some consequences of this perspective are presented, particularly in terms of the ideal of a unified biology. Finally, we defend an evolutionary pluralism that critiques the ideal of unification as a scientific objective, but still favors local integrations.

Keywords: biological evolution; history of biology; unification of biology; pluralism.

Biological evolution is often regarded as a central and unifying axis of biology (Smocovitis, 1996). The period known as the evolutionary synthesis, a movement that began in the early twentieth century and became more firmly established in the late 1940s, is considered an important milestone in promoting a unified biology (Largent, 2009).

The evolutionary synthesis refers to the beginnings of population genetics, characterized by academic mobilization around the reframing of Darwinian theory into Mendelian genetics (Mayr, 1980). A series of empirical and theoretical innovations that emerged between 1912 and 1918 made Mendelian thinking central to the study of biological variation and evolutionary causes (Provine, 2001, p.109). Since the transmission of hereditary factors is governed by statistical rules applicable to populations, the genetic explanation also had to involve statistics; for this reason, statistical techniques developed by biometrists were partially modified during the 1920s to allow a rapprochement between Mendelian genetics, Darwinian theory, and biometrics (Provine, 2001, p.130). To a large extent, this theoretical construction was driven by population geneticists such as Ronald Fisher (1890-1962), J.B.S. Haldane (1892-1964), and Sewall Wright (1899-1988).

Concepts derived from population genetics began to be incorporated into various biological disciplines between 1937 and 1947, largely through the efforts of Theodosius Dobzhansky (1900-1975). Dobzhansky's goal was to construct a place where all the heterogeneous and fragmented areas of biology could be "connected" through population genetics (Smocovitis, 1996).

Although the self-appointed "architects of synthesis" disagreed on more circumstantial evolutionary topics (such as gene interactions, the efficiency of natural selection in large and small populations, and the role of chance in evolution), these authors agreed that evolutionary biology was based on the mathematical structure of population genetics, which created a general framework capable of unifying various phenomena into one relatively simple theoretical synthesis. In this way, different phenomena, disciplines, and biological organisms began to be addressed from this theoretical framework (Stoltzfus, 2017).

This intentional movement toward the unification of biology took place at the same time as the intense activities of the Vienna Circle, an intellectual movement that envisioned (among other things) one formalized and unified science (Hahn, Neurath, Carnap, 1986, p.10). The unity of science proposed by the Vienna Circle involved the belief that all sciences – physical, biological, and social – could be translated into sentences addressing only physical objects, logically constituting a single "physicalist" language (Cunha, 2018). While belief in the unity of science was one of the fundamental principles of the positivist logic of the Vienna Circle in the 1920s, aligned efforts were seen across the biological sciences to unify biology (Smocovitis, 1992, p.3). In addition to the ideals of unification and formalization (mathematical, in the case of evolutionary synthesis, and logical in the case of the Vienna Circle), another element common to both movements was the tendency to purge metaphysical elements that did not apply to the human experience.

Hahn, Neurath, and Carnap (1986) state that biology was a science especially "contaminated" with metaphysical claims:

> Metaphysicians always had a penchant for distinguishing biology as a special domain. This was expressed in the doctrine of a special life force, vitalism. Modern proponents of this doctrine strive to bring it out from the dark and vague ways of the past to a version that is clearer from a conceptual point of view. Instead of the vital force, the 'dominants' (Reinke, 1899) or 'entelechiae' emerge (Driesch, 1905). Such concepts are rejected as metaphysical by the scientific conception of the world, since they do not meet the requirement of reducibility to the data (Hahn, Neurath, Carnap, 1986, p.16; emphasis in the original).[1]

At the turn of the twentieth century, biologists from different areas utilized intentional mechanisms of evolution, which the Vienna Circle had considered metaphysical speculations. In keeping with the Vienna Circle, evolutionary synthesis was an effort towards unification focused on making evolution a "positive science," and in doing so attempted to utilize experimental methods based on empirical evidence and generate results that could be generalized in mathematical terms. With the unacceptable metaphysical elements removed, the evolutionary synthesis was intended to be not only a strictly scientific approach to evolutionary biology, but to biology as a whole, uniting and underpinning the heterogeneous practices of this science (Smocovitis, 1996; Ferreira, Selles, 2005).

This unification plan provided a breakthrough in the dialog between different areas of biology, even though it did ignore some specific disciplines of this field. The architects of evolutionary synthesis contributed to the institutionalization of biology, organizing conferences, journals, and institutional environments where specialists from different areas could meet and form a relatively cohesive scientific community. One example is the Conference on Genetics, Paleontology, and Evolution held at Princeton (1947). This conference inaugurated the Society for the Study of Evolution, and brought together some of the leading evolutionists of the time. In creating these institutional conditions, evolutionists from different fields of biology were able to discuss and share their investigations. Delisle (2011, p.51) characterizes such institutional conditions for unifying biology as a genuine "sociological synthesis."

But even if the sociological dimension of evolutionary synthesis was successful, what can we say of its epistemological aspects and fundamental metaphysical commitments? According to Sahotra Sarkar (2004, p.1217), the reference to the concept of synthesis implies (at the very least) the union of two or more independent scientific structures – explanations, models, theories, or disciplines – brought together in such a way that they strengthen each other within an integrated structure. This author adds that epistemic parity would also be desirable in a synthesis, in order to distinguish it from other scientific changes such as reduction.

However, many philosophers and historians of evolutionary biology have discussed the limitations of considering the relationship between the scientific structures of the evolutionary synthesis in terms of synthesis (Gould, 1983; Provine, 1992; Smocovitis, 1996; Sarkar, 2004, 2017; Delisle, 2011). For example, if we consider disciplinary aspects it is difficult to contemplate an equal relationship between the different biological disciplines in the evolutionary synthesis, since evolutionary phenomena are explained in terms of microevolutionary processes that are ultimately based on population genetics (Sarkar, 2004). In this sense, population genetics takes priority over other disciplines in explanations.

Another criticism of unifying biology through the evolutionary synthesis is the lesser role of relevant biological disciplines such as morphology, paleontology, and embryology (Smocovitis, 1996). The evolutionary explanations sought by authors in these fields conflict with those presented by the architects of the evolutionary synthesis (Amundson, 2005). For these reasons, the proposal to unify biology through the evolutionary synthesis showed signs of its limitations from the very beginning.

Indications of the disintegration of the evolutionary synthesis

The evolutionary synthesis established some common assumptions that allowed biologists from different areas to work together, particularly in terms of evolutionary problems. Some of these assumptions are "genecentrism," strict gradualism, the extrapolation of microevolutionary explanations to macro-evolutionary patterns, and the preeminence of natural selection (Laland et al., 2015, p.2). This means that for the evolutionary synthesis, genetic inheritance is the only evolutionarily relevant inheritance system, evolutionary changes only occur in small steps leading to gradual evolution, macro-evolutionary patterns are explained by accumulated microevolutionary events via population processes, and natural selection holds a privileged position in explaining evolutionary change.

But between the 1960s and 1980s, different empirical and theoretical advances in evolutionary biology itself challenged these central elements of the evolutionary synthesis. According to Stoltzfus (2017, p.14), the emergence of molecular evolution was the first visible sign of the "disintegration" of the evolutionary synthesis. Research in molecular evolution during the 1960s reinvigorated the notion of genetic drift and led to a series of challenges to natural selection.

This was controversial even for the architects of the evolutionary synthesis, since up to the 1930s genetic drift was often considered to play a predominant role in phenotypic change (Gould, 1983). But from the 1940s, natural selection was more emphatically considered the main mechanism behind evolutionary change.

Meanwhile, molecular studies from the 1960s indicated the major role of genetic drift in the stock of genetic variants of species. Motoo Kimura's neutral theory of molecular evolution (1968) posited that most mutations do not have a noticeable phenotypic effect, and for this reason persist in populations due to genetic drift rather than natural selection. This molecular research pointed out a certain morphological and molecular "paradox:" what was observed at the morphological level, and prioritized by the evolutionary synthesis, did not seem to fit at the molecular level.

Shortly after this work by Kimura (1968), Gould and Eldredge (1972) presented the theory of punctuated equilibrium, challenging another assumption of the evolutionary synthesis: strict gradualism. These authors added the interpretation of a different pattern for some strains, considering the fossil record. Gould and Eldredge argued that certain species have certain stability in time (morphologically "unchanged"), followed by a period of rapid divergence. This pattern was not due to a failure in the fossil record, as strict gradualism had assumed, but instead a genuinely evolutionary process of stasis followed "suddenly" in the next sedimentary rock formation by a notable change in morphology and the origin of a closely related new species.

In the late 1970s, Gould was still fiercely criticizing the other central assumptions of the evolutionary synthesis. Together with the geneticist Richard Lewontin, he published an article entitled "The Spandrels of San Marco and the Panglossian Paradigm: A Critique" (Gould, Lewontin, 1979). This article contains two interesting metaphors that help us understand his critique. Spandrels are tapered spaces between arches that support a dome-shaped roof, such as in St. Mark's Basilica in Venice; these spaces are beautifully decorated, although they were not designed for this artistic purpose. The symmetry and consistency of the spandrels might indicate that they are the reason for the entire system of arches and domes that surround them, but they are simply an architectural byproduct resulting from the arches used to support the dome. Spandrels are consequently only explained as a byproduct of construction, rather than as an element designed for any purpose (architectural or artistic).

Gould and Lewontin used this example to refer to particular ways of interpreting living beings they considered problematic. Many biologists divide organisms into parts and assign a certain function to each part, when, in fact, we need to seek evolutionary explanations for the entire complex and indivisible organism. To understand spandrels we must consider the entire architectural structure that surrounds them, otherwise we might attribute the wrong original function to this structure. When biologists divide organisms into parts and assign functions to each part, they may also make the same mistake as an observer who sees spandrels as the original purpose of the basilica.

The evolutionary synthesis would make a similar error by seeking an adaptive origin for nearly all characteristics of organisms. As such, this approach does not consider the possibility that many characteristics may be byproducts of development, even if they acquire a particular function during evolution. Just as spandrels are architectural subproducts which took on an artistic function in the basilica, living beings also have phenotypic byproducts of development and evolution that were not originally "designed" (selected) for a functional characteristic.

Gould and Lewontin (1979) call the selectionist and atomist approach "Panglossian" in reference to a character from Voltaire's *Candide, ou l'Optimisme*: Professor Pangloss. This character believes that things exist in the world to improve it. Pangloss says "... nothing could have been different. Since everything was designed for a purpose, everything is necessarily meant to serve the best of all purposes. Observe how noses were designed to hold up eyeglasses, and therefore we have eyeglasses. Legs are obviously meant for wearing shoes, and so we have shoes" (Voltaire, 2006, p.10).[2]

The biological metaphor of the "Panglossian paradigm" refers to the notion that natural selection should have minimal restrictions so that the adaptation is the primary cause of all form, function, and behavior displayed by living beings. In this way, by believing in the omnipotence of natural selection as an idealization of an "optimal design" of living beings, this paradigm approaches a naive and functional Panglossian view of the world.

This criticism targeted evolutionists who hastily assumed that any characteristic found in living beings was functional, creating adaptive hypotheses and explaining their existence in a selective model. This involved proposing merely adaptive stories to explain the existence of functional characteristics, without necessarily empirically testing this hypothesis or considering other scenarios.[3]

These explanations, called "adaptationist," were considered mere just-so stories. As stated by Abrantes (2011, p.20), "the adaptationist thesis about the explanatory power of natural selection (to the exclusion of other mechanisms) is not testable, and the just-so stories generated from this thesis also could not be subjected to empirical evidence."

It is important to clarify that the criticism by Gould and Lewontin was not intended to undermine explanations of natural selection. Their goal was to highlight the blind spots of evolutionary theory that overvalued explanations involving natural selection while excluding alternative explanations. In the 1979 article, these authors pointed out that biologists should at least take a more serious look at genetic drift, restrictions related to development processes, structural constraints, and those related to the phylogenetic history of living beings.

Restrictions related to development processes and structural constraints related to phylogenetic history are not considered in the evolutionary synthesis, since this approach is based on a biology of parts and genes but not organisms. Organisms are integrated entities, in such a way that many of the characteristics observed result from structural constraints that affect the interactions of the elements that comprise the whole. Adaptationism is considered a functionalist position, and was therefore criticized by Gould and Lewontin, who indicated the need to prioritize other plausible evolutionary explanations, especially those that were structuralist in nature.

Functionalism and structuralism can be regarded as fundamental philosophical guidelines that distinguish different research proposals (Abrantes, 2011). The theoretical separation between studies of form and function led many authors to postulate the existence of a dichotomy between structuralism and functionalism in the history of biological thought. On the one hand, structuralists argue that evolutionary changes are modifications of form, and since morphology is the product of development, the study of biological evolution must include processes of ontogenetic changes; meanwhile, functionalists contend that evolutionary changes are essentially functional modifications, and that organisms can be partitioned in order to associate each part with a different function. Since embryology had a limited role in the evolutionary synthesis, structuralist approaches are understood to have had only a minor impact on evolutionary thought (Amundson, 2005, p.27).

In response to these criticisms from the 1960s and 1970s, during the 1980s some authors attempted to propose new forms of synthesis that could resolve the alleged gaps in the evolutionary synthesis and consequently lead to a higher unifying biology. Some examples are work by Gould (1980), Robert Reid (1985), and Niles Eldredge (1985). These efforts slowed in the 1990s, but during the aughts they resumed with the extended evolutionary synthesis (Pigliucci, Müller, 2010), which is currently being discussed in the scientific community. One example is a recent article entitled "Does evolutionary theory need to rethink?" (Laland et al., 2014), authored by evolutionary biologists who lead some of the world's main research groups and disagree on which processes should be considered fundamental in evolution. The authors are divided between the notion that without an extended evolutionary synthesis, evolutionary biology neglects key processes, or the contrasting idea that contemporary evolutionary theory accommodates empirical and theoretical novelties. This latter group argues that all is ultimately well with the standard evolutionary theory, since it was always able to incorporate innovations and extensions from different fields. After all, the evolutionary theory is far from stuck in the past, and currently the subject of vibrant research (Laland et al., 2014, p.163).

The future of this debate is uncertain, and as contemporaries of this historic process we do not yet have a clear view of its tendencies and consequences. Regardless of the position taken by the authors of the aforementioned article (whether the evolutionary synthesis really neglects evolutionary processes or encompasses them), evolutionists admit empirical and theoretical advances that have indicated a plurality in evolutionary biology (Futuyma, 2017). Contemporary evolutionary biology comprises multiple coexisting conceptual frameworks and perspectives that disagree on the nature and scope of evolutionary theory (Eldredge, 1985; Fábregas-Tejeda, Vergara-Silva, 2018). The evolution of living beings is approached from multiple perspectives and research strategies that focus on different areas and phenomena, such as genes, gene regulation, phenotypic plasticity, epigenetics, morphology, embryology, animal behavior, building niches, population structure, and macro-evolutionary patterns. A myriad of disciplines in biology conduct research with relevant evolutionary consequences. From macroecology to molecular biology, this pluralism broadens evolutionary biology for different levels of analysis, continents, and ecosystems to the biochemistry of life.

The complexity of the systems studied by evolutionary biology leads to a plurality of causal hypotheses that do not necessarily compete with those adopted by the evolutionary synthesis. The empirical evidence and recent theoretical advances explained that even despite the great importance of natural selection, the extrapolation of microevolution to macroevolution, strict gradualism, and "genecentrism," other evolutionary conjectures must be combined.

Such broad and diverse fields of research have experimental and theoretical impacts, expanding the empirical basis of evolutionary theory, boosting its explanatory power, and redefining concepts and terms. This diversity is also likely to have an impact on the structure of evolutionary theory itself, which is already not the same as it was decades ago (Pievani, 2002). In this way, a crucial question emerges: what exactly is the evolutionary biology of the twenty-first century?

As we shall defend below, contemporary evolutionary biology is best characterized as an "evolutionary pluralism." Evolutionary thought is currently being reformulated, in a process involving the proliferation of processes, standards, and heredity in evolutionary biology (Pigliucci, Kaplan, 2000; Doolittle, Bapteste, 2007; Danchin et al., 2011).

Evolutionary pluralism

Positioning in favor of pluralism in evolutionary biology has been common among historians and philosophers (Brigandt, 2010, p.296). There are many nuances about the type of pluralism adopted and its limits, which depend on the specific discussions.

Evolutionary pluralism has been defended in the literature according to the description of the scientific practice of the evolutionists (who participated in different disciplines, adopted different concepts, methods, explanations etc.), but also in reference to the complexity and hierarchy of biological phenomena (Pievani, 2002; Mitchell, 2003; Dieckmann, Doebeli, 2005; Brigandt, 2010). In this vision, both the research traditions among different evolutionary biologists as well as the heterogeneous and complex phenomena of evolution serve as justifications for the pluralism of evolution. In the former case, pluralism is defended from the description of the scientific practice, assuming this practice to be legitimate. In the latter case, pluralism is defended from a metaphysical basis, from theses on the content of the biological world as a whole (Dupré, 1993). In this way, evolutionary pluralism is founded on both practice and scientific discourse as well as the metaphysical plane. Below we shall explore each of these foundations.

Scientific practice as a base for evolutionary pluralism

The first major axis upon which evolutionary pluralism is built is the description of scientific activity; in other words, we inevitably have a pluralistic image of evolutionary theory when we characterize it today. When we look at science itself, we see a pluralism of theories, methods, research programs, research traditions, scientific topics, concepts, and so forth that are addressed by evolutionists. And this consideration is endorsed by both the scientists who seek to characterize their field as well as by historians of biology (Pievani, 2002; Mitchell, 2003; Dieckmann, Doebeli, 2005; Brigandt, 2010; Stoltzfus, 2017).

For this reason, when we compare the original evolutionary synthesis and contemporary evolutionary biology with the empirical and theoretical results of new approaches, we arrive at a pluralist perspective. It is in this sense that Pievani (2002, p.65) describes evolutionary pluralism in three dimensions: on evolutionary rhythms, on evolutionary units and levels, and on factors and causes involved in biological evolution.

While gradualism is considered an essential element of the evolutionary synthesis and of Darwinism itself, evolutionary rhythms increased from discussions on the theory of punctuated equilibrium (Gould, Eldredge, 1972). These patterns are not mutually exclusive, since they may explain the evolution of different lineages, comprising a more pluralistic scenario of evolutionary rhythms.

This is one of the reasons that lead us to another type of pluralism: what is called the pluralism of evolutionary patterns (Doolittle, Bapteste, 2007). For Doolittle and Bapteste (2007, p.2048), the belief that nature displays a unique pattern of relationships between the taxa exposes a standard monism as opposed to a standard pluralism – the recognition that different models and representations of evolutionary relationships are appropriate and true for different taxa. The evolutionary synthesis assumes a standard monism, representing the history of life as a large tree with well-established hierarchical relationships between ancestors and descendants.

Some processes of horizontal transmission described by biologists in recent years lead us to different standards than the one represented by the tree metaphor. Symbiosis, horizontal gene transfer (significant in bacteria), as well as hybridization between different species result in distinct patterns of well-established hierarchical relationships between ancestors and descendants. This implies not negating the standard represented by the tree, but instead recognizing that many standards represent the history of life when we consider the variety of taxa and the processes of horizontal and vertical transmission (Doolittle, Bapteste, 2007).

The evolutionary synthesis also limited discussions with regard to the units of evolution, preferring some biological entities that are causally involved in the evolutionary process. In recent years, a series of biologists and philosophers have proposed that genes, organisms, and species should be considered biological "individuals" in all aspects and consequently subject to selection. Natural selection can be formulated in a totally abstract way that does not involve references to organisms or any other biological units. Entities at many levels of the biological hierarchy can satisfy these conditions, including genes, chromosomes, organelles, cells, multicellular organisms, colonies, groups, and species. The hierarchical nature of the biological world, combined with the abstraction of the principle of natural selection, leads to a wide range of units upon which selection can theoretically act (Folguera, 2011).

Furthermore, some evolutionary biology debates on development also move away from populational thinking to favor the organism as the central concern of evolution. Since modifications in development mechanisms are central to organic evolution, ontogeny is considered a fundamental evolutionary unit (Amundson, 2005). We consequently are left with three distinct approaches to the evolutionary units and selection in contemporary evolutionary biology: (1) populational thinking: populations evolve, not organisms, and organisms or genes can be the targets of natural selection; (2) ontogenetic thinking: organisms do not evolve, but rather ontogenies evolve, and phenotypic characteristics are effects of the evolution of ontogenies; (3) macro-evolutionary thinking: species are subject to selection, and species constitute an evolutionary unit in their own right (Amundson, 2005, p.249).

In order to be considered an evolutionary unit, the changes that affect a biological level over time should accumulate, generating a double arrangement of identity and difference (Gould, Lloyd, 1999). For this reason, one requirement for evolutionary units is that they must be reproductive entities that allow continuity over space and time (Hull, 1976, p.182). For evolution to be cumulative and persistent, the changes to an evolutionary unit must be preserved until a certain point in the next generation. As for populational changes, this required persistence is guaranteed by heredity. And like the other aspects discussed here, biologists are increasingly indicating a need for a more "inclusive" concept of inheritance, proposing pluralistic models of biological heredity (Danchin et al., 2011; Walsh, 2015).

As previously mentioned, the evolutionary synthesis has a vision that can be considered "genecentrist" since it favors the gene as the basic unit of heredity. Gene theory in classical genetics (and as adopted in population genetics) does not address how genes are causally linked to the final product, the characters. For this reason, the study of heredity in the evolutionary synthesis focuses on the causes of genetic transmission between generations (Amundson, 2005).

This model of heredity has been enormously useful and successful in evolutionary biology. Despite its explanatory success, there are many critiques of describing biological heredity in purely genetic terms. With studies on molecular biology, genomics, developmental biology, and research on behavioral and cultural evolution, evidence is accumulating for the explanatory inadequacy of the genetics of transmission as the only model of biological heredity (Uller, Helanterä, 2014).

Mechanisms of genetic and non-genetic inheritance (as well as the interactions between them) are argued to have relevant evolutionary effects, may be an important trigger for divergence and speciation, and play an important role in adaptive evolution (Laland et al., 2015). Depending on the author, the emphasis and theoretical discussion on heredity may vary. For example, Eva Jablonka and Marion Lamb (2005) address heredity as information transfer between generations, establishing genetic, epigenetic, behavioral, and symbolic systems. Oyama, Griffiths, and Gray (2001), within the context of systems theory in development, do not regard inheritability as transmission of information through discrete channels (as Jablonka, Lamb, and others do), but instead emphasize the process of reconstructing life cycles in which the parental generation contributes. These perspectives about heredity seem different and are not clearly related; detailed analysis of this topic lies beyond the scope of this article.

Finally, in terms of evolutionary mechanisms and factors, we perceived that the evolutionary synthesis adheres to a functional and adaptationist vision. The so-called pluralism of processes is usually considered in opposition to adaptationist positions, focusing on natural selection (Orzack, Forber, 2017). For this reason, the profusion of evolutionary processes in recent years is in line with evolutionary pluralism, and is compounded by the factors favored by the evolutionary synthesis (natural selection, mutation, genetic drift, and gene flow).

It is argued that genomic, ecological, ontogenetic, and geological mechanisms must be considered in explanations of evolutionary change. Therefore, alongside classic evolutionary mechanisms we also have phenotypic plasticity, development biases, gene regulation mechanisms, niche building, mass extinction, selection at multiple levels, symbiogenesis, evolvability, and self-organization, for example (Almeida, El-Hani, 2010; Laland et al., 2015). It should be noted that selective explanations are not consequently rejected, but instead considered in conjunction or synergistically with these other evolutionary processes.

It is interesting to note how these processes consider not only genetic but also ecological, ontogenetic, and geological factors. Development is responsible for the production of organic form, influencing the course of evolution by producing morphological novelties as well as restricting the possibilities of their origin and modification. In this way, the plasticity of development is just as important a cause of evolution (for permitting the origin of evolutionary novelties) as phenotypic variation, which may be restricted by the processes of development. Development bias and restriction help us understand how some forms are more likely to evolve than others, clarifying examples of convergent evolution (Laland et al., 2015, p.3). Furthermore, understanding the processes of development helps explain complex evolutionary changes, such as changes in animal body plans.

As for ecological dynamics, another highlight is that living beings do not evolve to fit into existing environments, but rather co-construct and co-evolve with their environments, changing the structure of ecosystems. Some authors critique the evolutionary synthesis for seeing the environment as a “sieve” that passively determines which forms can survive in populations as time goes by (Reis, 2017). For this reason, authors like Odling-Smee, Laland, and Feldman (2003) state that niche building (the process by which organisms actively modify their own niches and those pertaining to other organisms) should be recognized as an evolutionary process in its own right. This process directs evolution via non-random modification of selective environments by the organisms themselves.

Finally, geological events are important for understanding macro-evolutionary processes that occur on large time scales. Glaciation and continental drift events are involved in the diversification and extinction of clades. Mass extinctions and background extinctions are important in macroevolution because they eliminate groups from certain geographical regions, stimulating evolutionary irradiations of other taxa. These stochastic events permeate the evolutionary history of lineages, altering them in such a way that the rates of speciation, increases in disparity, and extinction rates change. One example is the uplifting of the isthmus of Panama which allowed North and South America to connect, making it possible for many endemic strains to disperse across both continents; because of this event, many species emerged and others perished (Paes-Neto, Santos, Melo, 2017). Another evolutionary process related to geological events is species selection, a type of selection in which species function as individuals and exhibit rates of speciation and extinction in a manner analogous to reproduction and survival in classic natural selection. For this reason, some paleontologists argue that geological components which alter extinction and speciation rates are evolutionary processes in their own right (Lieberman, Miller, Eldredge, 2007).

We can also add to the discussion about evolutionary pluralism a series of core evolutionary theory concepts that can be seen from a pluralist perspective. One is pluralism on concepts of species. Mayden (1997), for example, listed 24 different concepts of species. Many of these concepts and their associated definitions are incompatible, to the extent that they may lead to differences in the limits and numbers of species classified.

The concept of environment is another example that can be taken from a pluralist perspective. In the monist approach of the evolutionary synthesis, the environment is considered as a selective pressure that affects the organism and determines the forms that will survive or become extinct in competition to replicate and multiply genes (Dawkins, 1996). In a pluralistic approach, living beings and the environment are part of an endless process of co-evolution in which different evolutionary paths interact: for example, in processes of phenotypic plasticity, in differentiation of populations due to geographical isolation mechanisms, in the rapid extinction of species due to environmental changes, followed by evolutionary divergence, and in "species selection" at the macro-evolutionary level (Vrba, 1983).

There is no consensus on many of the issues that involve evolutionary pluralism, since certain authors consider some processes more important than others. Caponi (2016), for example, believes that there is an explanatory subordination of niche building to natural selection. This author states that niche building should not have the status of an evolutionary mechanism, since it acts "in parallel" to natural selection as an agent of evolution.

In any case, when we look at the empirical and conceptual advances in evolutionary biology today, there is inevitably a pluralistic framework of evolution in terms of its main aspects. The next section discusses how evolutionary pluralism is also rooted in metaphysical concepts.

The metaphysical foundations of evolutionary pluralism

Scientists generally have strong assumptions about the world they investigate, which form a previous metaphysics (Dupré, 1993). A classic example is viewing the material world as a kind of mechanical system like the gears of a clock. In the case of biology, a metaphysical assumption that supports evolutionary pluralism considers the biological world as complex, multi-level, and contingent (Mitchell, 2003).

According to Sandra Mitchell (2003), organisms and ecosystems exhibit constitutive and procedural complexity. Constitutive complexity refers to their being composed of numerous parts, while procedural complexity is linked to the dynamic properties of life, such as extreme sensitivity to initial conditions, self-organization, and positive and negative feedback. Since it is impossible to address all these complex elements simultaneously, research approaches must inevitably select the aspects of biological complexity to be addressed. Each selection represents a different analysis of the causal universe, creating different sets of alternative causes. The explanations proffered in scientific exploration of this diversity in the biological world are responsible for creating some of this evolutionary pluralism (Mitchell, 2003, p.115).

If this is the case (in other words, if the nature of the biological world is such that important phenomena may not be completely and thoroughly explained by a single set of fundamental principles), then the goals, methods, and results of biology should not be understood or evaluated in reference to a monist search. Different approaches are appropriate for the conceptual and pragmatic goals of biology. For this reason, the type of knowledge and the very methods we use to study biological systems ultimately reflect this complexity (Kellert, Longino, Waters, 2006).

Another metaphysical foundation of evolutionary pluralism assumes that evolution involves processes that occur at multiple levels of organization (Mayr, 1961; Sherman, 1988). Evolutionary studies have focused on processes at different levels which are subject to different evolutionary factors and cannot be collapsed into a single one (Kellert, Longino, Waters, 2006). One simple and unified image of evolutionary biology would be inadequate to deal with complex, multi-component, and multi-level systems that populate the domain of living beings. Studies involving multiple causal processes and types of explanations offered for evolutionary phenomena on the molecular, behavioral, morphological, ecological, geological etc., levels create forms of explanatory and methodological pluralism in contemporary biology (Mitchell, 2003).

Finally, the so-called contingency theory of evolution is also a metaphysical foundation of evolutionary pluralism. As Stephen Jay Gould once said, evolution is like a videotape that, if rewound and replayed several times, has a different ending every time. Beatty (1995, p.221) expands Gould's thesis to state that the contingency of evolution not only creates regularities in nature, but also "breaks the rules" of the living world. For example, the Hardy-Weinberg law, one of the core principles of evolutionary biology, is a deductive consequence of Mendel's first law, which states that the characteristics of individuals are conditioned by pairs of factors (genes) that are separated during the formation of gametes, with only one factor in each pair going to each gamete. Mendel's first law (and consequently, the Hardy-Weinberg law) are consequences of the meiotic mechanism of gamete separation in sexual reproduction.

Meiosis, like any other biological process, does not cease to be a product of evolution (Beatty, 1995). This means that the biological generalizations derived from this mechanism (Mendel's first law and the Hardy-Weinberg law) are contingent upon evolution and therefore not laws of nature or a natural need. Exploring Gould's example, if we return to the history of life there is no need for evolution to have resulted in the mechanism of meiosis and gamete separation in the proportion expected by Mendel's first law in sexual organisms.

According to Beatty (1995, p.229), the fact that the contingencies of evolutionary history impede the existence of laws in biology forces biologists to be theoretical pluralists. Theoretical pluralism contrasts with the goal of explaining a domain of phenomena in terms of a small number of general mechanisms. This ideal was particularly adopted by Newtonian physics, an example of science for many architects of the evolutionary synthesis (Smocovitis, 1996). The models of evolutionary change were constructed according to the models of physics to demonstrate that evolution has regularities similar to physical laws. In the evolutionary synthesis, this inspiration was based on genetics and ultimately Hardy-Weinberg's mathematical principle of equilibrium, which has an explanatory scope for different biological levels.

The refusal to explain evolution in terms of a small number of mechanisms is also based on the understanding that life is essentially heterogeneous. Depending on the group of organisms, evolution may have created regularities that led to different evolutionary processes, inheritance mechanisms, and evolutionary patterns. Therefore, an extension of the contingency thesis is that there is not a single theory or mechanism – not even a theory or large multicausal synthesis – that is responsible for all explanations in the field of evolution (Beatty, 1995). Another consequence of this thesis is that nearly all the biological disciplines can contribute to the understanding of evolution. This is because by investigating how a certain group of organisms or biological level functions, a discipline can contribute to the understanding of processes, evolutionary patterns, and inheritance mechanisms. For this reason, embryology, paleontology, ecology, botany, zoology, and microbiology, along with other biological disciplines, can shed light on truly evolutionary questions.

The question of unity in biology

Pluralists need to answer difficult questions, especially those derived from the philosophy of science. One challenge is that a pluralistic stance would imply that the scientific approaches and theories do not provide a single complete and comprehensive truth for the evolutionary domain. In the absence of fundamental standards of justification, any and all forms of reasoning would be acceptable. In this way, some pluralist versions could lead to a biological free-for-all, at least in terms of truth and scientific demarcation (Boghossian, 2012).

Some proponents of evolutionary pluralism seek to distinguish its pluralist posture from relativism and establish minimum criteria of demarcation in science. From a relativistic perspective, there would be a denial of objective constraints on evolutionary pluralism, which may be part of this pluralism and place it on an equal footing with creationism and intelligent design, for example. One way of placing reasonable restrictions on what types of scientific knowledge are admissible is to return to the epistemic virtues of biological theories. There are many possible and real virtues such as sensitivity to empirical facts, plausible background assumptions, consistency with other knowledge, and exposure to criticism from a wider range of sources (Dupré, 1993).

Another criticism of evolutionary pluralism is the absence of a relationship between biological theories and disciplines (Mitchell, 2003). A pluralist could recognize that different types of questions require different responses, and consequently there would be no interaction between scientists who work with different levels; in extreme cases, this could lead to a form of isolation within the domain of evolution. The problem here is that explanatory closure is assumed within each level of analysis, and the narrow scope of scientific research prevents fruitful interactions between disciplines and theories that have accounted for much of the history of science (Mitchell, 2003).

An additional problem is that when we look at studies from different levels of research, we can see that in many cases they cannot be satisfactorily addressed without considering other levels. Even in the unlikely situation that a scientist is strictly concerned with only one level of analysis, it would be a mistake to think that the answers to other questions are unrelated to research at this level. For this reason, many discussions in favor of pluralism have left a philosophical vacuum to the extent that they do not look at how different fields, methods, and concepts are related in biological practice or how they could be integrated (Brigandt, 2010, p.296).

According to Kellery, Longino, and Waters (2006), a pluralistic stance does not immediately reject efforts at integration, but refuses to assume that the unit is always possible or that the synthesis is an end in itself. Pluralism does not assume that all disciplines are commensurable, and ultimately unifiable, nor does it presume that each discipline is necessarily isolated and incommensurable with others. The pluralism defended by Kellert, Longino, and Waters (2006) contends that for any and all disciplines, whether they can or should be united or integrated is a contingent and open question, one which should be answered on a case-by-case basis. For some issues, a multidisciplinary and cooperative approach seems to occur, while other problems seem to foster the creation of a new discipline. But pluralists argue that there are no good reasons to assume that isolation, cooperation, integration, or synthesis are good in all cases.

Against a pluralism that simply affirms that biology requires various disciplines and theoretical approaches, some authors have argued that solving complex biological problems (to meet some explanatory or epistemic objectives) requires at least partial integration of concepts and explanations from different fields. This is the case of authors such as Darden and Maull (1977), Sandra Mitchell (2003), Ingo Brigandt (2010), and Telmo Pievani (2016), for example.

Darden and Maull (1977) argue that the motivation for integration in biology in most cases is the existence of a scientific problem that cannot be solved by one field of research alone. When researchers recognize that they have common interests, this integration between different fields can result from the origin of what they call "interfield theory." Another example along these lines is the "integrative pluralism" described by Sandra Mitchell (2003). Integrative pluralism incorporates different levels of analysis by establishing small "local" integrations. This author argues that integrative pluralism is a better description of the multi-component evolutionary complexity involving varied levels seen in biological systems; complexity, she adds, invokes multiple levels of organization and multiple causal factors that in turn require an integration of approaches to exhaust biological problems. This type of integration is required to explain complex phenomena, but does not involve unification on a large scale.

More recently, Brigandt (2010) discusses a proposal for integration that can be carried out by smaller epistemic units (such as concepts, methods, and explanations) linked to specific scientific problems. While a synthesis/unification is a stable connection of disciplines, in the flexible model proposed by this author a discipline can maintain its independence and traditional identity while entering into closer relations with other transitional fields, depending on what problem is addressed.

Brigandt's idea (2010) is based on the history of science and a specific example of evolutionary biology, namely explanations of the origin of evolutionary novelties. This author states that a single discipline is not sufficient to solve problems related to the origin of major evolutionary novelties, and many of the solutions found in the history of biology required involvement from different fields. Some examples of evolutionary novelties include vertebrate jaws and the evolution of feathers in birds, which led to the involvement of phylogeny, paleontology, ecology, biogeography, and developmental biology for further clarification. For this reason, this author suggests that solving complex problems such as those found in evolutionary biology does not require a stable synthesis of different fields of biology, but instead integrations of smaller epistemic units in order to solve specific problems (Brigandt, 2010, p.297).

Finally, Telmo Pievani (2016) argues that an approach built from interactions between multiple levels of evolutionary changes (from genetic microlevels to geological macrolevels) can form the foundation of a "metatheory" proposal in evolutionary biology. Based on the hierarchical theory of Niles Eldredge (1985), this author believes that research on various levels and biological units should not be considered a sign of deunification, but instead an important opportunity for theoretical integration in evolutionary biology (Pievani, 2016, p.454).

Final considerations

As discussed throughout this article, the evolutionary synthesis presented a broad plan to unify biology. However, some visible limitations of this ideal appeared shortly after its establishment. Contemporary evolutionary biology comprises multiple coexisting conceptual frameworks and perspectives that disagree on the nature and scope of evolutionary theory. Evolutionary thought is currently undergoing reformulations that involve a proliferation of approaches, concepts, and processes that can be characterized as evolutionary pluralism.

In this way, when we look at scientific practice we do not find a broad synthesis in biology, but rather a series of integrations that do not involve a stable unification of different fields of biology. These forms of integration may be compatible with a pluralistic stance, without recourse to more traditional visions of the unity of science. Unification is not a goal in itself from the viewpoint of evolutionary pluralism, but local integrations occur and should occur in biology for specific epistemic purposes. Our criticism addresses the alleged broad unification of biology as a whole via biological evolution.

NOTES

[1] In this and other citations of texts from Portuguese, a free translation has been provided.

[2] This citation in English from Voltaire (2006) was sourced from Voltaire, *Candide or Optimism*. Translated by Burton Raffle. New Haven: Yale University Press, 2005. p.2.

[3] Although these critiques by Gould and Lewontin were imbued with academic prestige, discussions of the adaptationist program remain in vogue. More recently, Godfrey-Smith (2001) offered an overview of adaptationism and separated it into three versions (empirical, explanatory, and methodological), each with different uses in contemporary evolutionary biology.

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