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BIOLOGICAL INDIVIDUALITY AND THE EXTENDED EVOLUTIONARY SYNTHESIS

A PHILOSOPHICAL CONUNDRUM IN A (NEW) BIOLOGICAL FOCUS**

Abstract

There has been much debate in evolutionary biology concerning the extension of some of the central tenets of the modern synthesis (MS). Due to recent developments in evolutionary developmental biology (Evo-Devo), epigenetics, phenotypic and developmental plasticity, niche construction and ecological inheritance, and animal traditions, an increasing array of leading evolutionary biologists, theoretical biologists, and philosophers of biology agree that the structure of the MS needs to be reconsidered. This paper reflects on the connection between this scientific debate and the notion of biological individuality. The paper proposes a discussion of two levels at which the concept of individuality intersects with the extended evolutionary synthesis (EES), as well as the tension between two roles for individuals in such an extended theoretical framework. First, taken at face value, many developments in evolutionary thinking point to an organism-centered view of evolutionary processes. Second, the concept of individuality appears to have been hugely modified in the history of evolutionary thought. Indeed, both multilevel selection theory and the framing of Darwinian individuality transitioning among levels in evolution entail an expansion of the notion of individuality. Such an extended notion leaves room for aggregations of (classical) organisms counting as evolutionary individuals while (allegedly proper) organisms may coherently be viewed as populations. It follows that while individuality has become increasingly relevant for the renewed view of evolution that the EES presents, the boundaries of the notion seem blurrier and more fluid than ever. The paper concludes with a call for pluralism with regard to individuals (and many other evolutionary concepts).

Keywords: evolution, individuality, modern synthesis, extended evolutionary synthesis

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1. INDIVIDUALITY AND EVOLUTIONARY BIOLOGY

Questions of individuality and how to conceive of this traditional philosophical issue have received much attention in recent years from many areas of concern relating to biology and philosophy of biology alike (Buss 1987, Hull 1976, Clarke 2012, Godfrey-Smith 2013, Pradeu 2016a, b, Bueno, Chen, Fagan 2018). Much of this interest comes from a close examination of the role that either the concept of biological organism, the notion of individuals, or both can be made to play in our current understanding of the evolutionary process. However, there is another angle to the question at hand, which becomes apparent by examining the extent to which modern evolutionary thinking casts a new light in which to explore the traditional accounts of organismality and individuality. Granted that the classical philosophical notions of individuality may still have a role to play in the way we conceive of the evolutionary process in biology, it is also important to address whether such concepts need to be reconsidered in the light of the current biological frameworks for evolution. In this article, I examine how individuality functions in both classical evolutionary biology and the newly framed extended evolutionary synthesis (EES). I argue, first, that individual organisms have gained causal relevance in different areas of evolutionary biology within the EES. Secondly, I argue that, on closer inspection, this set of new developments in theoretical biology are rendering the concept of individuality increasingly convoluted and problematic. Finally, I will show how the issue of biological individuality, understood in the light of these new developments in evolutionary biology, is relevant to a broader number of epistemic ideas in general philosophy of science regarding the discussion about scientific pluralism as well as for a more process-oriented revision of what the ontology of our world is like. In particular, on the one hand, the allegation will be made that, as philosophers like John Dupré (2018) and Alison McConwell (2017) argue, such a variegated diversity of notions of individuality should persuade us to fully embrace scientific pluralism as the best epistemic policy at hand. On the other, I will show that pluralism with regard to biological individuals is best understood as providing evidence in favor of an ontological view of the world in which change gains prominence over substantial stability.

2. THE MODERN EVOLUTIONARY SYNTHESIS: ASSUMPTIONS AND IMPLICATIONS

Individual organisms have different roles in the intellectual history of evolutionary biology. On the one hand, I will discuss how organisms play a passive role in the modern synthesis (MS) despite thinkers like Darwin who previously focused on organism activity. On the other hand, I outline and explore the consequences of organismality in the EES. As we shall see, individual organisms play a much more active and central role in contemporary evolutionary explanations. Before exploring the role of organismality and individuality, both within the MS and the EES, it is worth presenting more broadly some of the central tenets of the MS in its historical making and show how recent research into evolutionary dynamics prove them insufficient.

There is a broad, though by no means universal, consensus (Huneman 2019) that the establishment of the scientific paradigm that Julian Huxley (1942) termed the modern synthesis shaped much of twentieth-century biology. Whereas many of the historical details concerning the construction of the MS have long been under scholarly revision (Smocovitis 1992, 1997, Huneman 2019), in what follows I present a selective historical account of the implications of this process of construction for the field of evolutionary biology: the formation of the MS went hand in hand with a process of scientific construction where the principle of natural selection alongside other factors, such as mutations and genetic drift, gained prominence as a factor explaining the evolutionary change of populations of organisms. This prominence of the principle of natural selection (Weismann 1893) led to the exclusion of various other mechanisms that had been contemplated by biologists earlier.

To understand what is missing in such an account of evolution, it is illustrative to consider the case of the so-called Lamarckian model of inheritance, also known as the Inheritance of Acquired Characters (IAC). Jean-Baptiste Lamarck (1914) envisioned a conception of evolution in which the IAC was given clear explanatory prominence. However, while the name of Lamarck has become uniquely associated in the history of biology with the IAC, Lamarck's theory of evolution makes other more substantial assumptions about the way evolution works that go clearly beyond this model of inheritance. It is also interesting to observe that Lamarck himself was by no means the only author advocating the IAC model: in particular, Charles Darwin (1868: vol. 2, 349-399) incorporates the IAC into his own very speculative theory of heredity. In any event, it has become customary to say that, by establishing a barrier between the somatic and the germinal lines, the experimental work developed

by Weismann paved the way for a debunking of the IAC and thus led modern biology to endorse a pan-selectionist account of evolution (Lewontin, Gould 1979), which represents the core of what George Romanes (1893) called the neo-Darwinian theory of evolution. Of course, Romanes' neo-Darwinism did not coincide exactly with the standard MS, which merged Mendelism, population genetics, and the principle of selection (Fisher 1918, Dobzhansky 1937, Mayr 1940, 1942). Much of the later results of statistical genetics were just not available when Romanes proposed his account of evolution by natural selection. But there is at least one element in Romanes' version of the Darwinian theory that other more recent frameworks do preserve. To see what this element is, it is worth considering Weismann's work.

There is no doubt that the so-called Weismann barrier between the somatic and the germinal lines of an organism constitutes one of the basic tenets of the MS. This is a way of thinking about the mechanisms of biological inheritance that was later buttressed by the so-called central dogma of molecular biology. Although the Weismann barrier and the central dogma are by themselves empirical contentions about how biological information about a certain range of traits is transmitted in different contexts (Ongay 2018b), they together suggest a view of evolution that goes beyond such a restricted domain to conclude that genetic variation transmissible through DNA, and natural selection acting upon that variation, are all that is necessary to explain the evolutionary change of populations. If this rather limited description of evolution suffices, then that would seem to entail a vision of the evolutionary process in which there is very little room, if any at all, for what Ernst Mayr and William B. Provine (1980) classically termed soft inheritance.

In effect, Mayr and Provine characterized the notion of soft inheritance as "the belief in a gradual change of the genetic material itself either by use and disuse, or by some internal progressive tendencies, or through the direct effect of the environment" (1980: 15). Notice that, so conceived, this idea is negative in character since it seems to include *any* mechanism of inheritance that happens not to be covered by the traditional Weismannian account of heredity. Notice further that the notion of soft inheritance that Mayr and Provine had in mind does not coincide exactly with the IAC as described by the Lamarckian theory of evolution. It is important to see that whatever the so-called neo-Lamarckian theories of the twentieth century may have proposed, Lamarck's original view of evolution emphasizes the role of organismal activity in the acquisition of traits by the use and misuse of certain body parts and makes no mention of the direct effects of the environment in initiating a change to the genetic material. Still, even though it is true that there is plenty more to the idea of soft inheritance than just the Lamarckian version

of the IAC (since there is clearly historical room for other versions of it), it is also the case that the IAC, as Lamarck conceived of it, would fall under the rubric of soft inheritance.

In any case, with this proviso in mind, let us note that Mayr and Provine (1980) go on to declare that the science of genetics shows that soft inheritance does not exist. According to the thesis they defend, the dismissal of soft inheritance as a viable mechanism accounting for the heredity of genetic variation is one of the greatest contributions of the "young science of [Mendelian] genetics" to the establishment of the MS (1980: 17). This is important because it shows that the MS is defined by some of its proponents in terms of what the theory excludes rather than what it proposes (for more on this, see Gould 2002).

But if the exclusion of all forms of soft inheritance is one of the pillars of the theoretical architecture of the MS, what are the other more positive components of the synthesis? A minimalistic articulation of the logic behind the MS would have to include at least the preeminence of natural selection as the major causal force driving the evolutionary process, alongside the principles of population genetics providing the material on which selection operates. Taken together, and in conjunction with other factors such as genetic drift, these two components set the stage for the clear-cut definition of evolution in terms of the statistical change in the genetic frequencies of populations classically formulated by Theodosius Dobzhansky (1937).

Philosophers of science and scientist alike, who are partial to the principle of parsimony, often feel that simplicity is a virtue. This is perhaps why carving away soft inheritance could be viewed as a positive contribution to the MS. However, and leaving aside the heated debate on the epistemic justification of parsimony (Bunge 1963, Sober 2015, Ongay 2019), I hope the reader agrees that there might be cases in which the appeal of parsimony can mislead us. I take the exclusion of soft inheritance to be detrimental to our understanding of evolution. A wealth of scientific research presently suggests that both evolutionary biology and biology in general study processes that are much more complex in nature than such an austere view of evolution, no matter how enticing, allows. A recently developed extended evolutionary synthesis (Pigliucci, Müller 2010, Laland et al. 2014, Laland, Matthews, Feldman 2016, Müller 2014, 2017) points to some ways in which the minimalistic tenets of the MS may prove insufficient to accommodate the intricacies of the evolutionary process (but see Wray et al. 2014 for a discussion). Rather than a precisely defined theory, the EES constitutes an extraordinarily diverse and colorfully variegated research program with a multi-dimensional scientific purview. While a clear theoretical articulation of the different components of the EES

is not yet forthcoming, it encompasses areas of research as diverse — and, at times, as controversial — as transgenerational epigenetic inheritance (Jablonka, Lamb 2008), developmental and phenotypic plasticity (West-Eberhard 2005, Fusco, Minelli 2010, Lea et al. 2017, Lafuente, Beldade 2019), niche-construction and ecological inheritance (Odling-Smee, Laland, Feldman 2003, Laland, Matthews, Feldman 2016), social transmission of information and behavioral traditions in animals (Avital, Jablonka 2000), multi-level selection theory (Sober, Wilson 1998, Wilson, Wilson 2007), evolution of evolvability (Pigliucci 2008), and plenty more. All these contributions differ with respect to subject matter as well as in the empirical details of the processes they attempt to describe. However, whatever the sometimes substantial differences between their proponents, they do share some common ground: that the representation of evolutionary dynamics should appeal to an array of factors that proponents of the MS did not recognize and that the conception of causation in biology needs to be extended so as to accommodate large networks of multi-level feedback loops (Buskell 2019, Laland et al. 2011, Laland et al. 2013, Uller, Laland 2019) rather than holding on to a steadfast distinction between proximate and ultimate causes (Mayr 1961, 1993). Such a more pluralistic understanding of causality in evolution crucially includes a reference to processes in which the activity of individual organisms plays a causal role in evolutionary dynamics. There is much debate about whether many of the developments of the EES are really new (Wray et al. 2014) or how to measure the alleged superiority of the explanatory power of the ESS to the MS (Baedke, Fábregas-Tejeda, Vergara-Silva 2020). Instead of focusing on these debates, I will address one point of contrast in which the MS and the ESS do differ: the role of the individual organisms in evolution.

3. EVOLUTIONARY BIOLOGY AND THE MISFORTUNES OF THE (INDIVIDUAL) ORGANISM

It may seem paradoxical that although biology is an investigation into the properties of living individuals, the role of organismal activity has long been absent from the center of the modern synthesis's evolutionary dynamics. Consider for example the definition of the evolutionary process as change of gene frequencies in (Dobzhansky 1937). Consider also the later gene-centered view of evolution (Williams 1966, Dawkins 1976) that has dominated much of evolutionary biology from the second half of the twentieth century onwards. Although both conceptions differ in some important respects, they concur

more broadly in an interpretation of evolution where the role of the individual organism is considered as explanatorily inert. Notice that with this I do not mean to say that individual organisms are completely ignored in this framework. This is by no means the case: in fact, the importance of organisms in most evolutionary accounts is impossible to overstate: in the MS, organisms are understood as the basic target of natural selection, and so twentieth-century biology is replete with theoretical mechanisms that put organisms at the very center of evolutionary dynamics.

Rather than alleging that organisms are just ignored in the MS, I contend that the MS treated organismal activity as an effect to be explained away by referring it to an explanatory level outside the individual organism. In this sense, the MS treated individual organisms as passive recipients of causal processes. To put this point philosophically, both the classic MS and the gene-centered view of evolution are reductive models (Hempel, Oppenheim 1948, Nagel 1970) in that they tend to construe the activity of the individual organism as one of the *explananda* to be dealt with in evolutionary biology and correspondingly indicate other, more fundamental causal factors that would screen off such activity. For example, organisms are pictured to respond passively to their environments or to their genotypes. The reason for adopting such a reductive account lies in the fact that, in contrast with the robustness of genes, organismal activities, much like the rest of the phenotype, are seen as too ephemeral and temporary a process to be accorded any causally active agency in the long run. This is clearly not to say that there is not a role for the individual organism to play in biology, rather what is involved here is the claim that such a role, when it is recognized, remains passive in character and construed as an explanatory effect rather than as a causal mechanism in its own right.

Notice that this position contrasts with some previous ideas about the importance of organismal activity in evolution. Charles Darwin, for example, takes a different view in *On the Origin of Species*, *The Descent of Man*, and *The Expressions of Emotions in Man and Animals*, where he deploys a much more organism-centered image of how the evolutionary process works. Actually, in contrast to many neo-Darwinian accounts from the twentieth century, the Darwin's original theory (1859, 1871, 1872) recognizes plentifully the behaviors of individual organisms as causes and not merely effects of the evolutionary dynamics he is attempting to account for.

I am invoking the classic work of Darwin not because I intend to accuse biologists working under the MS of betraying his legacy. After all, scientists often improve on theories in the light of more recent findings. However, Darwin's emphasis on a more organismal-centered understanding of evolution

corresponds quite closely to the modern multidimensional approach presented by the proponents of the EES. In spite of his alleged defense of group selection (Chancellor 2005), Darwin constructed his view of evolution by focusing on the activity of individual organisms considered as paradigm cases of unitary individuals defined by such criteria as cohesiveness, delineation, sameness over change, and uniqueness (Santelices 1999, Folse, Roughgarden 2010). As we will see in the next section, this traditional representation of what a biological individual is, largely shared by the MS, has later become problematic in view of a multitudinous array of puzzle cases. However, it is fair to say that the active role of organisms is one of the long-forgotten aspects of evolution in much of twentieth-century biology. This does not mean that the MS is wrong about the evolutionary factors it positively contemplates, although it presents an unnecessarily restrictive theoretic framework that leaves out a variety of biological phenomena that have recently (and with good reason) received a lot of philosophical and biological attention. While too numerous to list exhaustively, this work includes references to non-genetic inheritance, exogenetic information, multi-dimensional heredity or niche-construction, and ecological inheritance. While the empirical details are to be worked out by biologists working in the emerging EES tradition, there is still a general point to be made: there is mounting evidence that evolution is much too complex and multidimensional to be captured succinctly by the narrow tenets of the MS. Attempts to extend the synthesis are a response to what was previously ignored: there is nothing wrong with understanding alterations in gene-frequencies as a cause of evolution, but that should hardly be a motivation to obscure the fact that at times organismal behavior takes priority, and then the replicators follow suit by means of a plurality of mechanisms of canalization and genetic accommodation (Waddington 1942, 1953, Noble 2015). In this regard, the right order of events of evolutionary change appears to be as multifold as it is eclectic.

Perhaps surprisingly, a familiar analogy from the Hindu tradition could be helpful by demonstrating exactly how the view of evolution derived from the MS goes astray. Confronted with an elephant, three blind wise men produce three diverse representations of what the animal is like. It would be a mistake to conclude from the parable that any of such depictions of the anatomy of the elephant is false even though it is easy to see that each of them is one-sided and incomplete. The mistake that each of the blind men makes is not to affirm what they know but to let each one's partial representations delude them into a wholesale denial of other aspects of the elephant that are equally relevant. Much like the elephant of the story, evolution exhibits a variety of dimensions, and, to many of them, the organismal activity is not just

a passive effect that needs to be explained away but also a causal factor that can be central to evolutionary analysis.

4. THE EES AND THE PARADOXES OF INDIVIDUALITY

In the previous section, I discussed some of the variety of evidence that the EES has recently marshaled in favor of giving the individual organism a more active role in our understanding of evolution. These are the prevalence of niche construction and ecological inheritance, the importance of exogenetic information, animal traditions, mechanisms of genetic accommodation, epigenetic inheritance, and developmental and phenotypic plasticity, to name but a few. It might be tempting to believe that this new state of affairs in evolutionary biology suggests a vindication of the more organism-centered view of evolution proposed by Darwin leading up to the MS. This would be an oversimplification, however, and misses the point of the elephant parable. To see why such an interpretation of what the EES entails is flawed, let me outline what I take to be a paradox concerning the expansion on the ontological category of biological individuality in light of recent developments in biology.

My line of argument so far has considered the observation that the present state of affairs in theoretical biology points to a multifactorial view of evolution. I have further argued that many of the dimensions of this comparatively convoluted image of what is at stake in evolutionary biology presupposes a description of the mechanisms driving evolution where organismal activity is given increasing importance. I now approach a different path that explores the consequences of the passive role for individuals in evolution traditionally endorsed by MS. I will show how the EES does not merely place the individual at center stage of the evolutionary scheme of things, but it also alters the very notion of individuality to make it much more multi-faceted and blurrier than one might expect. There are many aspects to the EES that imply such a complication of the traditional account of individuality, and I will not attempt to survey them all here. But there are two ways in which current biological research renders the concept of the individual more intricate that are worth considering briefly in what follows.

First, much of the philosophical discussion about individuality both inside and outside the biological realm has traditionally revolved around conceptual clarity concerning the biological individual organism. While there exist myriads of organisms for which criteria of individualization appear to be notably more problematic — from cicadas to amphibians or to hydrozoans, from

modular and clonal organisms (Clarke 2012) to biofilms of micro-organisms (Doolittle 2013, Ereshefsky, Pedroso 2013, Clarke 2016), the traditional notion tends to be mirrored in the image of our day-to-day paradigmatic mammals and other taxa in the *Metazoa* where relatively limpid spatial and temporal boundaries can be posited readily. The EES confronts us with a view of evolution in which this type of individual, which might include more than one organism within its bounds, is far from limiting itself to responding to the environment in a passive fashion. Individual metazoans, for example, are actually given a protagonist role in producing the conditions that define their own evolutionary process either by actively modifying the niches they adapt to or by reconstructing their phenotypes by means of engaging in plastic behavior (West-Eberhard 2005). That more nuanced depiction of the agency of individuality is only one of the facets to consider here. The second part of the story follows from a variety of conceptual analyses showing that individuality is not only a causal driving force moving evolution forward, it also, and conversely, constitutes a causal result of an evolutionary process, bringing about new sorts of Darwinian populations (Godfrey-Smith 2009) by establishing novel boundaries and the singling out of new entities exposed to the dynamics of selection and drift. Leo Buss' *The Evolution of Individuality* (1987), John Maynard-Smith and Eörs Szathmáry's *The Major Transitions in Evolution* (1995) and the late E. O. Wilson's *The Social Conquest of Earth* (2012) all concur to indicate the ways in which newly defined individuals can start to exist out of a process marking the evolutionary transformation of previously extant biological entities by means of spatial-temporal integration at higher orders of biological interaction as well as the corresponding de-Darwinization of the phenomena taking place at lower levels (Godfrey-Smith 2009). In that respect individuality is an evolutionary novelty arising across evolutionary levels and timescales, and not something to take for granted at the very outset of the process.

But what is a biological individual? Biologists working on different domains of the EES will give different answers depending on a multitude of local criteria pertaining to the conceptual requirements of immunology, epigenetics, behavioral biology, botanic, embryology, cell biology and cancer research, or metabolism research, among a plurality of other fields. In some of these areas, individuals can be assemblies of different organisms. For example, we might consider humans and their microbiome, or the human holobiont, as an individual that consists of communities of micro-level entities in light of the ubiquity of endo-symbiotic interactions (Gilbert, Sapp, Tauber 2012, Gilbert, Tauber 2016, Pradeu 2013, 2016a, b, Stencel 2019). In other respects, immunology helps redefine in a more fluid manner the constantly

changing frontiers separating the biological self and the non-self by virtue of the interactions between the immune system and the environment of an organism (Pradeu 2019, 2020). A similar logic governs the functioning of phenomena like selfish DNA and intragenomic conflict (Orgel, Crick 1980, Hurst 1992, Werren 2011, Gardner, Úbeda 2017), or even selfish neurons in the connectome (Seung 2011, Dennett 2017).

Irrespective of whether scientists working on these research programs would think of themselves as contributing to an extension of the MS, one consequence of the above revisions of classically defined individuals is that the traditional boundaries among single organisms are much less clear, which may turn out to take a toll on any prospective revision of such traditional temporary boundaries as those of birth (Gilbert 2014) and death (Nowak 2019). I suspect that such a dis-unified array of non-overlapping criteria of what individuality means may be seen as scientifically problematic (Clarke 2010, 2013) or, more generally, as a reason for intellectual dissatisfaction. Nonetheless, I do not see any principled reason for believing that there needs to be a general framework uniquely valid for the totality of all these areas and a plurality of others. Rather than understanding plurality of criteria as a problem calling for a decision on how to arbitrate over it, I propose to take plurality at face value: as an inherent feature of biology as a scientific endeavor as well as an inescapable characteristic of the living world of evolutionary biology (Dupré 1993, 1999, Bueno 2013, Ongay 2018a) to be taken notice of instead of resolved. As Thomas Pradeu (2019) points out, the concept of biological individuality depends on the question being asked. This plea for a maximally liberal sort of scientific pluralism resonates with Sinan Şencan's (2019) point that earlier proposals in favor of integrative pluralism (e.g., Mitchell 2002) do not suffice to accommodate for both single and multi-species individuals. Simply put: instead of a uniquely defined point at which the notion of individuality is to be unambiguously specified, what a multifarious assembly of lines of converging evidence stemming from various areas of research in present-day biology seems to entail is the existence of an entanglement of fluid individuals, each consisting of other individuals definable *ad libitum*. Rather than looking at this perplexingly plural situation as a theoretical conundrum calling for a solution, I suggest that we adopt a different attitude here: in current biology there are myriads of non-overlapping notions of individuality, *and that is just scientifically fine*.

Apart from fluidity regarding criteria of biological individuation, there is a second source of complication to be noted. So far, I have listed problem cases where entities previously thought of as individuals are technically or "really" composed of collections of organisms. The flip side stems from considering

sets of organisms as *real* biological individuals of sorts. Michael Ghiselin (1974), David Hull (1976), and Elisabeth Vrba and Niles Eldredge (1984) among a number of others all provide an interpretation of systematics that treats certain taxonomic classes as constituting higher-order biological individuals with an evolutionary trajectory of their own. Even if such positions represent a controversial (and remarkably ambitious) way to look metaphysically at the properties of some units of taxonomic analysis as real entities, the idea that there are supra-organismal individuals is one that connects elegantly with other directions in current biological theory concerning for example multilevel selection theory (MST), group selection, or the important notion of super-organism (Hölldobler, Wilson 2008). Much of the discussion about MST signals that levels of individual integration can be variously specified for a multiplicity of selective dynamics. Some of these specifications include traditional group selection, intragenic selection, selfish DNA, selfish cells, and so on. Depending on what range of selection pressures one chooses to focus on, all biological levels (including those that are clearly supra-organismal, such as eusocial colonies) may be principally computed as involving different types of equally legitimate Darwinian individuals — that is, members of assemblies subjected to Darwinian change (Godfrey-Smith 2009, 2013) and the process of natural selection (Clarke 2012, 2013).

Notably, I do not think that there is a *fact-of-the-matter* about which level in the biological hierarchy (i.e., genes, cells, organisms, populations, species, etc.) biological individuals occupy. If that were the case, the debate over individuality would lead to an inescapable conundrum as the levels of individualization are indefinitely many and depend crucially on the theoretical interests one decides to pursue on each occasion. This claim may seem to involve a conventionalist interpretation of the topic, but that is not the line of reasoning I would like to endorse. Instead, I submit that even though there are multiple sorts of non-overlapping individuals depending on the disciplinary research interests at stake, each of them is as real as any other.

Does this plurality represent an unmanageable proliferation of levels of individuality? Although some philosophers may be tempted to answer this question in the affirmative, I do not see any *prima facie* good argument to be so pessimistic. We ought not mistake super-abundance for inexistence: the relevance of individuality to an extended evolutionary synthesis is undeniable and the concept itself has become indispensable in many evolutionary scenarios. However, when those scenarios are contemplated in detail, what we are left with is a promiscuously varied proliferation of *real* individuals in any number of biological realms. This landscape suggests that the prospects for any monolithically fixed account of individuality are in fact quite dim, but

that alone is no reason for rejecting individuality realism altogether. Rather, the proliferation of levels of biological individualization ought to be considered as an admonition against a monistic interpretation of this and other important concepts in biology as well as an opportunity for scientific pluralism of the sort proposed by philosophers such as Hasok Chang (2012), John Dupré (1993), or Gustavo Bueno (2013). I expand further on bringing individuality realism and pluralism together before concluding the paper.

5. BIOLOGICAL INDIVIDUALS IN THE ONTOLOGY OF A WORLD OF PROCESSES

I have outlined the vast and complicated considerations of individuality in the extended evolutionary synthesis (EES). With that in mind I have considered the ways in which some recent work regarding the EES can accommodate a more actively causal role for organismality in defining evolutionary dynamics. Also, in light of the diversity of puzzle cases of biological individuals, such as holobionts and eusocial colonies, it is well-received that we should be pluralists about biological individuality. I have mainly focused on the active nature of individuality in the EES as opposed to the passive and static nature of biological individuals mainly confined to organisms in the MS. To close this discussion, I briefly outline the ontological implications of individuality pluralism *as conceived in its active role within the EES*. Ellen Clarke (forthcoming) persuasively argues that the way current biological research and theorizing carves out the world has ontological consequences worth considering. In what follows, I focus solely on two ontological frameworks (substance first versus processes ontologies) with a view to spelling out the implications of scientific pluralism about biological individuality to such an ontological scheme. As I show, recent developments within the EES strongly call for a pluralistic understanding of the notion of individuality. Such expanded understanding is in turn much better accommodated by a metaphysical view of the world which stresses the central role of processes over substances.

Under the influence of Parmenides, Aristotle, and Descartes among many other major philosophers, the basic furniture of our world has traditionally been conceived of as one of substances. Substance-first ontologies rely on a view of the world that emphasizes permanent objects that sometimes happen to change. This is a perspective that accommodates nicely some of the core pre-philosophical intuitions of the layperson concerning a world that seems

to exhibit stability at most crucial levels. It is no coincidence therefore that such a basic ontological scheme has been enormously influential for many centuries. Now, to say that substantialism has been an influential doctrine hardly implies that its appeal is universal or irresistible. Another tradition, represented by an egregious list of thinkers from Heraclitus of Ephesus to Hegel or from Alfred North Whitehead to Martin Heidegger, resists the allure of thinking of the world as composed of *things* and conversely stresses change and temporality as inherent features of any sound depiction of what there is. Again, that this family of doctrines tends to focus on how objects change does not mean that they are committed to the negation of stability and permanence. Rather than going that far, the point that such an ontological view advances is that permanence is a secondary and comparatively abstract moment in a world that is primarily made of processes of evolving realities and relations (Dupré 2018).

If the familiar scheme of substance-first ontology has the advantage of fitting well with the outlook of the layperson, an ontology based on processes has something to be said in its favor, too, as it captures more naturally the description of relevant phenomena in many of the most successful scientific theories of the day. Since the beginning of the twentieth century, for instance, quantum mechanics and the theory of relativity have experienced an enormous growth. Whatever their other irreducible mutual differences, these are two scientific theories that depict physical objects as arising from processes and relations instead of permanent things fixed once and for all as the fundamental building blocks of the physical universe. John Dupré and Daniel J. Nicholson (2018) have lately argued that a similar point holds, too, of the consequences of evolutionary biology and other areas of biology alike in that they, too, encourage the philosopher to revisit the process ontology (Dupré 2012). Here is what is key to consider: stressing processes in the living world does not imply that there are just no living *things* out there, even if it brings to the fore the very consequential implication that *things* are not to be thought of as substances but as sets of evolving processes which become carved out in a variety of ways for a set of pragmatic reasons.

I believe that the situation regarding the status of individuality in current biology fits rather well with a more mobile ontological description of the *furniture of nature*. Although the sort of pluralism regarding the spectrum of concepts of individuality that I have laid out may be seen as a call for a *tout-court* denial of the existence of *real* individuals, I assert no such negation. What is important, though, is to de-emphasize the substantial character of our traditional understanding of individual living things while taking the vast plurality of kinds that the reservoir of individuals in the biological world implies at

face value (McConwell 2017, Durpé 2018). It is true that this move may lead us to see the living world as consisting of a set of processes that get individualized by our pragmatic practices of scientific abstraction and not so much as a world-composed-of-things out there. If this picture seems unsatisfactory for the layman, my answer is simply put: such is *life*. The EES has the goal of expanding the scope of the MS to account for aspects and dimensions of evolutionary dynamics that were left previously unattended. Among many other things, this objective has implied the attribution of a protagonist role to organismal activity in defining evolution, as well as a revision of biological individuality in a more pluralistic direction. This does not, however, commit us to an anti-realism: there are suitable ontologies that emphasize processes to complete our philosophical picture. I hold that, when reasoning about what such an extension of the MS suggests for traditional metaphysical discussions, there is an interesting way in which the EES seems to lend support to process ontology over substance-first theoretical orientations. The emergence of biological individuality of numerous types by the integration of lower level entities exposed to variability and natural selection, as well as the corresponding abundance of criteria of individuation in different areas, point to a process-like interpretation of biological individuals. Individuals, the way they are pluralistically conceived of in current biology, are not substances but are best understood as being brought about by a never-ending process of evolution.

CONCLUSION

I will conclude this paper by bringing to the fore something that philosophers of biology may easily find surprising: there is some insight to be gained from reflecting on one lesson from the philosophy of Hegel. The Hegelian insight to be adopted here consists in an account of individuality where individuals are to be thought of as results of a dynamic process rather than metaphysically stable substances underpinning the process of change.

Hegel famously thought of individual entities as involving the laborious abstraction of a whole array of much more fundamental ontological notes that are mobile and temporary in character. What Hegel had in mind in deploying this dialectic criticism of substantialism was not the process of evolution as biologists think of it nowadays. However, I think that there is a rather modest Hegelian insight to be preserved by the philosopher of biology. The take-home message connects well with what many areas of scientific endeavor, including biology, suggest about our world. This paper has attempted to

highlight how the vicissitudes of the notion of individuality in the EES lends support to such a more process-centered representation of the biological realm. I have shown that the role of individuals in the biological process of evolutionary change has been handled in various ways along the history of modern evolutionary theory. Much has changed in biology with regard to the role of the individual within (its) evolution: from the protagonist place it was given in Darwin's original theory of evolution by natural selection to its treatment as a phenomenon to be causally reduced to other factors in the MS. Organismal activity and the behavior of individuals is shown to recover a much more active role in present-day accounts of the intricacies of how evolutionary change is brought about. Nevertheless, the situation we are presented with when it comes to scrutinizing the impact of the EES and its ramifications for the concept of the individual is rather twofold: no matter how indispensably relevant it may prove to be, *individuality* does not represent a uniquely singled out concept. Instead, it constitutes a scruffy spectrum of notions to be carved out in many ways depending on the disciplinary interest of the occasion. It is also a moving concept in that various levels of Darwinian individuality result from the same evolutionary process to which they contribute.

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