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Perspective

Are we really seeing the big picture? Some reflections on the current debates in evolutionary biology

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Abstract After more than one hundred fifty years of the publication of *On the Origin of Species* by Darwin, scientists are still arguing on the relative importance of mutation and natural selection, on the driving force of organismal evolution, on microevolution and macroevolution, etc. Such periodically repeated debates appeared to have introduced more chaos than musings. What happened and why? Have we really considered our views, opinions and arguments under the big picture of evolution before posing the questions? Or are we talking past each other? We do need some reflections. While we believe that the current evolutionary theory is doing fine, perhaps a refinement or re-encapsulation of its knowledge framework can help promote a better understanding of the evolutionary science as a whole and blow off the mist over the big picture [*Current Zoology* 61 (1): 217–220, 2015].

Keywords Mutation-driven evolution, Development-driven evolution, Macroevolution-driven evolution, Evo-Devo, Natural selection, Tool-kit genes, *Hox* genes

Six years ago, scientists world-wide celebrated the one hundred fiftieth anniversary of the publication of Darwin's *On the Origin of Species*; and this historic publication has become unquestionably "the most important book of science ever written" (Wilson, 2009). Evolution as a thought has penetrated almost every aspect of human exercises. Can Darwin now finally feel reassured? Probably not, given the mushrooming one upon another of criticisms and debates on the key tenets of evolutionary theory over the last ten years, including the very issue of natural selection which is the backbone of Darwin's and modern evolutionary theory. Then, have we really considered our views, opinions and arguments under the big picture of evolution before posing the questions?

1 The Major Debates

Below I attempt to outline some of the major topics under the current debates, referred to as, by mimicking Nei, "mutation-driven evolution", "development-driven evolution", and "macroevolution-driven evolution" for convenience; and all of them are much stimulated by recent fascinating progresses in developmental biology, particularly evolutionary developmental biology (Evo-Devo). Note that these are interconnected issues with differential emphasis.

Mutation-driven evolution. The central argument of this proposition is that "mutation is the driving force of evolution and natural selection is of secondary importance" (Nei, 2013). Note that mutation here is defined in a broad sense, including the conventional mutation (nucleotide substitution and small insertion/deletion), gene/genome duplication, recombination, chromosomal rearrangement, transposition, etc., i.e. any change of DNA molecules. In his retrospective, Nei traced his earlier thought of this heresy of view to the 1970s (Nei, 2013). Nevertheless, his argument of mutation as the driving force of phenotypic evolution was modernized and more formally launched in 2007 (Nei, 2007).

The rationale of Nei's argument is that "natural selection and genetic drift are ultimately determined by the differential rates of birth and death of individuals, which are again the consequences of metabolism and reproduction", which are "governed by the function of DNAs and RNAs" and mutations of which are unavoidable (Nei, 2013). Hence, "natural selection occurs as a consequence of mutational production of different genotypes, and therefore it is not the fundamental cause of evolution" (Nei, 2007, *p.*12241). In his new monograph, Nei further emphasized that "evolution occurs primarily as a result of constraint-breaking mutations rather than a result of struggle for existence" (Nei, 2013, *p.*197).

Development-driven evolution. The central argument

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of this proposition is that non-random mutation associated with developmental constraint or developmental bias is the direct cause of adaptation and speciation, and thus sets the rates and patterns of evolutionary change. An archetypal perception was the "Revolution #3" proclaimed by Carroll (2005a), as a generalized variation of some of King and Wilson's (1975) pioneering ideas. That is, Carroll praised the Evo-Devo achievements as the third revolution in biology, with the other two being Darwin's theory of evolution and the discovery in molecular biology on how DNA acts as the basis of heredity. Carroll suggested that mutations in regulatory regions change the action modes of the controlling genetic switches, that alter the spatial and/or temporal expression patterns of developmental "tool-kit genes" (e.g. *Hox* genes) that in turn regulate the development of different modules, and thus these regulatory mutations play the predominant role in organismal evolution.

While King and Wilson (1975) anticipated that regulatory mutations may account for the major organismal differences between humans and chimpanzees (here "organismal differences" refer to differences in anatomy, physiology, behavior, ecology, etc.), Carroll, on the one hand, extrapolated it into the animal kingdom, and on the other hand, restricted it to morphological evolution (i.e. evolution of forms or anatomy), that is, "the evolution of anatomy occurs primarily through changes in regulatory sequences" (Carroll, 2005b). But other evo-devo biologists (evo-devotees) are even more radical, with a more fanciful claim that "evolution is not so much the result of wholesale genetic variation in terms of mutation as it is a matter of changing when and where genetic switches will be turned on and off in the development of an organism" (Ayala and Arp, 2010; *p.*196). Other developmental phenomena were also suggested to be the fundamental causes of evolutionary change, including evolvability, phenotypic plasticity, epigenetic variation, etc. (Pigliucci, 2007; Laubichler, 2010; Laland et al., 2014).

Macroevolution-driven evolution. The central argument of this proposition is that there exist macroevolution-unique evolutionary processes (i.e. processes that are uniquely operating at macroevolutionary level but not at microevolutionary level) (see Gould, 2002 for an extraordinary spacious discussion). The discontinuity of biological (or "organic" in Dobzhansky's word) diversity is the most striking feature of life on earth, which has puzzled generations of naturalists. The effort to distinguish between microevolution and macroevolution actually reflected a historical attempt to examine and explain the puzzle. Nevertheless, some paleontologists and evo-devotees believed that as discontinuities are accompanied by hierarchical structures at various levels, such structures will "impede, obstruct, and even neutralize the effects of microevolution" (Erwin, 2000), and some higher order processes such as developmental bias, species selection (hierarchical selection), niche construction, punctuated equilibrium, etc, should be invoked to explain macroevolution (Gould, 2002; Erwin, 2010; Laland et al., 2014).

2 Talking Past Each Other?

Although the debate on development-driven evolution is mainly developed since 1990s (see Laubichler, 2010), the other two debates have a much longer history. The mutation-selection debate should not be unfamiliar to those who have some knowledge on the history of evolutionary biology. It has gone through several ups and downs over the last one hundred and twenty years (for historical accounts, see Provine, 1971; Gould, 2002; Nei, 2013). Among the distinguished opponents who (exclusively) supported mutation as the driving force of evolution (or saltatory origin of species by mutation) and largely denied the role of natural selection, are figures such as Hugo de Vries, Thomas Morgan, and now Masatoshi Nei (who nevertheless does no reject selection) (For reviews, see Gould, 2002; Nei, 2013).

Similarly, whether macroevolutionary processes are reducible to microevolutionary processes has been one of the persistent debates in evolutionary biology, ever since the concept of macroevolution was introduced to English speaking biologists by Dobzhansky. Actually, Mayr's (1982) analysis indicated that such a debate existed well before the inception of the two terms of macroevolution and microevolution. Well, in his extensively long argument on evolutionary theory, Gould (2002) reckoned that Hugo de Vries had actually visioned the issue of macroevolution and even coined in 1905 the term of "species selection" in English. Interestingly, Dobzhansky himself appeared to have never really accepted the notion of discontinuity between microevolution and macroevolution (*cf.* Dobzhansky, 1937, preface, *p.*12 and Dobzhansky, 1970, *p.*429).

Noticeably, various dissenters in the current debates still habitually fired on the Modern Synthesis as if evolutionary theory has fossilized since the Synthesis. Actually, evolutionary theory has never stopped being upgraded in the last six to seven decades, achieving a breadth far beyond the substance of the Synthesis, as testified by modern textbooks of evolutionary biology (e.g. Futuyma, 2013). As one of the major figures in the Synthesis, some thirty years ago when commenting on macroevolutionary discontinuities, Mayr wrote: "Undoubtedly regulatory genes are participating in these changes or are largely responsible for them, but this does not require saltations" (Mayr, 1982, *p.*618). Clearly, Mayr updated himself.

In retrospect, earlier debates apparently introduced more chaos than musings. This was true with de Vries, Morgan, and perhaps even Gould. It is generally expected that discussions and debates would stimulate further thinking and in depth investigation, and which then bring back a better understanding of the topics in question. However, this is only possible when discussions and debates were under a common knowledge framework. A conventional wisdom is that when a subject has been repeatedly debated without consensus or argued with no echo, it would suggest that there exists some great misunderstanding or misconception, and/or there is a lack of common framework such that the two sides are talking past each other. The ongoing debates in evolutionary biology appear to be self-trapped as such again, worryingly managed only to increase the dimension of chaos.

This is bad for the community, particularly for students and young scientists (not to mention the general public) just stepping into the research field of evo-devo and evolution-related areas (such as molecular ecology, conservation biology, biogeography, ecology, developmental genetics, etc.), who are relatively short of time (and perhaps patience as well) in reading deeply and widely evolutionary literature. We do need some reflections on the possible unexpected outcomes of such debates, on why these issues have been debated again and again without coalescence, and on whether we who are still labeled, willingly or not, as neo-Darwinists by some dissenters are a bit obstinate or not.

3 A Need for a Refinement of the Current Framework?

An important reason for the disagreeable "state of affairs" is perhaps due to the somewhat lopsided focus of current studies and emphasis (e.g. zooming rather exclusively in a few detailed forces such as natural selection, mutation and drift, and in mechanisms of developmental evolution). The consequence is that there is a lack of general understanding of both the modern evolutionary science as a whole and the big picture of biological evolution, which then put us at risk of confusing the particular with the general, and an incidental consequence with the causal mechanism. This leads to a state of not seeing the forest for the trees. While Wray et al. (2014) may be sensible that the evolutionary theory does not need an overall rethink, perhaps a refinement or re-encapsulation of its knowledge framework can help promote a better understanding of the evolutionary science and thus settle down some serious debates and confusions.

Essentially, biological evolution can be alternatively formulated into the following spectrum of contiguous processes:

(1) Process **"0 → 1/N"** (the origin of novelty, e.g. the origin of the first RNA/DNA molecule, first replicator systems, first translation systems, first cell, first eukaryote cell, first multicellular organism, ...; the generation of new alleles, new genes, new genomes, new functions, new forms, new behaviors, ...);

(2) Process **"1/N → 1"** (the increase in the frequency of a novelty in an environment (including genetic background), e.g. the fixation of a mutant in a population, the adoption of a new pathway in a species, the formation of a new species, the establishment of the first multicellular organism in Nature, ...);

(3) Process **"1 → N"** (the increase in the diversity, e.g. from a singleton to a gene family, intraspecific polymorphism, species diversification and evolution of biodiversity, ...);

(4) Process **"N × N"** (connections and interactions between/among genes, pathways, genomes, cells, individuals, species; between organisms and environment, earth and asteroids, ...; e.g. developmental constraint, epigenetic inheritance, phenotypic plasticity or genetic assimilation, mutualism, coevolution, social and behavior evolution, evolution of parasites and hosts, ...); and

(5) Process **"N → 0"** (extinction, reduction, degeneration and loss of function, e.g. decrease in frequency and diversity, gene and pathway loss, regressive evolution, species extinction, population bottleneck, decrease in genomic, organismal and ecological complexity, ...).

Clearly, various mechanisms (forces) are responsible for these heterogeneous evolutionary processes, and mutation, selection, drift are among such mechanisms (surely there should exist other yet-to-be-identified mechanisms). Therefore, under this perspective, the Modern Synthesis was largely a theoretical realization of the second process; also, it is not really rational to argue on the relative or absolute importance of natural selection and mutation as the driving force of evolution, because they play different roles in different processes. Similarly, the intriguing findings of evo-devo on "tool-kit genes" and their regulations (or the "secrets of evolutionary innovation" in Carroll's words) are actually the working genetic principle of development which is the outcome of evolution through the above processes. Also, the so-called macroevolution appears to be just one outcome of evolutionary processes in pursuit of diversification which stems ultimately from genomic variation at the limit of our current knowledge, the rule of which follows the mechanisms of microevolution. Appealing and thoughtful it may be as a concept, hierarchical selection needs more than contemplative thinking. What has been largely ignored in the current discussion, however, are the roles of the process of interactions in adaptation, in maintaining stability, in creating biological diversity and in their almost unlimited potential to trigger innovation. This should be a grand area open to evolutionary biologists, developmental biologists, ecologists and alike.

Among these five heterogeneous evolutionary processes, the first process is fundamental to all biological evolution, the second one is obligatory because for any innovation to be evolutionarily meaningful, it has to at least succeed from (1) to (2), and the fourth one apparently accompanies all the others in the real biological world. The first four processes can be regarded as forward-leading endeavors, while the fifth is more or less the destination from a long-term viewpoint (but it may also lead to novel rounds of innovation cycles). Evolutionary discussions under a background of the big picture, whether as the one proposed here or as other alternatives, would be better orientated, while stimulating musings it would induce less costly chaos. Moreover, such a big picture will help junior researchers or students to better enter the grand field of evolutionary biology regardless of its intrinsic heterogeneity or complexity as demonstrated by these numerous debates.

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