Recent Developments in Evolutionary Biology and Their Relevance for Evolutionary Economics

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Abstract The paper gives attention to the question of whether the development of evolutionary theories in biology over the last 20 years has any implications for evolutionary economics. Though criticisms of Darwin and the modern synthesis have always existed, most of them have not been widely accepted or have been absorbed by the mainstream. Recent findings in evolutionary biology have started to question again the main principles of the modern synthesis. These findings suggest that phenomena of co-operation, communication, and self-organization have been underestimated, and that selection is not the predominant factor of evolution, but only one among many. Thus, in evolutionary economics, the question is whether the popular variation-retention-selection principle is still up to date. The implications for evolutionary economics with respect to analogies, generalized Darwinism, and the continuity hypothesis are also addressed.

1 Introduction

In the last 20–30 years, there have been discoveries in evolutionary biology that, on the one hand, have led to the inclusion of new fields of research, such as embryology and ecology, and on the other hand, to the emergence of new factors of evolution and thus to a shift in the significance of chance, genes and selection. The relationship of these findings towards the modern synthesis—the standard theoretical paradigm of evolutionary biology—is not yet clarified and agreed upon in the scientific community, but the new empirical evidence is so overwhelming that a new assessment of the theory of evolution is inevitable. The reason why this development could be interesting for evolutionary economics is that some approaches in evolutionary economics draw upon evolutionary biology, mainly

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through the form of metaphors and analogies or in unifying concepts such as generalized Darwinism. Thus, since evolutionary economics itself is a research program outside the mainstream, and since there are obvious similarities between the modern synthesis and neoclassical economics (Foster 2001, p. 118), it would be inattentive not to consider—or at least not to have a look at—these recent developments outside mainstream evolutionary biology.

Charles Darwin's intention was to provide evidence of evolution being a historical matter of fact and to explain evolution. Darwin's own explanation of the rise, change and decline of species was complex: in some respect clear and distinct, but in others vague, even contradictory, and since genetics had not yet been established, some explanations remained speculative. At the beginning of the twentieth century, with the rise of genetics, the explanation of evolution was still not generally accepted, as may be seen, e.g., in the scientific controversy between the geneticists and the researchers on populations about the relative significance of discrete mutations, the impact of the environment and selection. It was only later in the 1930s and 1940s when the main principles of genetics had become more widely accepted that the pluralistic view narrowed down to that of the modern synthesis (or synthetic view of evolution), which is with modifications the standard theoretical paradigm in evolutionary biology today.

The basic tenets of the modern synthesis might vary slightly from interpretation to interpretation (e.g. Reif et al. 2000), but there is a kind of common quintessence on which most of the exponents would agree. According to the modern synthesis, stochastic changes in gene frequency (caused by mutation, recombination and gene flow) produce small, heritable variations in the phenotype. Some of the individual organisms are, then, better adapted to the environment, have a higher fitness and spread in the population through positive selection. The ongoing modification of the genome furthers the morphological evolution and the only factor directing morphological evolution is the selection of better adapted phenotypes (Wieser 1994, p. 160).

In the following, and to avoid any misunderstandings, I would like to emphasize that the modern synthesis is considered here as a theory on how evolution took place. The issue, then, is the explanation of evolution and not the historical record of evolution which from a scientific perspective in this paper is taken to be a matter of fact. Including the research areas presented in the following, there is no disagreement about conceptions of evolving species in general, and about the principle of common descent.

Challenges to the modern synthesis in the second half of the twentieth century have been manifold, e.g. the neutral theory of molecular evolution by Kimura (1955, 1983), today better known under the label of "gene drift", endosymbiotic theory (Margulis 1970), theories of internal selection and development constraints (e.g. Gould 1980; Maynard Smith et al. 1985), system theories of evolution (e.g. Riedl 1975), theories of discontinuous evolution, the punctuated equilibrium theory (Gould and Eldredge 1972, 1977), theories of self-organization (Kauffman 1993), theories of skin, group and species selection and the corresponding hierarchical theory of evolution (e.g. Maynard Smith 1964; Vrba and Eldredge 1984;

Eldredge 1985), the theory of autoevolution (Lima-de-Faria 1988) etc. Most of these critical approaches did not reject the modern synthesis completely, but acknowledged at least some of its achievements, while extending, qualifying or putting into perspective certain tenets of the modern synthesis and also adding new factors of evolution. A lot of the critique of the modern synthesis implied the predominant roles of (random) mutations, genes and selection in biological evolution. Some discoveries, such as gene drift, were absorbed by the modern synthesis, whereas others, such as the endosymbiotic theory and punctuated equilibrium theory, entered standard text books on evolution but still were presented mainly as side effects that completed the standard explanation without questioning the main tenets of the modern synthesis. The modern synthesis would definitely have remained the standard theoretical paradigm in evolutionary biology had criticism in the last decades ebbed away. But the contrary has taken place. More and more empirical findings and new hypotheses critical to the standard theories have come up in the last 25 years. They draw on new insights into molecular underpinnings, genetics, ecology and developmental biology, giving new support to the old criticism of the modern synthesis. Apart from the publications in scientific journals, a set of books have been released that summarize and assess these discoveries, among them are Carroll (2006), Gilbert and Epel (2009), Jablonka and Lamb (2005), Kirschner and Gerhart (2005), and Pigliucci and Müller (2010a).

Thus, in Sect. 2, I will present essential research programs and research findings in evolutionary biology. The choice has been made according to the principles of (1) novelty—which will roughly be defined as what has emerged in the last 25 years (a period that admittedly is to a certain extend arbitrary but the history of the theory of biological evolution is not the main focus of the paper), (2) divergence from mainstream, and (3) ongoing research activities in this field. It should be mentioned that many of the recent research findings to be presented here are not completely new, but have been either better confirmed or have become clearer, so there might be an overlap with earlier approaches. There is no claim that the list of recent approaches in evolutionary biology is complete, since the aim of the paper is not primarily to give a comprehensive record of the developments in biology, but to hint at some methodological consequences for evolutionary economics from a choice of unorthodox biological theories. In Sect. 3, an assessment of the findings mainly by biologists is presented. In Sect. 4, possible implications for evolutionary economics are given. Sect. 5 concludes.[1]

[1] Since I am an economist and not a biologist and have had no training in biology, I apologize for any remaining obscurities and errors, in particular in the sections dealing with biology. Any comments and corrections are very welcome.

2 Recent Developments in Evolutionary Biology: Findings

A major motivation for biologists to explore evolution further was the fact that some phenomena of evolution have still not been explained satisfactorily. Among them is the so called Darwin's dilemma, since this problem had already been raised by Darwin himself. The question is: How can complex organs or parts of the body like an eye, a limb or a wing be the result of a gradual selection process? An eye, for example, is a complex system of a lens, a retina, tissue, nerves and so on. If an eye is indeed the product of gradual selection, it has not developed as a whole, and all of a sudden. There must have been intermediate forms with which the individual organism was not only viable but which were also selected, since according to the modern synthesis, every intermediate form, including incomplete ones, must have shown a selective advantage. It is obvious, then, that this explanation of the emergence of complex new structures was not satisfying (Kirschner and Gerhart 2007, p. 16). It was shown that this deficiency of the modern synthesis lies in its disregard of the rules of transformation from genotype to phenotype. The modern synthesis concentrates on two research areas, genetic and phenotypic evolution, implicitly assuming that the space between genetic evolution and phenotypic evolution is not relevant (Müller 1994, p. 185) and not knowing whether the genetic changes responsible for big changes in form were the same as those for small variations within species (Carroll 2006, p. 284). Thus, the modern synthesis was blamed for only explaining what body forms can be maintained in organismal evolution, but not what forms are generated. It was reasoned that mutations only produce small variations from what already exists, but do not create new forms (Kirschner and Gerhart 2007, p. 23) and mutations are often the result of negative impacts such as radiation and hence destroy more than they create. In addition, selection is a mechanism that can only work on what already exists (Müller and Newman 2003, p. 3). Thus, a theory of how completely new organs, structures and body plans come into existence was still lacking.

This scientific challenge has given rise to a research program called evolutionary developmental biology (or informally "evo-devo"), which combines two research areas that had existed quite independently until roughly 1990: developmental biology and evolutionary biology (Müller 2005, p. 87). Developmental biology deals with the development of organisms and ontogenetic rules of the development of forms and structure, in particular, the origin and evolution of embryonic development. Evo-devo seeks to extend this research by concentrating on interdependencies between ontogenesis and evolution, in particular, the analysis of causal relationships between embryonic and evolutionary processes (Müller 1994, pp. 155–160).[2] One of the main questions posed by evo-devo is: Does

[2] According to Müller (2005, pp. 98–102), evo-devo comprises four research programs: (1) The Comparative Morphology Program (2) The Epigenetic and Experimental Program (3) The Evolutionary Developmental Genetics Program (4) The Theoretical Biology Program.

developmental (embryonic) evolution bias the produced phenotypic variations or constrain certain paths of evolution? (Futuyma 2007, p. 474).

Some exponents of evo-devo have concentrated on physical processes that guide the way in which cells organize organs and tissues. The stickiness, elasticity, and chemical reactions within and between cells affect the body plan of an organism (Pennisi 2008, p. 196). Since body plans have internal inertia, evolution is not completely arbitrary, but works around these stable body plans. Consequently, there is a multitude of development constraints. The modern synthesis implicitly assumes that genetic and morphological variation and evolution are highly positively correlated. However, results in molecular genetics show that this is not the case and, even from the complete knowledge of the genome, one cannot infer the anatomy of an organism. The ontogenetic formation of morphological structures is not determined by genes only, but is due to an interdependent activity of genes, cells, tissue and external factors (Müller 1994, p. 162).

One of the discoveries of evo-devo in contrast to the modern synthesis has been that the same or similar organs and structures in different animals (such as eyes, limbs, hearts, legs, wings etc.) have not been "invented repeatedly from scratch", which means they would have emerged from distinct changes in the number and sequence of genes (Carroll 2006, p. 132). Instead, similar organs and structures have "evolved by modification of some ancient regulatory networks under the command of the same master gene or genes" (Carroll 2006, p. 286). In other words, common and very old genes or master genes have existed latently in the genome of all animals for a very long time (since early evolution), and they are the reason for similar body plans and organs in very different animals (in different branches of the genealogical tree) (Carroll 2006, p. 71). Genes that code for body plans are called Hox-genes. These old and complex genes are activated in embryonic development. Hox-genes together with transcription factors (proteins that bind to DNA and turn transcription on or off) and signaling pathways (communicating cells leading to traveling proteins that induce changes in the cell and in gene expression) are considered to be elements of a genetic tool box (Carroll 2006, p. 74). Similar sets of Hox-genes and sometimes even identical single genes can produce a variety of body plans because the genetic tool box has been differently combined by the function of genetic switches (promoters, enhancers), regions of DNA that are typically located near the genes upstream on the same strand of DNA, which can turn genes on and off in reaction to transcription factors (specialized signal proteins). Genetic switches allow the same tool kit genes to be used differently and thus are a central factor in the creation of variety. As a result, these genetic switches are considered to be the "key actors" in embryonic development and evolution (Carroll 2006, p. 111). Though the discovery of Hox-genes was important, it was discovered that it is not a single Hox-gene that is responsible for one new organ or structure, but groups of gene switches and proteins that build networks that regulate the formation of whole organs and structures (Carroll 2006, p. 129). Changes in genetic switches trigger a shifting in the zones of Hox-genes and thus are responsible for all kinds of changes in the body form, including the creation of new species. Therefore, not the invention of new

Hox-genes caused evolution but the genetic switches triggered by ecological conditions worked on the genetic tool kit. According to this view, natural selection is not responsible for the creation of new body forms, but determines only which forms are actually been realized (Carroll 2006, p. 287).

Kirschner and Gerhart argue on similar lines with their hypothesis of facilitated variation. They say organisms restrain some components of their phenotype from certain changes while, on the other hand, other components are released for change. Restricted elements are called conserved core components and they consist of a sequence of several protein components. These core components have remained relatively intact through time, and have not been subject to gradual change but rather to discontinuous waves of change (Kirschner and Gerhart 2007, p. 299). Specific features of these core processes make them robust and flexible, e.g. weak regulatory linkage, modularity, and compartmentalization. These features have not changed in the course of time but have provoked regulatory changes (Kirschner and Gerhart 2007, p. 354). The greatest amount of change (since the Cambrian) is not due to changes within core components, but is due to regulatory changes of core processes. Among these regulatory changes are changes in the date, place, amount, and circumstances of gene expression, cell signaling, the role of Hox genes in embryonic development, the program for developing extremities, etc. As a result of these regulatory changes, core components are used in new combinations and in different amounts at other times and in other places. Under the new conditions, the flexible core components might show different performance and new phenotypes (Kirschner and Gerhart 2007, p. 300). Carroll argues along the same line: "At an anatomic level, multifunctionality and redundancy are keys to understanding the evolutionary transitions in structures" (Carroll 2006, p. 288) and Müller states "[t]he new tenets by evo-devo may be called "emergence" and "inherency" (Müller 2005, p. 106). Core components are adaptive, and have been selected due to their robustness in embryonic development and anatomic stability. Consequently, phenotypes that have emerged from regulatory modifications of core components are presumably less lethal, more viable and better adapted than completely new phenotypes. In this way, variation is facilitated and accelerated (Kirschner and Gerhart 2007, p. 301). Organisms combine a limited number of components to transform a small amount of random mutations into new phenotypic forms. However, organisms and not mutations are the protagonists in the realization of concrete body forms (Kirschner and Gerhart 2007, p. 354). This view also stresses the existence of established and approved components for innovation (Kirschner and Gerhart 2007, p. 303).

It is well known that genomes consist of DNA with coding sequences (genes in the narrow sense) and DNA with non-coding sequences, also called "dark matter of the genome" (Carroll 2006, Chap. 5). In the last decades, it has emerged that, in the non-coding sequences—the larger part of the genome—specific elements, called "transposable elements" (or transposons) can change the structure of the genome, including changes to germ cells. Transposable elements can double single genes or groups of genes; they can reorganize genes by combining them differently, and they can change the local position of genes (the reason they are sometimes also called jumping genes) and thus bring genes under the control of other genetic switches (Pennisi 2007). These phenomena can be interpreted as a form of "self-organization" of the genome, but they also include the possibility of the creation of new genes. The activity of the transposable elements is under the control of the cell, which, according to some biologists, is considered to be a cognitive entity. The cell in turn is under the impact of ecological conditions. The cell has several possibilities to exert an impact on the activity of transposable elements. It can create new transposable elements, or can control and even restrict their activity. In the latter case, the deactivation of transposable elements—a mechanism that is called RNA-interference because it blocks or destroys RNA molecules—exerts stability in the phenotype of an organism when there is no drastic change in the ecological conditions. However, if, by contrast, radical and lasting ecological changes prevail, the organism gives information to the cells which—through the weakening of the RNA interference and easing of the control of transposable elements—in turn induces a creative process of reorganization of the genome. From these findings, some biologists have concluded that changes to the genome are not mainly a consequence of random point mutations, but are due to reactions of the cell, which responds to radical and stressful changes in the ecological conditions, in the form of nuclear radiation, contact with varmints, extreme diet, water scarcity, injuries, etc. (Bauer 2008, pp. 23–30, 84–94).

One of the most surprising new findings in this context was the discovery that changes in the environment can exercise a permanent influence on the gene regulation and gene expression, and through this mechanism heritable changes in the phenotype can be induced, e.g. in the form of RNA-interference (Bauer 2008, p. 26). Epigenetics is the study of heritable changes in the phenotype or gene expression caused by non-genetic mechanisms. In a wider sense, it refers to all mechanisms other than changes in the underlying DNA-sequence that influence the embryonic development. Epigenetics can hence be interpreted as a (counter-) reaction to the dominance of genetics in the modern synthesis. Typically, changes in the environment induce chemical modifications of the DNA, which turn a gene on or off. This process does not represent a mutation; rather, it exerts effects similar to a mutation and hence constitutes an epigenetic mark that can be passed on to the next generation. Epigenetic inheritance can lead to changes in the phenotype that can last for generations. For example, it has been found that extreme diet during gestation can change epigenetic patterns of the descendants and new traits can arise that can last for generations and also affect fertility (Pennisi 2008, p. 197). Thus, environmental conditions influence the heritable phenotype (Jablonka and Lamb 2005, p. 143). At first glance, epigenetic inheritance seems to question one of the dogmas of the modern synthesis, the so called central dogma of molecular biology (articulated by Francis Crick in 1958) according to which information moves only from nucleic acids (DNA and RNA) to proteins, and not vice versa. But since epigenetic inheritance is more about the impact of RNA on DNA, it is said not to contradict the central dogma (Jablonka and Lamb 2005, p. 152). However, the findings according to which epigenetic variations in somatic cells can indeed induce changes in germ cells (Jablonka and Lamb 2005, p. 149) are evidence for the breakthrough of the Weismann barrier. In addition, the theory of epigenetic inheritance has posed the question of a rehabilitation of Lamarckism, since the theory postulates that changes in phenotypic variants are inherited (Jablonka and Lamb 2005, p. 143). Contrary to popular interpretations, this view is mostly rejected by most of the more unorthodox evolutionary biologists. They mostly argue that Lamarck explained the inheritance of the acquired characteristics differently, namely through physiological adaptation. Though epigenetic inheritance has been confirmed in countless experiments, whether it represents an evolutionary principle is still an open question. Some doubt it, because epigenetic traits are gradually lost over a few generations and thus are reversible. There is also no sound empirical evidence that epigenetic variants are adaptive (Jablonka and Lamb 2005, p. 153).

These discoveries in molecular biology have also led to a reassessment of mutations, which are unevenly distributed, as an analysis of the genome of several species has shown. It seems that the cell has the capacity to allow only some parts of the genome to be subject to mutations, mainly those parts that have been duplicated by transposable elements, whereas Hox-genes and other important sequences are less subject to mutations. In other words, the original Hox-genes have been retained, while the copied genes have been released for change, e.g. for the reorganizations of mutations. The conclusion to be drawn here is that mutations are not completely random and that the cell shows a high capacity to control the genomic architecture (Bauer 2008, p. 66, pp. 121–125, p. 135).

Furthermore, it has been widely recognized that, in the early stages of evolution and also in more recent times, not only gene transfer from one generation to the next (vertical gene transfer) took place but also massive horizontal gene transfer, i.e. gene exchanges between individuals of completely different species. Transposable elements (transposons) cannot merely change the structure of a genome within an organism (see above), but can also transfer genes from the genome of one organism into the genome of another organism (Bauer 2008, p. 27). This phenomenon was an important creative factor of recombination. For example, mammals took over genes from viruses, and today it is known that more than 220 genes in the human genome are due to horizontal gene transfer (Bauer 2008, p. 49). The empirical evidence of horizontal gene transfer also implies that phylogenetic trees have to be reconsidered in the sense that they no longer have to be presented as linear lines that branch out, but can be conceived as networks. On this view, evolution is no longer considered to be linear but may be viewed as reticulate.

Another form of inheritance, called "ecological inheritance", has caused attention. It is also a phenomenon that brings ecosystem ecology and evolutionary biology together. Ecological inheritance is due to niche construction, that is, the construction of the environment out of elements of the external world by individual organisms. In this way, they alter the selection pressure of the environment. Ecological inheritance occurs when transformed habitats—by niche construction modified selection pressures—are transmitted to the descendants. Niche construction is considered to be incompatible with the so called external view of the modern synthesis, according to which the internal properties of organisms are only determined by characteristics of the external environment. By contrast, the niche construction theory postulates that organisms cause changes in their environment, which makes niche construction not only a consequence of the evolution, but a discrete factor of evolution (Odling-Smee 2010, pp. 176–180).

In another research branch, a multitude of findings in the last decades suggest that co-operation is an important principle of evolution, in particular, in the creation of new species. For example, in early evolution, eukaryotic cells came into existence because archaea-cells imported bacteria and let them become part of their cells, the so called endosymbiosis (Margulis 1970, 1981). This important evolutionary step was a precondition for the evolution of animals and humans and cannot be explained with the principles of the modern synthesis, but only with co-operation (Bauer 2008, pp. 52).

Since phenomena such as endosymbiosis, horizontal gene transfer, and gene duplication, recombination of genes, and changes in the regulation of genes have played a considerable role in the creation of variety, it is argued that the role of point mutations in the creation of new species has been overestimated by the modern synthesis. Recent discoveries suggest that speciation has primarily arisen from radical changes in the genome, which in turn was mainly induced by eruptive activations of the transposable elements (Bauer 2008, p. 56, p. 84). Furthermore, extensive paleontological studies provide more and more evidence that the incidence of species disappearance is mainly due to punctual mass extinctions, such as volcanism, mega-ice ages, etc. Consequently, natural selection appears not to be the predominant cause either of speciation or of species disappearance (Bauer 2008, p. 100). Whereas the randomness on the micro-level is being more and more questioned (see the discussion of mutations above), on the macro-level, randomness seems to be still an evolutionary factor.

3 Recent Developments in Evolutionary Biology: Assessment

In this section, the question is addressed as to the way in which biologists have assessed the recent findings, before turning to its relevance for economics in Sect. 4.

The research program of evo-devo has led to a complete change in the view of the manner of the evolution of complex biological systems. Already in 1994 Müller wrote: “Of course, Neo-Darwinist theory has in its core statements been confirmed, and generally been accepted” (Müller 1994, p. 160).[3] But then: “The inclusion of internal ‘organismic’ factors would not only mean an extension of the synthetic theory but would amount to a paradigm shift” (Müller 1994, p. 186).[4] Müller argues that, in the modern synthesis, the only forces that give evolution a direction are external factors, whereas under a system theory of evolution, variations would be

[3] Translation from German by the author of this paper.

[4] Translation from German by the author of this paper.

considered to be dependent on internal factors, namely the path-dependent rules of embryonic development (Müller 1994, p. 186).

Another representative of evo-devo, Carroll, says: "First, I assert that Evo Devo constitutes the third major act in a continuing evolutionary synthesis. Evo Devo has not just provided a critical missing piece of the modern synthesis—embryology—and integrated it with molecular genetics and traditional elements such as paleontology. The wholly unexpected nature of some of its key discoveries and the unprecedented quality and depth of evidence it has provided toward settling previously unresolved questions bestow it with a revolutionary character" (Carroll 2006, p. 283). However, Carroll does not see any contradiction with the main principles of the modern synthesis. In the last chapter of his book on evo-devo, he adheres to the traditional view of evolution as a combination of "completely random ...[ ]... genetic variation(s) by mutation" as well as "nonrandom" and "powerful" sorting or selection proceses (Carroll 2006, p. 290).[5] As Müller puts it: "Some regard evo-devo as perfectly compatible with a strictly selectionist theory of evolution; others claim it represents a strong departure from it" (Müller 2005, p. 88).

Kirschner and Gerhard see their theory of facilitated variation as a supplement to and completion of Darwin's theory (Kirschner and Gerhart 2007, p. 304, p. 319). They also raise the question of whether their theory can contribute to an understanding of social, political or technical elements. Subsequent to some careful suggestions in the form of analogies, they conclude that at least their proposition provokes metaphors other than those of Social Darwinism. They suggest that history (in general) is not only the product of selection determined by external factors and competition, but also the structure and capacity of societies and organizations to evolve, to adapt and to renew (Kirschner and Gerhart 2007, p. 357).

Prominent representatives of epigenetic inheritance, Jablonka and Lamb, write in the foreword of their influential book "Evolution in Four Dimensions": "Our basic claim is that biological thinking about heredity and evolution is undergoing a revolutionary change. What is emerging is a new synthesis, which challenges the gene-centered version of neo-Darwinism that has dominated biological thought for the last fifty years." (Jablonka and Lamb 2005, p. 1) Their main critique is thus not the focus of the modern synthesis on natural selection, but its gene-centrism mainly in heredity. They state that "evolutionary change can result from instruction as well as selection", the meaning of instruction being "internal or external regulatory signals" that control the activity in cells and organisms (Jablonka and Lamb 2005, p. 102). In their study, they not only discuss the genetic inheritance system, but also the epigenetic, behavioral and symbolic ones. In doing so, they suggest classifications of the four systems according to their predominant hereditary transmission, unit and origin of variation, target of selection, unit of evolution,

[5] "... the sorting of these variations as to which will persist and which will be discarded is determined by a powerful, selective and nonrandom process "(Carroll 2006, p. 290).

reproduction of information, transmitting of information, and so on (Jablonka and Lamb 2005, p. 39, p. 234, p. 236).

What makes an overall assessment difficult is the fact that the same discovery leads exponents of the modern synthesis and radical critics to converse interpretations. For example, in a standard textbook on evolution, one can still read "The genes of most TEs [transposable elements] do not contribute to development or function of the host organism; rather, they encode only proteins essential for replication and transposition of the retroelement itself. They are an example of a selfish genetic element, or 'selfish gene'"(Futuyma 2007, p. 459). This is in contrast to Bauer, who states that genes cannot be interpreted as egoistic since they are under the control of the cell and not autonomous (Bauer 2008, p. 37). Being familiar with recent discoveries concerning transposable elements, Bauer claims: "Genes and respectively genomes follow three basic biological principles [ ] : co-operation, communication and creativity" (Bauer 2008, p. 17).[6] In Bauer's understanding of evolution, selection plays a role, but only in the sense of a tautology: Individual organisms that are nonviable cannot survive and those that are not propagable will not reproduce (Bauer 2008, p. 104, p. 188). In an introduction to the extended synthesis, Pigliucci and Müller state: "On this view, natural selection becomes a constantly operating background condition, but the specificity of its phenotypic outcome is provided by the developmental systems it operates on. Hence the organisms themselves represent the determinants of selectable variation and innovation" (Pigliucci and Müller 2010b, p. 13).

Though it is definitely too early to give a conclusive appraisal of the recent findings in evolutionary biology, the least one can say is that a thorough reassessment of the significance of chance, genes and selection in biological evolution is inevitable. From an evolutionary economics viewpoint, the most interesting question concerns the role of selection as an evolutionary principle, since this is the one that has been the most transferred to economics and the least questioned in economics. Most of the representatives of the recent research findings presented here (Jablonka and Lamb 2005 are an exception), as well as those of the critical approaches before 1990 (as hinted at in the introduction), agree that the predominance of natural selection is one of the weakest elements of the modern synthesis. As mentioned above, the modern synthesis has acknowledged the phenomenon of genetic drift (Senglaub 1998, p. 574), which implies that, even within the modern synthesis, the statement "no evolution without selection" cannot be maintained.[7] By contrast, in the extended synthesis, not primarily due to genetic

[6] Translation from German by the author of this paper.

[7] Genetic drift is the change in the relative frequency with which a gene variant occurs in a population when changes in the frequency of gene variants occur randomly. Genetic drift is acknowledged as an evolutionary principle, since it can reduce genetic variability. Changes in the gene pool are then considered to be either the consequence of random fluctuations in proportions (gene drift) or of non-random adaptations due to better adaptation (natural selection) (Futuyma 2007, p. 10). Depew/Weber's interpretation in 1994 was: "If this theory [neutral theory by Kimura] is generally true, natural selection can no longer be presumed to be even heuristically

drift but to other discoveries such as the importance of internal regulation or of niche construction, the significance of natural selection as a factor of evolution is not completely denied but definitely pushed back. Instead, internal factors and regulatory changes (also in the creation of new species) are emphasized.

It can be concluded that the recent findings in biology outside the mainstream suggest a shift away from random mutations, competition, and selection, towards co-operation, internal regulation, networks, self-organization, and path-dependency. In particular and contrary to the modern synthesis, some findings in evolutionary biology suggest that (amongst others) (1) mutations are not completely random and variety is not only triggered by mutations, (2) selection is not the predominant evolutionary factor in the modification of species, the origin of new species and the extinction of species, (3) the systemic character of the genome, including phenomena of co-operation, self-organization and communication, has been underestimated (also in the generation of novelty), and (4) there is more and more evidence on discontinuous evolution.

The presented research programs in biology have in common the fact that their representatives do not reject the modern synthesis completely, all of them being convinced of evolution and the principle of common descent.[8] It should also be stressed that the research findings presented above are generally confirmed and accepted. Many of these findings and theories are not inconsistent with the modern synthesis, but that does not necessarily imply that they are fully covered by the modern synthesis framework (Pigliucci and Müller 2010b, p. 4). Thus, the overall assessment and interpretation with respect to the modern synthesis is still quite controversial. Some say they are still satisfied with the modern synthesis, others suggest an extension of the modern synthesis[9] or even a new evolutionary synthesis and "some say it's time for modern synthesis 2.0" (Pennisi 2008, p. 196). Then there are those who have declared "the end of Darwinism" (Bauer 2008).[10]

the primary agent in evolutionary processes, and genetic drift, or something like it, can no longer be blithely treated as a trivial or merely annoying secondary evolutionary force" (Depew and Weber 1994, p. 363). Though the empirical evidence of genetic drift is now unambiguous, the question of the relative importance of selection and genetic drift still prevails in evolutionary biology today and is another instance of a possible completely divergent interpretation of the significance of an empirical phenomenon. (For a discussion of the different perspectives, see Kutschera and Niklas 2004, p. 269). For example, according to new findings, some exponents of the modern synthesis argue that genetic drift can no longer be considered to be crucial for speciation and they conclude that "[n]obody really doubts that most of the body parts have been formed by selection" (Orr 2009, p. 15). This demonstrates that, though genetic drift is recognized in the modern synthesis, it is degraded to a side effect or exception.

[8] En passant it shall be noted that the recent findings in evolutionary biology—e.g. the finding of the ancient origin of the genes for building all kinds of animals—confirm the principle of common descent (Carroll 2006).

[9] In some textbooks on biological evolution, the extended synthetic theory is already explicitly mentioned as the successor of the Synthetic Theory (Kutschera 2008, p. 83).

[10] In the latest edition of his book, Bauer (2010) substituted the subtitle "evolution as a creative process" for "the end of Darwinism", intending to avoid any confusion about his belief in the fact of evolution. Indeed, he declares the fact of evolution to be "irrevocable" (Bauer 2010, p. 9).

Actually, the concept of a new framework, called the "extended synthesis", seems to be gaining ground. Though the term indicates that the modern synthesis has only to be expanded (to embryology and developmental biology and ecology) yet will remain untouched in its core principles, the claims of the exponents of an extended synthesis are much higher: According to their conception, evolutionary biology also has to carry out a shift in the importance of evolutionary factors. From a methodological point of view, they postulate a shift away from statistical correlation analysis (common in population dynamics) to mechanistic causation research, e.g. "a theory of the mechanistic conditions for the origin and innovation of traits." (Pigliucci and Müller 2010b, p. 13) These are important aspects because some economists seem to have the conviction that whatever new discoveries in biology might emerge, the main explanation of evolution will always center on mutations, genes and selection, everything else being extensions, side-effects or exceptions. To take the recent developments in evolutionary biology seriously means to renounce this false conception.

The variety of theoretical approaches in biology can also be viewed in a broader context. In the philosophy of science, it is argued that, since 1970, in science in general, and not only in biology, there has been a tendency from a monolithic towards a pluralistic understanding of science. In biology, this would imply that the modern synthesis will not be substituted for but be supplemented by a range of distinct alternative approaches (Beurton 1995, p. 119).[11] This would be (or already is), by the way, a very similar development to that of economics.

4 Consequences for Evolutionary Economics

We have seen that, at present, there is a pluralism of scientific interpretations of evolution: Traditional interpretations within the modern synthesis go along with new ones that explicitly break with the modern synthesis without denying common descent and without completely rejecting the role of random genetic modification and selection. This pluralism cannot be denied. What makes an assessment for economists really difficult is that those biologists who have come up with the new concepts and principles do not agree on the significance of these new findings and their relation to the mainstream paradigm, the modern synthesis.

One reason why biological scientists draw different conclusions from the new findings is not so much grounded in professional controversies as it is due to the implications of the research results for the social and cultural life in the human societies in which we actually live. For example, Carroll's motivation to adhere to the random variation-selection-paradigm is—according to my interpretation—his aim to support teaching in biological evolution based on scientific results and to provide a multitude of arguments against creationism and intelligent design (Carroll

[11] Quoted from Senglaub (1998, p. 577).

2006). Considering the anti-Darwinian and anti-evolutionary movements of creationism and intelligent design, my impression is that it seems to be too difficult for scientists—mainly in the U.S.—to make clear to the public that, in the scientific community, there is unanimity that evolution has definitely taken place but a controversy on how it has happened. In a non-scientific public discussion, a scientific discipline (evolutionary biology) that is not united in the explanation of its main research object (evolution) is much weaker than one that adheres to common principles. In addition, critics of the modern synthesis risk—not only in the U.S.—being expelled from the scientific community (Bauer 2008, p. 110). Consequently, most of the biologists in the profession strive to avoid this dispute. This is not the case for Bauer, whose goal is to stress the role of co-operation and communication in evolution in order to demonstrate that the idea of egoism as a central evolutionary principle as well as the consideration of living beings as machines is not based on solid scientific research. He argues that this is important to acknowledge since concepts such as those of egoistic genes generate anthropological models that have negative consequences for the way we actually live in human societies (Bauer 2008).

Although not all scholars of evolutionary economics are inclined to resort to theories in biology, there are two arguments as to why these recent findings in evolutionary biology should be of interest to the scientific community of evolutionary economists: (1) For those evolutionary economists who have always found that the fact of evolution in general is more inspiring than the theory, new findings in evolutionary biology still will have effects but only indirect ones. Theories always influence mental attitudes and the way in which studies are conducted and empirical results are looked at. As Zimmerli put it: “Each scientific theory sediments into human consciousness in a way that its theorems are eventually considered to be elements of reality” (Zimmerli 1990, p. 138). (2) In biology, critics of the modern synthesis argue that (mainstream) biology is very much shaped by mechanical physics and economics, and that, in general, beings are considered to be machines and not living systems (Bauer 2008, p. 13). Thus, the danger in evolutionary economics is that, in resorting to the modern synthesis, indirectly all the mechanical aspects this research area has intended to avoid are re-imported. One of the common characteristics of biology and economics—in contrast to physics—is that they deal with living organisms. Consequently, in evolutionary economics, one of the crucial questions should be: What are the main and specific properties of living systems[12] and, in particular, human beings? The mechanistic models in parts of the extended synthesis unfortunately are neither very helpful in answering these questions nor in providing fruitful heuristic devices towards these questions.

In the past, the influences of theories of evolutionary biology on economics were manifold and can be summed up by different heuristic strategies (Witt 2004, 2008), two of which will be dwelled on further in the following.

[12] It is not the subject of this paper to discuss this question, but important characteristics are sentiments and perceptions. See also Capra (1996, part IV).

First, an important way in which biology has had an influence on economics is by the methodological device of analogies. It is widely acknowledged that analogies in sciences can have important heuristic functions and they can be used as a method to build new hypotheses. It should be emphasized that the method of analogy as a heuristic device in science (Klamer and Leonard 1994, p. 35) as such cannot be criticized. In particular, it cannot be argued that the analogy is inadequate because some characteristics, elements or relations from the original theory (in one science) do not correspond with those of the destination theory (in another science), because it is the essence of the analogy that not all aspects match. Thus, the statement that an analogy is inadequate or useful, or more general, good or bad, is illegitimate since the analogy is a method and not the correspondent, counterpart or equivalent itself. The problem with these kinds of analogies is that they might become a justification in the sense that, without further arguments, studies or proofs, the findings from one science are directly transferred to another science (Ruse 1986, p. 33). Analogies hence run the risk of starting a life of their own without being reassessed and verified. This holds in particular for analogies based on the variation-retention-selection paradigm. Theories based on these analogies often fail to inquire as to whether the principles of variation, retention and selection are indeed the core principles of evolution in economic reality and whether omitting specific economic, social and cultural factors is a proper approach.

Reflecting on biological evolutionary theorizing in the last 50 years, the impression arises that a lot of analogies are based more on the original Darwinism of the nineteenth century or the early modern synthesis of the 1930s and 1940s. This is astonishing even in light of the state of evolutionary biology in the second half of the twentieth century. Some, thus, have wondered how economists could, on the one hand, criticize neoclassical economics and, on the other hand, prefer competition to self-organization (Foster 2001, p. 123).[13] The concentration on selection analogies would not have been a major problem if analogies had only the function of inspiration and would not become independent. In light of the recent developments in evolutionary biology, is it then advisable to build analogies in economics based on evo-devo, plasticity, epigenetic inheritance and niche construction? As hinted above, the main function of metaphors and analogies is to create hypotheses and, in fulfilling this function, they cannot be preferred to any other. New hypotheses in biology do not necessarily provide better hypotheses in economics than old ones, since biology and economics are not congruent anyway.

Second, since the explanation of biological evolution is undergoing a reassessment, in which the traditional core principles of evolution, such as blind mutation and selection, lose significance (although as argued above, they do not become completely irrelevant), concepts such as generalized Darwinism (Aldrich et al. 2008) are probably no longer up to date. As has already been argued by Cordes (2006, p. 532), generalized Darwinism does not even take into account all those

[13] Exceptions were e.g. Silverberg et al. (1988), Foster (1997), Witt (1997).

principles that mainstream biologists consider to be essential to Darwin's theory. For example, the principles of descent and of speciation are not chosen to belong to generalized Darwinism. Buenstorf (2006, p. 515) states that, since generalized Darwinism turned the heuristic frame into an ontological fact, subjects that are not covered by the assumed three core principles of evolution are excluded from examination, e.g. certain forms of learning and knowledge transfer. In this paper, I further argue that generalized Darwinism does not take into account the principles of co-operation and self-organization. Though the representatives of generalized Darwinism concede that to explain evolution sufficiently "auxiliary" principles are required (Aldrich et al. 2008, p. 592), the question that arises is why co-operation and self-organization are not considered as core principles of generalized Darwinism and what the selection criteria are that make the difference between core and auxiliary principles of evolution.

As mentioned above, not all evolutionary economists are inclined to let themselves be inspired by theories of biological evolution. In particular, analogies and concepts such as generalized Darwinism bear the danger of neglecting specific human, social and economic aspects of evolution and, in addition, their explanative power is rather humble. Events other than economic crises should remind us that there is still much to learn about human behavior and economic systems. Thus, instead of looking for common principles with other scientific disciplines, I would argue in favor of concentrating more on the specific characteristics of human, social and economic evolution. This kind of analysis can acknowledge that human beings have animal bodies and hence are to a certain extent subject to biological evolution. However, in addition, the evolution of societies and economies follows certain rules and norms, some of which are, at least in part, the result of deliberate decisions and not subject to biological evolution. The continuity hypothesis (Witt 2004, pp. 129–133) is, for example, a heuristic strategy which is in line with these requirements.

5 Conclusion

In this paper, it has been shown that, in addition to modern synthesis principles such as random mutations and selection, the principles of co-operation and self-organization are considered by quite a number of researchers in biology today to be core principles of biological evolution. With respect to the identification of important factors of evolution, it must also be taken into consideration that the scientific development of evolutionary biology will continue. The recent discoveries can be interpreted as an indication of the deep changes (maybe including paradigm shifts) that this science might still undergo in the next decades.

The short review above hopefully has documented that nobody in biology really doubts the existence of mutations and natural selection. But some researchers question their assumed significance which is magnified and stylized to a transdisciplinary variation-retention-selection paradigm. The problem with this paradigm is that it ignores certain important aspects, in particular, internal regulation, co-operation and self-organization.

As indicated in the introduction, in the second half of the twentieth century, the modern synthesis had already shown quite a remarkable resistance towards a wave of critique. In our own area of expertise, we have experienced that mainstream paradigms are highly innovative and adaptable in order to insure their survival. A similar development can take place in evolutionary biology and the modern synthesis might absorb the recent findings. Fortunately, evolution—also the one of sciences—can lead to surprises. Though it seems as if genes and natural selection will continue to be considered as core factors of evolution, the focus of attention can also shift to other evolutionary principles. How things develop is not only dependent on the critical reception in biology, but also on debates in other sciences as in economics.

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