

PAPERS on Economics & Evolution



MAX-PLANCK-GESELLSCHAFT

0911

Recent Developments in Evolutionary Biology and Their Relevance for Evolutionary Economics

by

Karin Knottenbauer

The *Papers on Economics and Evolution* are edited by the Evolutionary Economics Group, MPI Jena. For editorial correspondence, please contact: evopapers@econ.mpg.de

ISSN 1430-4716

© by the author

Max Planck Institute of Economics
Evolutionary Economics Group
Kahlaische Str. 10
07745 Jena, Germany
Fax: ++49-3641-686868

Recent Developments in Evolutionary Biology and Their Relevance for Evolutionary Economics

Karin Knottenbauer
Department of Economics
RWTH Aachen University
Templergraben 64
D-52056 Aachen, Germany
Email: Karin.Knottenbauer@rwth-aachen.de
Tel. (0049) (0)241 80 97031
Fax. (0049) (0)241 80 92649

30 September 2009

Abstract

The paper gives attention to the question of whether the development of evolutionary theories in biology over the last twenty 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 amongst others that the 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.

Keywords:

Analogies, evo-devo, evolutionary economics, evolutionary biology, co-operation, genes, Lamarckism, modern synthesis, neo-Darwinism, selection, self-organization.

1 Introduction

Charles Darwin's intention was to provide evidence of evolution being a historical matter of fact and to explain evolution. Although during Darwin's lifetime the revolutionary aspect and his own main interest was to find proof of evolution, today's scientific interest is focused more on the theory of 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 and even contradictory and since genetics had not yet been established some explanations remained speculation. At the beginning of the 20th century with the rise of genetics the explanation of evolution was still not unanimous, given e.g. 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, 1940s and 1950s when the main principles of genetics had become more widely accepted that the pluralistic view narrowed down to that of *Modern Synthesis* (or *Synthetic View of Evolution*, sometimes also called *Neo-Darwinism*).¹ According to *Neo-Darwinism*, here considered as the mainstream theory of biology from 1930 to date, holds: 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, 160).

In the following, and to avoid any misunderstandings, I would like to emphasize that *Neo-Darwinism* is considered here as a theory on how evolution took place. The issue, then, is the explanation of evolution rather than the historical record of evolution which from a scientific perspective is taken to be a matter of fact here. 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 *Neo-Darwinism* have been manifold, e.g. the neutral theory of molecular evolution by Kimura (1983), today better known under the label of "gene drift", 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 so called punctuated equilibrium theory (Gould, Eldredge 1972, 1977), theories of self-organization (Kauffmann 1993), theories of skin, group and species selection (e.g. Maynard Smith 1964, Vrba, Eldredge 1984), etc. What all these critical approaches in the second half of the 20th century had in

¹ In the following, I will mainly use the term *Neo-Darwinism*, though being aware that this is rather the term used in popular science than in the science of biology.

common was that they did not reject Neo-Darwinism completely. Most of them acknowledged its achievements, but extended, qualified or put into perspective Neo-Darwinist factors of evolution *and* also added new factors of evolution. It can further be deduced that the weakest points in *Neo-Darwinism* were considered to be the predominant roles of mutation, genes and selection. Despite the critiques mentioned above Neo-Darwinism showed an astonishing inertia. Though some of the counter positions such as *Punctuated Equilibrium* have even been considered in textbooks on evolutionary biology, the main explanatory factors of evolution remain those of mutation and selection.

Owing to this inertia and its capacity to absorb additional aspects, for many decades it has looked as though *Neo-Darwinism* is a verified theory. However, a theory can only be considered to be verified as long as there is no falsification. Now we have come to realize that with regard to biological evolution there are still a lot of puzzles to be solved. Recent developments – in the last twenty years – draw on new insights into molecular underpinnings, genetics, ecology and developmental biology. Since evolutionary economics itself is a research program outside the mainstream, it would be inattentive not to consider – or at least not to have a look at – these recent developments outside mainstream evolutionary biology.

Thus, in section two 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 twenty years – (2) divergence from mainstream and (3) ongoing research activities in this field. Many of these recent research findings are not completely new but have either been better confirmed or have become clearer. To make a division roughly at the year 1990 is to a certain extent arbitrary and there is an overlapping with critical approaches before 1990. There is no claim that the list of recent approaches in evolutionary biology is complete. In section three, an assessment of the findings mainly by biologists is presented. In section four, possible implications for evolutionary economics are given. Section five concludes.²

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 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

² Since I am an economist and not a biologist and had not any training in biology I apologize for any remaining obscurities and errors, in particular in the sections dealing with biology. Any kinds of comments and corrections are very welcome.

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 *Neo-Darwinism*, 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, Gerhart 2007, 16f). It was shown that this deficiency of *Neo-Darwinism* lies in its disregard of the rules of transformation from genotype to phenotype. *Neo-Darwinism* concentrates on two research areas: genetic and phenotypic evolution, implicitly assuming that the sphere in between genetic evolution and phenotypic evolution is not relevant (Müller 1994, 185) and not knowing whether the genetic changes responsible for big changes in form were the same as for small variations within species (Carroll 2006, 284). Thus, *Neo-Darwinism* 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, Gerhart 2007, 23) and mutations are often the result of negative impacts such as radiation and hence they destroy more than they create. In addition, selection is a mechanism that can only work on what already exists (Müller, Newman 2003, 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 rather new research program called *Evolutionary Developmental Biology* (or informally “*EvoDevo*”), which combines two research areas which had existed quite independently until roughly 1990: developmental biology and evolutionary biology (Müller 2005, 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. *EvoDevo* seeks to extend this research in concentrating on interdependencies between ontogenesis and evolution, in particular the analysis of causal relationships between embryonic and evolutionary processes (Müller 1994, 155-160).³ One of the main questions posed by *EvoDevo* is: Does developmental (embryonic) evolution bias the produced phenotypic variations or constrain certain paths of evolution? (Futuyma 2007, 474).

Some exponents of *EvoDevo* have concentrated on physical processes that guide how cells organize organs and tissues. The stickiness, elasticity, and chemical reactions within and between cells affect the body plan of an organism (Pennisi, 2008, 196f). Since body plans have internal inertia, evolution is not completely arbi-

³ According to Müller (2005, 98-102) *EvoDevo* 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.

trary, but works around these stable body plans. Consequently, there is a multitude of development constraints. *Neo-Darwinism* 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, 162f). *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 *Neo-Darwinism*.

One of the discoveries of *EvoDevo* in contrast to *Neo-Darwinism* 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, 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, 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, 71f). 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 lead 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, 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*). Genetic switches are regions of DNA that are typically located near the genes upstream on the same strand of DNA, and they can turn genes on and off reacting 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. Thus, these genetic switches are considered to be the “key actors” in embryonic development and evolution (Carroll 2006, 111). Though the discovery of *Hox-genes* was important, it came out that it is not a single *Hox-gene* that is responsible for one new organ or structure but groups of gene switches and proteins build networks that regulate the formation of whole organs and structures (Carroll 2006, 129f). 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 (Carroll 2006, 287). Thus, 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, 287f).

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 whereas 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, Gerhart 2007, 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, Gerhart 2007, 354f). The greatest amount of change (since the Cambrian) is not due to changes within *core components* but 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 a different amount at other times in other places. Under the new conditions the flexible core components might show different performance and new phenotypes (Kirschner, Gerhart 2007, 300f). Carroll argues in the same line: “At an anatomic level, multifunctionality and redundancy are keys to understanding the evolutionary transitions in structures” (Carroll 2006, 288) and Müller states “(T)he new tenets by *EvoDevo* may be called “emergence” and “inherency” (Müller 2005, 106). *Core components* are adaptive, and have been selected due to their robustness in embryonic development and anatomic stability. Consequently, phenotypes which 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, Gerhart 2007, 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, Gerhart 2007, 354). This view also stresses the existence of established and approved components for innovation (Kirschner, Gerhart 2007, 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, chapter 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 reorganise genes by combining them differently, and they can change the local position of genes (the reason why 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, on the contrary, 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 reorganisation 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 varmint, extreme diet, water scarcity, injuries etc. According to this view, 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, 23-30, 84-94)

Furthermore, an analysis of the genome of several species has shown that mutations are unevenly distributed. 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, whereas the copied genes have been released for change, e.g. for the reorganisations 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, 66f, 121-125, 135).

One of the most surprising new findings in the new research areas 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. These mechanisms can take place in the form of *epigenetic inheritance* or in form of *RNA-interference* (Bauer 2008, 26). 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 but it exerts effects similar to a mutation and hence constitutes an *epigenetic mark* that can be passed on to the

next generation. This *epigenetic inheritance* is a sensation because it questions one of the dogmas of *Neo-Darwinism*, the so called *Weismann barrier* according to which hereditary information moves only from germ cells to somatic cells and not vice versa. However, according to *epigenetic inheritance* changes in somatic cells can indeed induce changes in germ cells. Epigenetic inheritance can even be considered to be *Lamarckian* since gene regulation and gene expression react to environmental stimuli and the phenotypic results 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 arise that can last for generations and also affect fertility (Pennisi 2008, 197). It should be mentioned that in contrast to mutations *epigenetic marks* are reversible but like mutations they can be subject to selection. Though epigenetic inheritance has been confirmed in countless experiments and recent studies rather confirm than refute it (see e.g. Singer 2009), whether it represents an evolutionary principle is still an open question – even in the progressive research community which challenges *Neo-Darwinism*.

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 (so called *endosymbiosis*). This important evolutionary step was a precondition for the evolution of animals and humans and cannot be explained with Neo-Darwinian principles, but only with co-operation (Bauer 2008, 52ff).

Furthermore, it has been widely recognized that in the early stages of evolution but 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* or “*jumping genes*”) can transfer genes from the genome of one organism into the genome of another organism (Bauer 2008, 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 come from horizontal gene transfer (Bauer 2008, 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 as networks of lines branching out. In this view, evolution is no longer considered to be linear but reticulate.

Since phenomena like endosymbiosis, *horizontal gene transfer* as well as gene duplication, recombination of genes, and changes in the regulation of genes have played a considerable role in the creation of variety (Bauer 2008, 56, 85f), it is argued that the role of point mutations in the creation of new species has been overestimated by *Neo-Darwinism*.

With regard to macro-evolution, it has been generally acknowledged (also in *Neo-Darwinism*) that it is characterized by periods of stasis in which changes in the genomes were minor (Futuyma 2007, 504). 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 of species disappearance (Bauer 2008, 100f.) and on the makro-level randomness is still an evolutionary factor.

3 Recent Developments in Evolutionary Biology: Assessment

In this section the question is addressed of how biologists have assessed the recent findings, before turning to its relevance for economics in section four.

The research program of *EvoDevo* has led to a complete change of the view of how complex biological systems evolve. Already in 1994 Gerd B. Müller wrote: “Of course, Neo-Darwinist theory has in its core statements been confirmed, and generally been accepted” (Müller 1994, 160).⁴ 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, 186).⁵ Müller argues that in Neo-Darwinism the only forces that give evolution a direction are external factors whereas in a system theory of evolution variations would be considered to be dependent on internal factors, namely the path-dependent rules of embryonic development (Müller 1994, 186).

Another representative of *EvoDevo*, Sean B. 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, 283). However, Carroll does not see any contradiction with the main principles of Neo-Darwinism. In the last chapter of his book on *EvoDevo* 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 process (Carroll 2006, 290)⁶. As Müller puts it: “Some regard *EvoDevo* as

⁴ Translation from German by the author of this paper.

⁵ Translation from German by the author of this paper.

⁶ “... 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, 290).

perfectly compatible with a strictly selectionist theory of evolution; others claim it represents a strong departure from it” (Müller 2005, 88).

Kirschner and Gerhard see their theory of *facilitated variation* as a supplement to and completion of Darwin’s theory (Kirschner, Gerhard 2007, 304 and 319). They also raise the question of whether their theory can contribute to the 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 other metaphors 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, Gerhard 2007, 357).

Some of the presented research results are acknowledged by *Neo-Darwinism* and are then often interpreted as an exception, e.g. in the case of *horizontal gene transfer* (Bauer 2006, Kutschera 2008). In other cases the same discovery leads *Neo-Darwinists* and *Non-Neo-Darwinists* 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, 459). To Bauer genes cannot be interpreted as egoistic since they are under the control of the cell and not autonomous (Bauer 2008, 37f). Bauer claims: “Genes and respectively genomes follow three basic biological principles ... : co-operation, communication and creativity” (Bauer 2008, 17).⁷ In Bauer’s understanding of evolution, selection plays a role, but only in the sense of a tautology: Individual organisms which are nonviable cannot survive and those which are not propagable will not reproduce themselves (Bauer 2008, 104 and 188).

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, mutations and selection in biological evolution is inevitable. The most interesting question concerns the role of selection as an evolutionary principle. Most of the representatives of the recent research findings presented here as well as those of the critical approaches before 1990 (as hinted at in the introduction) would agree that the predominance of natural selection is one of the weakest elements of *Neo-Darwinism*. Until recently, even in *Neo-Darwinism* because of the findings of *genetic drift* (Senglaub 1998, 574)⁸ the statement “no evolution without selection” was no longer be maintained. But according to new findings some Neo-Darwinists argue that *genetic drift* can no longer be considered to be crucial for

⁷ Translation from German by the author of this paper.

⁸ 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. In contrast to selection genetic drift is a random process.

speciation. Instead they emphasize the significance of natural selection: “Nobody really doubts that most of the body parts have been formed by selection” (Orr 2009, 15).⁹ It is obvious that in *Neo-Darwinism* natural selection has not really lost importance. This is different in the research areas presented here. In *EvoDevo* and in some branches of genetics and molecular biology the significance of natural selection is obviously pushed back. Instead, internal factors and regulatory changes (in the creation of new species) as well as mass extinctions (in the distinction of species) are emphasized.

It can be concluded that the recent findings in biology outside the mainstream suggest a shift away from random mutations, competition, selection, towards co-operation, regulation, networks, self-organisation and path-dependency. In particular and contrary to *Neo-Darwinism* 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 have been underestimated (also in the generation of novelty) (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 Neo-Darwinism completely, all of them being convinced of evolution and the principle of common descent.¹⁰ It should also be stressed that the research finding presented above are generally confirmed and accepted. Yet, the overall assessment and interpretation with respect to *Neo-Darwinism* is quite controversial. Some say they are still satisfied with *Neo-Darwinism*, others suggest an extension of *Neo-Darwinism* or even a new evolutionary synthesis and “some say it’s time for *Modern Synthesis 2.0*” (Pennisi, 2008, 196).¹¹ Only a minority – among them the German medical researcher Joachim Bauer – have declared “the end of Darwinism” (Bauer 2008).

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 Neo-Darwinism will not be substituted but be supplemented by a range of distinct alternative approaches (Beurton 1995, 119).¹² This would be (or already is), by the way, a very similar development to that of economics.

⁹ Translation from German by the author of this paper.

¹⁰ 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).

¹¹ Even in some Neo-Darwinian textbooks on biological evolution the Extended Synthetic Theory is already explicitly mentioned as the successor of the Synthetic Theory (Kutschera 2008, 83).

¹² Quoted from Senglaub 1998, 577f.

4 Consequences for evolutionary economics

We have seen that at present there is a pluralism of scientific interpretations of evolution: Traditional Neo-Darwinist interpretations go along with new ones which explicitly break with Neo-Darwinism 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 of Neo-Darwinism.

One reason why biological scientists draw different conclusions from the new findings is not so much grounded in professional controversies but rather due to the implications of the research results for the social and cultural life in the human societies we actually live in. 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 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 taken place. 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 traditional principles. In addition, critics of *Neo-Darwinism* risk – not only in the U.S. – being expelled from the scientific community (Bauer 2008, 110f.). Consequently, most of the biologists in the profession strive to avoid this dispute. This is not the case for Bauer. His goal to stress the role of co-operation and communication in evolution is – according to his own statement – 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 like 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 will still have effects but only indirect ones. Theories always influence mental attitudes and the way 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, 138). (2) In biology, critics of *Neo-Darwinism* argue that (mainstream) biology is very much shaped by mechanical physics and economics, and that, in general, beings are considered to be machines not living systems (Bauer 2008, 13). Thus, the danger in evolutionary economics is that in resorting to *Neo-Darwinism* 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 properties of living systems?¹³

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 and 2008), some of which will be hinted at in the following.

An important way in which biology has had an influence on economics was by the methodological device of analogies. It is widely acknowledged that analogies in sciences can have important heuristic functions and they are used as a method to build new hypotheses. It should be emphasized that the method of analogy in science 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 proves the findings from one science are directly transferred to another science (Ruse 1986, 33f). Analogies hence run the risk of starting a life on 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 study 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.

Furthermore, 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 like *Generalized Darwinism* (Aldrich et al., 2008) are probably no longer up to date. As has already been argued by Cordes (2006, 532), *Generalized Darwinism* does not even take into account all those principles

¹³ 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).

that mainstream biologists consider to be essential principles of Darwin's theory. For example, the principles of descent and of speciation are not chosen to belong to *Generalized Darwinism*. Buenstorf (2006, 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, 592), my questions are: Why are co-operation and self-organization not considered as core principles of Generalized Darwinism and what are the selection criteria 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 like *Generalized Darwinism* bear the danger of neglecting specific human, social and economic aspects of evolution and, in addition, their explanative power is rather humble. Not only economic crises like the one we are actually in should remind us that there is still much to learn about human behaviour and economic systems. Thus, instead of looking for common principles with other scientific disciplines I would argue in favour 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 are not subject to biological evolution. The *continuity hypothesis* (Witt 2004, 129-133) is, for example, a heuristic strategy which is in line with these requirements.

5 Conclusions

In this paper, it has been shown that today, in addition to other traditional *Neo-Darwinian* 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 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 aspects, in particular internal regulation, co-operation and self-organization.

As indicated in the introduction, in the second half of the 20th century *Neo-Darwinism* 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 *Neo-Darwinism* might absorb the recent findings. Fortunately, evolution – also the one of sciences – can lead to surprises. Though it seems as if mutations and natural selection will continue to be considered as 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.

Bibliography

- Aldrich, H.E. et al (2008), In Defence of Generalized Darwinism, *Journal of Evolutionary Economics*, vol. 18, 577-596.
- Bauer, J. (2008), *Das kooperative Gen – Abschied vom Darwinismus*, Hoffmann und Campe.
- Beurton, P.J. (1995) Neo-Darwinism or Synthesis?, in: Wolters, G., Lennox, J.G. (eds.), *Concepts, Theories, and Rationality in the Biological Sciences*, Universitäts-Verlag Konstanz/Pittsburgh Press.
- Buenstorf, G. (2006), How Useful is Generalized Darwinism as a Framework to Study Competition and Industrial Evolution?, *Journal of Evolutionary Economics*, vol. 16, 511-527.
- Capra, F. (1996), *The Web of Life: A New Synthesis of Mind and Matter*, HarperCollins, New York.
- Carroll, S. B. (2006), *Endless Forms Most Beautiful. The New Science of Evo Devo and the Making of Animal Kingdom*, Weidenfeld & Nicolson, London; German translation: *Evo Devo – Das neue Bild der Evolution*, Berlin University Press, 2008.
- Cordes, C. (2006), Darwinism in Economics: From Analogy to Continuity, *Journal of Evolutionary Economics*, vol. 16, 529-541.
- Futuyma, D.J. (2005, 2007), *Evolution*, Sinauer Associates, Sunderland (USA), 2005; German Edition (in English) Elsevier München 2007.
- Gould, S.J. (1980), Is a New and General Theory of Evolution Emerging?, *Paleobiology*, no. 6, 119-130.
- Gould, S.J., Eldredge, N. (1972), Punctuated Equilibria: An Alternative to Phyletic Gradualism, in: Schopf, T.J.M. (ed.), *Models in Paleobiology*, San Francisco, 82-115.
- Gould, S.J., Eldredge, N. (1977), Punctuated Equilibria: The Tempo and Mode of Evolution Reconsidered, *Paleobiology*, vol. 3, 115-151.
- Kauffman, S.A. (1993), *Origins of Order: Self-Organization and Selection in Evolution*, Oxford, Oxford University Press.
- Kimura, M. (1983), *The Neutral Theory of Molecular Evolution*, CUP, Cambridge.
- Kirschner, M.W., Gerhart, J.C. (2005), *The Plausability of Life*, Yale University Press, New Haven; German translation: *Die Lösung von Darwins Dilemma* (2007), Rowohlt Reinbek.
- Kutschera, U. (2008), *Evolutionsbiologie*, 3. Aufl., Eugen Ulmer, Stuttgart.
- Maynard Smith, J. (1964), Group Selection and Kin Selection, *Nature*, vol. 201, 1145–1147.
- Maynard Smith, J. et al (1985), Development Constraints and Evolution, *Quarterly Review of Biology*, vol. 60, 265-287.

- Müller, G. B. (1994), Evolutionäre Entwicklungsbiologie: Grundlagen einer neuen Synthese, in: Wieser, W. (ed.), *Die Evolution der Evolutionstheorie – Von Darwin zur DNA*, Spektrum Akademischer Verlag, Heidelberg, 155-193.
- Müller, G. B. (2005), Evolutionary Developmental Biology, in: Wuketits, F.M., Ayala, F.J. (eds.) (2005), *Handbook of Evolution*, Wiley VCH, 87-115.
- Müller, G. B., Newman, S. A. (2003), Origination of Organismal Form: The Forgotten Cause in Evolutionary Theory, in: Müller, G. B., Newman, S. A. (eds.), *Origination of Organismal Form – Beyond the Gene in Developmental and Evolutionary Biology*, MIT Press, 3-10.
- Orr, H.A. (2009), Selektion im Test, *Spektrum der Wissenschaft Spezial*, no.1, 12-19.
- Pennisi, E. (2007), Jumping Genes Hop Into the Evolutionary Limelight, *Science*, vol. 317, 984-895.
- Pennisi, E. (2008), Modernizing the Modern Synthesis, *Science*, vol. 321, 196-197.
- Riedl, R. (1975), *Die Ordnung des Lebendigen*, Parey, Hamburg, Berlin.
- Ruse, M. (1986), *Taking Darwin Seriously*, Oxford, Basil Blackwell.
- Senglaub, K. (1998), Neue Auseinandersetzungen mit dem Darwinismus, in: Jahn, I. (ed.), *Geschichte der Biologie*, 3. ed., Spektrum Akademischer Verlag, Heidelberg, 558-579.
- Singer, E. (2009), *A Comeback of Lamarckian Evolution?*, Technology Review (MIT), February 4.
- Vrba, E., Eldredge, N. (1984), “Individuals, hierarchies and processes: Towards a more complete evolutionary theory”, *Paleobiology*, vol. 10, 146-171.
- Wieser, W. (1994), Gentheorien und Systemtheorien: Wege und Wandlungen der Evolutionstheorie im 20. Jahrhundert, in: Wieser, W. (ed.), *Die Evolution der Evolutionstheorie – Von Darwin zur DNA*, Spektrum Akademischer Verlag, Heidelberg, 15-48.
- Witt, U. (2004), On the Proper Interpretation of ‘Evolution’ in Economics and Its Implications for the Production Theory, *Journal of Economic Methodology*, vol. 11, 125-146.
- Witt, U. (2008), What is Specific About Evolutionary Economics?, *Journal of Evolutionary Economics*, vol. 18, 547-575.
- Zimmerli, W.C. (1990), Grenzen des evolutionären Paradigmas – Metakritische Bemerkungen zu einer auslaufenden Denkmode, in: Jüdes, U., Eulefeld, G., Kapune, T. (eds.), *Evolution der Biosphäre*, Hirzel, Stuttgart, 137-152.