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Natural and Economic Selection - Lessons from the Evo-Devo and Multilevel Selection Debate

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Abstract

This paper sheds new light on the concept of selection in evolutionary economics. The interpretation of natural evolution has experienced significant changes in the last decades, while these developments have been often ignored by economists. This is especially true for the concept of selection, a key concept in many evolutionary approaches. In economics as well as in biology, selection is seen as a central mechanism, which mediates for example the spread of information and innovation, the coordination of groups of agents and the optimization of their behavior. In this article we are aiming to explore the actual significance of selection as a major explanatory principle in economics. Starting with an analysis of a modern and modified understanding of the selection mechanism in nature we will draw some conclusions for its use in economics.

Keywords: Selection – Bioeconomics – Evo-Devo – Cultural Evolution - Multilevel Selection – Economic Theory

JEL Codes: B15 – B40 – B52 – D03

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1 Introduction

Few economists are aware of the fact that economics and evolutionary biology have developed in parallel for a long time. Especially fruitful was the interdependence of both sciences in the very early days of modern biology, culminating in the discovery of natural evolution by Charles Darwin. At this time economics was already a well-established science. The insemination of ideas, however, flew mainly in one direction: from economics to biology. Darwin was much influenced by the economic theories of the day, mainly by Adam Smith and Thomas Malthus, when he developed his theory of natural evolution. He was aware of the similarities of both approaches: Both, economics as well as biology, deal with complex, dynamic systems, where historic contingencies heavily influence future developments. In both cases, much insight can be gained by population thinking, where multiple agents interact at small scales. Thereby, some characteristics are spreading faster through the population then others, leading over time to changes on a macro level (see for a detailed comparison: Hodgson and Knudsen 2010 or Gowdy et al. 2013). However, at the end of the 19th century, economic theorists where attracted more and more by the physical sciences. The outstanding success of mechanics and electrodynamics caused many economists to consider physics as the archetype of a proper science. Since then, the majority of economists - with some notable exceptions like Thorsten Veblen (see Veblen 1898) - neglected biological and evolutionary concepts.

In recent decades economist show a renewed interest for biological thinking. The motivation for having a closer look on biology has been quite diverse. In search for a less stylized description of economic agency, psychological and biological approaches towards human behavior are taken into account: The fields of behavioral economics, organizational theory or management sciences are heavily influenced by evolutionary psychology, brain science and sociobiological approaches. Another influential stream of evolutionary economics is dealing with the role of innovations for industrial dynamics and economic change (Nelson and Winter 1982). Analogous to biological mutations, innovations may alter the development of industries or replace existing industries in an ongoing process of creative destruction, as it was described by Schumpeter (Schumpeter 1942). Other scholars even argue that a direct application of general biological principles, such as variance, inheritance and selection may serve as basis for a meta-theory for economics and other social sciences (Hodgson and Knudsen 2006, Dawkins 1983). Since the 1970s, evolutionary game theory helps to analyze strategic interactions of economic agents (Weibull 1995). Ecological theories are transferred to an economic context to explore firm competition from a population based perspective (Hannan and Freeman 1989). One common element in most of these evolutionary approaches is that (market) selection plays a crucial role as an explanatory mechanism and analytic tool. Neo-Schumpeterians, organizational ecologists or scholars of generalized Darwinism use economic selection in close analogy to the biological concept of natural selection: economic optimization or at least some degree of adaption to the environment is the outcome of a selective process, where only the best adapted survive or prosper.

As a matter of fact, not only in evolutionary economics, but also in neoclassical economics natural selection is used as an explanatory metaphor. One cornerstone of orthodox economics – the rational actor model – is often justified using a natural selection argument. In his famous 1953 article, Milton Friedman defended the assumptions of rational, utility maximizing and uniform agency in standard economics using a naïve interpretation of natural selection. Paraphrasing Friedman's argument may read like this: Whether agents are fully rational or not does not matter. In the long run agents will act ***as if*** they are fully rational and therefore uniform. This is because in the economy, as well as in nature, all those agents behaving sub-optimal will be driven out of the market quickly by a mechanism closely analogous to natural selection (see for a detailed discussion: Hodgson 2002). There is a substantial literature criticizing *as if* arguments as generally problematic (see for a recent one: Berg and Gigerenzer 2010). We want to develop a different argument in this paper. We want to show that an economic adaption by selection is no innocent assumption and often unrealistic because of a misinterpretation of the natural selection concept itself.

Usually biologists consider four types of evolutionary modes of causation, the famous Tinbergen questions (Tinbergen 1963). All four forms of causation should be considered if you give an evolutionary explanation for a given phenomenon. Firstly, you have to differentiate between ultimate and proximate causation. Ultimate causation explains why a trait exists. It explains its adaptive value and its phylogenetic history. On the other side proximate causation explains how a trait is working in a physical, chemical or biological sense. The latter is also influenced by the ontogeny of the organism who is the carrier of the trait. Applying the four Tinbergen questions, D.S. Wilson explains in a recent essay why Milton Friedman's argument is therefore evolutionary, but not "evolutionary enough" (Wilson 2012). Friedman assumed that considering the undoubtedly adaptive value of being a rational market participant proofs that evolution by natural selection has to lead to rational actors in the end. All non-rational actors are driven out of the market by selection. However, Friedman did not consider that behavior – from an evolutionary point of view - is not only determined by its current adaptive value.

As it is argued by D.S. Wilson (2012), the phylogenetic influences on behavior as well as proximate causation have to be considered too. The phylogenetic heritage of humans does, for example, include certain pro-social attitudes like a sense for fairness and spontaneous cooperation (see e.g. Henrich et al. 2001). These human characteristics are part of our genetic endowment and influence our economic behavior. Proximate causation like the architecture of our brain and cognitive limitations due to limited neural capacities also set boundaries to economic selection and the evolution of rational, self-interested actors. According to the Tinbergen principles, the hypothesis that certain traits will be favored by selection, because they seem to be adaptive is a good one to start with. Thus, the next step has to be the investigation of the properties of the units that are subject to selection processes. This includes their structural properties, their ontogeny or individual history as well as their phylogenetic history. In addition, someone has to be sure that she indeed identified the selection pressures correctly, which is not trivial as we will find when we discuss multilevel selection effects. The Tinbergen's four were developed to analyze the biology of behavior. However, we will show later that the interpretation of economic selection has to occur with even more caution, as it is constrained by cultural means.

We will start our analysis of selection in evolutionary biology and sociobiology, where it has undertaken a considerable refinement during the last years. Especially progress inside the fields of evolutionary developmental biology (Evo-Devo) and multilevel selection theory (MLS) put the central role of natural selection for biological evolution into perspective. However, this new view on a key concept in natural science has taken place without much attention outside the natural science community. Whereas possible economic applications of multilevel selection and especially its cultural pendant cultural group selection are recognized more and more (Samuelson 1993, Henrich 2004, van den Bergh and Gowdy 2009, Gowdy and Wilson 2013), the progress in the field of Evo-Devo catches only sporadic attention. In addition, the few works on economic theory in the light of Evo-Devo are characterized by overstatements of its main results. Knottenbauer (2009) comes to the conclusion that Evo-Devo biology is incompatible with Darwinian evolution or its current form, the "modern synthesis"; she therefore rejects any selection involving argument as outdated. This view is not shared by the vast majority of biologist and may result from a lack of understanding of the cellular and molecular mechanisms involved. Pelikan (2011) presents an Evo-Devo inspired model which tries to contribute to a Generalized Darwinism approach to economics. We will discuss later, why we think that this line of reasoning is unlikely to be fruitful.

The paper will proceed as follows: Section 2 gives an introduction to the field of evolutionary developmental biology, section 3 to multilevel selection theory. Section 4 will propose some implications for the use of the selection concept in economics. Section 5 concludes.

2. Evolutionary Developmental Biology: A Paradigm shift?

Basically, evolutionary developmental biology or Evo-Devo is a combination of two sub-fields: evolutionary biology and developmental biology. In a nutshell, evolutionary biology deals with the process of phylogeny. In contrast, developmental biology deals with mechanisms of ontogeny, i.e. the exploration of the incredible complex cellular and biochemical processes leading from one single fertilized cell, the zygote, over a series of cell divisions to the unfolding of a new organism. Over the last decades the rapid progresses in molecular biology and biochemistry as well as the decoding of whole genomes of different organisms (like the human genome project) and their analysis by computational methods expanded human knowledge on embryonic self-organization dramatically. Beside other findings, two of them surprised developmental biologists most.

First, the DNA sequences of all living organisms are surprisingly similar while the total number of different genes is far smaller than expected. Not only closely related species like humans and chimpanzees share the lion's share of their genes, but also very far related ones. Gerhard and Kirschner (2007) give an overview over different classes of genetic “conserved core components” that most organisms share today (including such diverse phyla as yeast, insects, and mammals), although their common ancestors lived millions or even billions of years ago. The structural actin proteins of yeast and humans for example, share their amino acid sequence to 91%. Other parts of the genome are highly variable and subject to frequent random changes, especially in the non-coding DNA strands. It seems that the basic structure of most of our genetic endowment has been conserved for ages, whereas other parts of the genetic endowment were allowed to mutate without experiencing much selective pressure. Indeed, the non-coding areas of the genome make up more than two thirds of DNA, providing space for mutational experimentation (Jobling et al. 2004, p.30). The genomic material is therefore not at all perfectly organized as previously supposed. It contains lots of energetically costly “waste” accumulated during phylogeny and is far less “optimized” than some strong selectionist views might suggest.

The second most stunning result is the degree of genomic organization and the similarity in regulatory components across biological phyla. It is of particular interest for our analysis. The genome of an organism is a highly organized structure, incorporating regulatory genes at the top level that guide the activity of structural genes at the bottom. The regulatory genes as well as the structural ones are embedded in networks which get activated or silenced depending on the progress of the ontogenetic process. During embryonic development gene regulating networks are activated stepwise. In the first step they guide the development of general structures such as body axes which determine the "Anlagen" for the nervous system or the inner organs. Afterwards more specialized gene networks are brought into action. Complex cascades of signaling peptides and proteins influence transcription factors which regulate, in turn, "molecular switches" that are located on special areas at the DNA. The pattern of activation and deactivation of these regions determine the morphogenesis of more specialized body structures.

Some of the most famous examples for such regulatory gene groups are the Hox- Gene- Clusters. These gene groups can be found in various animal phyla, for example in arthropods (e.g. flies) or in vertebrates (mice, humans). In both taxa these genes regulate the design of the anterior-posterior axis in early embryonic development. The sequence of these regulating genes is to a high degree very similar. What is differing across phyla is the number of copies of these gene clusters and the temporal and spatial order in which they get activated. Indeed, it is a widely held conjecture that the main changes in evolution, at least since the Cambrium, consisted in the rearrangement, duplication, or differential expression of higher order gene regulating networks (Carroll 2008). A rough analogy comparing the genome with a toolbox or construction kit is given by Gerhard and Kirschner (2007):

> "This, we argue, was such a powerful and versatile toolkit that post-Cambrian animals could largely omit further functional innovation at the gene product level (protein and functional RNA evolution) and instead exploit regulatory innovation to diversify anatomy, physiology and development. "

This is, of course, not meant to imply that any conscious or unconscious decision is being made by an individual animal or even an individual cell in order to rearrange its genetic material. Claiming that the "animals could omit further innovation at the gene product level" is but a loose form of saying: Over many generations natural selection altered the gene pool of a (meta-) population of individuals of one species in such a way that mutations in structural gene products were almost always fitness diminishing and therefore selected against. Yet, a few mutations in gene regulating networks had beneficial outcomes on anatomy, physiology, or development so that they spread among the descendants and ultimately in the entire population. The genuine new insight on the evolutionary process provided by Evo-Devo thus is the following. While it is true that natural selection is the central shaping force at the population level (with the exception of very small populations, were genetic drift and chance events play an important role), the raw material on which it is operating is a highly structured one. It incorporates historical adaptations, highly protected by various mechanisms. This amounts to a pre-selection of new combinations on which natural selection can act, and that constrains its shaping power more than often assumed. This is true at least since the Cambrian times. Since then no fundamentally new organismic "Bauplan" has emerged.

Hence, the abstract principles of variation, selection, and retention (inheritance) as such are of little value for reconstructing how natural evolution proceeded. The new findings in Evo-Devo show that it is essential to understand how the source of possible variation is biased and limited to historical grown and path dependent elements of the organismic blueprint. Accordingly, the creative power of evolution is strongly diminished. As De Robertis (2008, p.193) states:

> "What we are learning from Evo-Devo is that the source of variation of importance for evolution resides in deeply homologous developmental gene networks shared by all animals. A key question is to what extend these genetic homologies discovered by Evo-Devo have channeled, or constraint, the outcomes of evolution."

Theorizing on evolution in biology therefore focuses now on the particular structure and developmental limitations that determine the material and the ontogenetic mechanisms on which natural selection works. The reorientation has important implications. First, the main mechanisms of evolution appear in a new light. Unlike in the standard textbook interpretation, historical contingencies condition the influence of natural selection enormously. It is important to notice that, because formal models based e.g. on replicator dynamics usually ignore these. Second -- and closely related – it provides support for critics of a strong adaptionist view of evolution like Gould and Lewontin (1979; see also Gould 2002, pp. 1025-1055). The main critique of these authors is directed at the claim that evolution by means of natural selection generally leads to optimal adaptation in response to environmental problems. If true, this claim would imply that animal (and plant) anatomy, physiology, and also (social) behavior are optimized with respect to their functions. Making such a claim neglects, however, the abundant trade-offs between selective necessity and blueprintal feasibility that evolution has been forced to make during phylogeny. Vestigial structures, atavisms, and apparently maladaptive behaviors of various kinds are consequences of this trade off[2]. The forms of strong “adaptionism”, prominently represented by many socio-biologists and evolutionary psychologists, require a strong belief in an overwhelming power of natural selection. The idea of Evo-Devo rejects this strong selectionist view to a considerable degree, emphasizing other, additional constrains to evolution.

If natural selection becomes less pronounced wherever complex blueprints, especially of higher organisms, limit possible further adaptations and reduce the potentiality of fundamental reorganization, what does this mean for our species today? Obviously, the power and the speed of natural selection is reduced here further, by a huge, almost pan-mictic and nearly exponentially growing human population? It is clear that under such conditions, substantial genetic rearrangement or the dispersion of new, highly fitness enhancing genes or genetic variants is at best very slow and overall unlikely to occur. The main source of evolutionary change in modern society is therefore not genetic but cultural, and the comparatively rapid cultural adaptations have little, if any, time to systematically feedback on the human genetic endowment. Thus, unlike in the case of early hunter-gatherers and stone age humans, for which evolutionary anthropology postulates a co-evolution of culture and human genetic endowment, i.e. a “gene-culture co-evolution“, today almost all observable adaptations are exclusively culturally induced. They arise from individual and collective learning and knowledge accumulation processes.

However, the substrate on which this cultural evolutionary process is based is the human mind with the various pre-adaptations it carries, i.e. cognitive and social dispositions, acquired by natural selection in pre-historic times. While cultural features like technology, science, political and economic systems etc. proceed and develop, every generation of humans is genetically endowed anew with the same emotional and cognitive apparatus as, say, the Cro-Magnon was already endowed with. The environment in which this apparatus was shaped and to which it became adapted was very different from that of present days: food intake was insecure, the living conditions were generally much more hostile and dangerous, and the range of social interactions much smaller. The question thus arises to what extent the corresponding pre-adaptations constrain life in modern times which is of main interest in this paper.

[2] Gould (1991) proposed the concept of “exaptation” to stress the point that many traits present in organisms may have had previous adaptive value in the past, but are without function today. Very often exaptations provide raw material for new adaptations, often in entirely different contexts. In behavioral biology the term “preadaptation” is more common in the recent literature.

In biology, the ability of an individual organism, characterized by its fixed genetic blueprint, to adapt to different conditions is called "phenotypic plasticity". To put the question in analogous terms it could be asked: Is human cultural phenotypic plasticity unlimited? Or are there innate limitations and boundaries which constrain the possible forms of social interactions, organization, and institutions? This problem reminds of the controversy about unlimited vs. constrained adaptationism that the Evo-Devo paradigm shift triggered in evolutionary biology.

3. Multilevel selection theory – a further challenge towards strong adaptionism

The question of the levels of selection already bothered Darwin. In his analysis of the descend of man he argued that natural selection was probably not only working between individuals but also between social units, such as human tribes (Darwin 1871, p.166). In subsequent years the question of the units and the levels of selection did not receive much attention. This changed dramatically during the 1960s and 1970s when this question became a most important issue in context of explaining the evolution of sociality (Wynne-Edwards 1962, Williams 1966, Wilson 1975). Today, the idea that natural selection is operating on different levels simultaneously and causes specific adaptations at each level is a matter of hot debates between leading scholars (see as an example, Wade et al. 2010).

Biological evolution can be technically defined as change of gene or allele frequencies at the population level from one generation to the next. Besides genetic drift and mutation, natural selection is the most important force in changing gene frequencies. By drawing mainly upon formal models that describe differential growth of gene frequencies in a gene pool, many theorists argued that the gene or the molecule carrying the genetic information should be seen as the only relevant level of selection. However, in most species, especially higher organized ones, genes are not organized in a homogenous "pool" of free floating units like water molecules in a swimming pool. They are arranged in compartments, cells, tissues, individuals and social groups, characterized by an amazing degree of division of labor and cooperation. In social insects even individuals seem to act more as organs of a greater organism than as autonomous organisms, abstaining actually from own reproduction (Hölldobler and Wilson 2008).

To give an explanation for the stunning degree of cooperation in nature, which is compatible with a gene-level selection view, Hamilton (1964) proposed the concept of inclusive fitness which was in later years mainly interpreted as kin- selection. The idea of kin selection is based on the relatedness between reproducing entities of alleles or genes. From the point of view of a gene, it would pay off to reduce own reproduction, if reproduction of identical or very closely related genes- carried by related individuals - is enhanced sufficiently. If relatedness is too low, cooperative behavior cannot evolve. Consequently, also the carrier of the genes – the organism - should only cooperate, as long as she is closely related with another individual. Due to limited space, we cannot go into more detail here, so this rough idea of a much elaborated theory has to suffice. However, this concept was understood as a milestone in evolutionary biology. It seemed now possible to reduce even complex organismic behavior such as social behavior to selection processes at the gene level and to population genetics.

The emerging field of sociobiology was initially based entirely on this gene centered perspective on animal interaction. Phenomena such as altruistic behavior between two individuals were interpreted as the outcome of a hidden self-interest of their genes. A perspective on behavior which could be reduced to the gene level seemed to be universally applicable. Even obviously pathological behavior, such as genocide or some kinds of infanticide has been interpreted, especially in early studies, as adaption on the gene level using a sociobiological argumentation (see for a critique Ruse 1979) .

Until perhaps the 1990s the mainstream of evolutionary biologists and sociobiologists was optimistic that social behavior like the behavior of state building insects like ants and bees could be satisfactorily explained by gene-centered theories. Nowadays it becomes more and more clear that these expectations were delusive. There is still a consensus, that under standard conditions - for mathematical reasons - lower level selection is stronger than higher level selection. That means, speed and strength of the selection mechanism diminishes, the higher we climb the ladder of levels of integration (cells, individuals, groups etc.). On the other hand the path-breaking work of theorists like D.S. Wilson (see for a summary of the argument: Sober and Wilson 1996), showed that - given certain circumstances - group selection or multilevel selection is plausible to occur. Moreover, the genetic analysis of highly social insects proofed that the degree of kinship in these animals is too low to explain their evolution by kin-selection. Nowadays many biologists, including eminent authorities of the field like Hölldobler and E. O. Wilson, accept the importance of MLS as part of the explanation for the evolution of sociality (Wilson and Hölldobler, 2005, Wilson 2012). In a recent publication, Nowak et al. propose a set of general conditions for the emergence of eu-sociality, including multilevel selection mechanisms and behavioral pre-adaptations which can be understood as a kind of mixture of Evo-Devo arguments and MLS (Nowak et al., 2010). However, not only social insect experts became more open to MLS. Also in human evolution group level adaptations seem to have been very influential. Several evolutionary anthropologists are arguing that the evolution of culture strengthened selection on the group level in human phylogeny, especially during the period of an intense gene-culture coevolution (Henrich 2004, Bell et al., 2009).

Sociobiology was for the last decades the predominant paradigm in behavioral biology. However, the gene-centered view on social behavior it provided proofed to be too simple: it neglected selection influences from other levels, but also the importance of phylogenetic constrains. Many followers of E.O. Wilson were inclined to use “strong adaptionist” explanations of social behavior. This adaptionist bias has been a major point of criticism against sociobiology from evolutionary theorists like Gould and Levontin (1979). The initial success of the strong forms of adaptionism in sociobiology and later on in evolutionary psychology fed back also to the social sciences and to economics. Laland and Brown (2011) give a very comprehensive overview over different biologically inspired streams of literature that deal with human behavior. They focus also on problems and misinterpretations of human behavioral biology that arise from strong adaptionist viewpoints.

There exist several recent attempts to make use of ideas from multilevel selection theory for economics. Van den Bergh and Gowdy (2009) give a broad overview over the concept of MLS and discuss some possible applications. D.S. Wilson and Gowdy (2013) propose an argument how central features of human social and economic systems can be interpreted as a product of multilevel selection (Wilson and Gowdy 2013). In our paper, we are not so much interested in direct applications of MLS, but on its implications for our understanding of the explanatory power and the scope of the selection mechanisms. One important insight is that it proves to be extremely difficult to find an evolutionary explanation for social behavior that arises from the interaction of selfish players only. More important for our analysis however is that we can identify again the close interconnection between an excessive use of (mono-layer) selection based explanations and the problems of adaptionism. If we consider the insights provided by MLS as plausible, we reach similar conclusions as for Evo-Devo biology: The interpretation of a given phenomenon as an adaption mediated by selection is not straightforward. There might exist contrarious selection pressures on different levels, leading to unexpected forms of adaption or even mal-adaption. In the following section we will discuss possible implications for economic theorizing.

4. Implications for the use of the selection concept in economics

Economic selection processes are different from natural selection. Economic or market selection is a subject of culture. Natural selection is a subject of genes and the change of gene frequencies in a population's gene pool over generations. Indeed, making such a distinction does not seem to be trivial. Over the last years, proponents of a *Generalized Darwinism* approach to economics argue, that selection processes (together with variance and heredity of traits) could serve as cornerstones of a meta-theory that describe all sorts of evolving systems, biological as well as social and economic ones (see Hodgson 2002, Hodgson 2004, Hodgson and Knudsen 2006). Though adherents of a Generalized Darwinism admit that there exist clear differences between economic and natural evolution, these differences are treated as accidental, while the central mechanisms are interpreted as transferable to any evolving system. Following this line of argumentation, it should be possible to identify corresponding elements that fulfill the same role in natural as well as in cultural and economic evolution. However, the identification of evolutionary *analoga* proved to be difficult, unsatisfactory and very hard to use in explaining concrete phenomena. First of all, there are no clear matching parts of genes in cultural evolution. The meme concept, as it was introduced by Richard Dawkins (1976) faces severe problems (Fracchia and Lewontin 2005, Richerson and Boyd 2005); organizational routines that take the role of genes and replicators in the Nelson and Winter approach (1982) are also very limited in scope (see for a detailed discussion Vromen 2006). An identification of analoga for the biological concepts of phenotype and genotype in form of cultural or economic replicators and interactors has been not very successful. Further, a main requirement for economic selection to work in similar ways as in nature, would be a substantial degree of inertia of the subjects of selection. The assumption of inert economic actors, such as firms who are unable to learn and to adapt, is at least questionable. All these and several more problems that arise in a Generalized Darwinism framework are discussed *in extenso* for example by Witt (2003, 2004), Cordes (2006, 2007a, 2007b), Levit et al. (2011) or Vromen (2007).

One lesson that can be derived by resent results of Evo-Devo biology and MLS suggests that a top-down approach, as it is proposed by Generalized Darwinism, is unlikely to work. The installation of a general theory that puts the selection mechanism *a priori* in a central position necessarily has to lead to adaptionistic failures. An economic theory which is built on the individualistic perspective and interprets the selection mechanism as main evolutionary force could run soon into similar problems as sociobiology. Even if pro-social traits of humans and multilevel selection forces could be implemented in a generalized Darwinism framework, the role of self-organization of social entities, the cognitive and emotional predispositions of humans, individual ontogeny and learning, idiosyncratic mechanisms of cultural transmission or path-dependent and historic properties of cultural evolution would be ignored. The latter, however represent essential boundary conditions that influence cultural and economic evolution substantially, comparable to phylogenetic blueprints and genomic organization in Evo-Devo biology.

Instead of thinking about generalizable evolutionary forces and accidental cultural influences, we would prefer to suggest the opposite approach. Human behavioral predispositions and cultural causes for behavior should not be treated as accidental, but should be placed at the heart of analysis. Cultural and therefore also economic evolution is characterized by its own features and mechanisms that are distinct from natural evolution. However, cultural evolution is shaped by natural selection. Natural selection provided the original conditions for culture by creating brain structures and emotional dispositions hard-wired in our genome. Since the invention of agriculture approximately ten thousand years ago, human evolution has taken place mainly as a cultural phenomenon[3]. Today the impact of natural selection is comparatively small, at least for relevant economic timescales. The transition from natural to cultural evolution, however, was not an abrupt one. According to Robert Boyd and Peter Richerson (1985, 2004), during this transition period an intense gene-culture coevolution took place. Natural selection favored traits that enhanced our capability of cultural knowledge accumulation. Those groups who were able to store knowledge via cultural transmission were hugely successful in their ability to survive and produce offspring, so enhanced cultural abilities fed back towards natural selection. Our human dispositions towards culture, including the cognitive apparatus which is needed to make use of culture e.g. the ability to transmit cultural information, was acquired and genetically hard-wired to our genome by natural selection. As this process came to an end with the agricultural revolution, natural selection left stage leaving our genetic endowment on the whole untouched.

One main result of the gene-culture coevolution is the specific human ability for cumulative social learning (Boyd and Richerson 1985, Richerson and Boyd 2004, Tomasello 1999). The evolution of cultural information transmission represents an alternative mechanism to acquire and store complex information over generations, which does not rely on differential reproduction or survival of the actors involved. To a substantial degree culture replaced genetic selection as the main means of information

[3] This is at least true for complex genetic adaptation. Cochran and Harpending (2010) argue that humans have developed some genetic modifications since agriculture was introduced. However, most of these adaptations are small in scale and concern resistances against certain infectious diseases, such as malaria, or enhanced ability to digest carbohydrates or lactose. Fundamental changes in our behavioral repertoire have not been altered.

transmission and opened a new way for adaptation. Adaption in the cultural sphere does not necessarily rely on the selection of better adapted selective units. Those who are less adapted are able to learn from others via imitation or teaching. Information transmission and accumulation is further not restricted to take place on a generational or vertical basis but takes place within generations. Cultural information transmission and social learning therefore provide a more powerful tool and a much faster mechanism than selection to achieve adaption. A crucial difference between selection that is driven purely by the environment (e.g. market selection) and cultural transmission has to be recognized. Adaption by cultural transmission is biased by our psychological endowment, whereas environmental selection does only measure success *ex post*. Again, we have to be cautious: like natural evolution also cultural transmission may lead sometimes to maladaptive and non-optimal behavior (Richerson and Boyd 2004, p. 148-190). Products of cultural and economic evolution like firm structures or other economic institutions could be results of transmission processes that are non-adaptive and therefore non-efficient. Examples are differing size distributions and organizational structures of firms within one single industry (see e.g. Coad 2009, 14-24). Although these firms share a common environment, they are not at all completely uniform, which is a clear indicator that their size and structure are probably no products of a selection process. The postulate that the mere existence of a characteristic or structure has to be an adaptive solution against a selective environment is not valid. The specific boundary conditions under which these structures evolved have to be considered, to be sure if they indeed adaptive or not.

One obvious application of cultural learning in economics is the study of social groups, for example in the context of organizational development and corporate culture. According to our analysis so far, we would suggest that an evolutionary analysis of organizational structures should be based to a lesser extent on competitive processes and market selection between firms, as it has been done in the past (Winter 1965, Nelson and Winter 1982, Hannan and Freeman 1989, Metcalfe 1993). On the contrary, cultural transmission and behavioral predispositions towards social organization shift the focus on developmental and self-organizing processes such as social learning within firms in the tradition of Cyert and March (1963), Penrose (1966) and Rathe and Witt (2001). Biased transmission of cultural traits can contribute to our understanding of growth crisis in firms (Cordes et al. 2010) or the initialization of new industries by spin-off formation, due to a changed corporate culture in the mother firm (Cordes et al. 2013). The perspective provided by MLS may contribute in future considerably to an evolutionary understanding of the economy that goes beyond simple adaptionism. There are attempts for instance, to use MLS based arguments to improve the concept of the invisible hand and self interest in the context welfare economics, by analyzing the influence of multiple interacting social levels (Wilson and Gowdy 2013, Gowdy et al 2013). These approaches, however, are fundamentally different from a Generalized Darwinism perspective. They are following a bottom-up strategy in applying methods and insights provided by evolutionary biology, anthropology or behavioral biology, when appropriate. Methods and results derived by biology or psychology are applied to economic questions in form of a tool kit (Wilson and Gowdy 2013). If methods from these or other disciplines are available and can be used to provide additional insight, it is reasonable to use them. If not, you should stay with economic concepts.

5. Conclusions

Recent progress in Evo-Devo biology and multilevel selection theory suggests that a Generalized Darwinism approach to economics is unlikely to be fruitful. A top down theory that puts the selection mechanism *a priori* in a central position necessarily leads to adaptionistic failures. Economic selection is a cultural phenomenon and is distinct from natural selection.

What remains of the selection concept in economics? Selection, if interpreted as differential success of economic agents in a competitive process can still be a valuable concept. It may, for example, serve as a good predictor for short term changes in market shares of firms. However, given other and more effective modes of information transmission in cultural systems, selection in economics cannot play a similarly powerful role as it does for natural evolution. Especially the interpretation selection as the central mechanism leading to fast and optimal adaption to market conditions has to be questioned. Not even natural selection acting biological populations is able to lead to adaption in such a way. Instead of trying to establish an evolutionary understanding of economic processes in close analogy to abstract principles of evolution, we suggest to take another way. Our understanding of human behavior, cultural evolution and other specific human characteristics that contribute to economic behavior have to be identified in the first place and taken into account for the analysis of economic evolution.

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