



UvA-DARE (Digital Academic Repository)

Universal Darwinism from the bottom up: An evolutionary view of socio-economic behavior and organization

Stoelhorst, J.W.

Publication date

2008

Document Version

Author accepted manuscript

Published in

Advances in evolutionary institutional economics: Evolutionary mechanisms, non-knowledge and strategy

[Link to publication](#)

Citation for published version (APA):

Stoelhorst, J. W. (2008). Universal Darwinism from the bottom up: An evolutionary view of socio-economic behavior and organization. In H. Hanappi, & W. Elsner (Eds.), *Advances in evolutionary institutional economics: Evolutionary mechanisms, non-knowledge and strategy* (pp. 35-58). (Studies in evolutionary political economy). Edward Elgar.
<http://www1.fee.uva.nl/pp/bin/339fulltext.pdf>

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, Singel 425, 1012 WP Amsterdam, The Netherlands. You will be contacted as soon as possible.

UvA-DARE is a service provided by the library of the University of Amsterdam (<https://dare.uva.nl>)

**Generalized Darwinism From the Bottom Up:
An Evolutionary View of Socio-Economic Behavior and Organization**

J.W. Stoelhorst

Amsterdam Business School
University of Amsterdam
Roeterstraat 11
1018 WB Amsterdam
The Netherlands

Tel. 31-20-525 5689

j.w.stoelhorst@uva.nl

Published in:

Stoelhorst, J.W. (2008), Generalized Darwinism From the Bottom Up: An Evolutionary View of Socio-Economic Behavior and Organization. In: Wolfram Elsner and Hardy Hanappi (Eds.), *Advances in Evolutionary Institutional Economics: Evolutionary Mechanisms, Non-Knowledge, and Strategy*. Cheltenham: Edward Elgar Publishers, pp. 35-58.

Generalized Darwinism From the Bottom Up: An Evolutionary View of Socio-Economic Behavior and Organization

J.W. Stoelhorst

1. Introduction

Institutional and evolutionary economists have recognized that organizations are social as well as economic entities, but in modern evolutionary theories of the firm the social aspect of economic organization is typically lost. This is a result of the fact that these theories take the existence of firms as given, focus on the explanation of market and industry level phenomena, and in doing so use notions such as routines to abstract from individual behavior within the firm. This paper takes another approach and reasons from the bottom up. It is argued that for both historical and ontological reasons, individual behavior should be seen as the starting point of theorizing about socio-economic organization. Organizations are a social solution to the individual problem of survival, and while they introduce an additional level of analysis with its own emergent properties, any theory of economic organization should both acknowledge and be consistent with the nature of individual behavior.

Making individual behavior central to evolutionary theories of socio-economic organization raises a number of fundamental questions. An evolutionary view of individual behavior that recognizes the social aspect of economic organization would see individuals as competing in a socio-economic environment, with their success depending on their socio-economic fitness. But what is socio-economic fitness? While an evolutionary analysis of socio-economic behavior necessarily involves such a concept, its nature is not at all clear. A concept of socio-economic fitness implies social as well as economic selection pressures, but what is the nature of these pressures? And is adaptation to socio-economic pressures not an ontogenetic rather than a phylogenetic process that defies explanation in terms of the population logic of evolutionary theories?

The purpose of this paper is to answer these questions by applying Generalized Darwinism to the analysis of socio-economic behavior and organization. Its intended contributions are threefold. First, the paper presents an argument for the importance of building theories of socio-economic organization on an evolutionary understanding of what drives individual behavior. Second, the paper demonstrates how Darwinism can be used to understand the evolution of individual behaviors in socio-economic contexts. Third, the paper

shows how such an understanding can be used to advance evolutionary theories of economic organization.

The paper proceeds as follows. It asks how Generalized Darwinism can ground theories of economic organization and argues that the historical and ontological primacy of individual behavior calls for theories of economic organization that are grounded in an evolutionary understanding of human behavior. The paper takes Nelson and Winter's (1982) seminal contribution to modern evolutionary economics as its starting point and shows how their treatment of the firm abstracts from individual behavior. It is furthermore argued that this treatment of individual behavior goes against their own research agenda, and it is shown that Generalized Darwinism can help develop an evolutionary theory of economic organization in which individual behavior has the place that Nelson and Winter originally envisaged. The paper demonstrates how the ontogenetic nature of individual learning in socio-economic contexts can be understood in Darwinian terms by modeling the evolution of individual behavior in terms of the selective retention of successful behaviors in an individual's behavioral repertoire. It asks what socio-economic selection pressures shape individual behavior and develops a typology of four selection mechanisms (market, hierarchy, social network, expert) that may operate in socio-economic contexts. The firm is discussed as an example of a socio-economic selection environment, and implications for an evolutionary theory of the firm are derived. The paper concludes by developing the contours of Darwinian theory of socio-economic organization that links the traditional concern for selection between firms with an additional concern for the selection of individual behaviors within them.

2. Evolutionary economics and Darwinism

It has recently been argued that there is both a need and a possibility to move beyond the truism of survivor selection that is characteristic of much evolutionary theorizing in economics (Knudsen 2002). There is a need for more rigorous explanations of economic evolution that go beyond the use of biological metaphors (Hodgson 2002), and there is the possibility to develop such explanations by building on the premises of what has become known as 'Generalized Darwinism' (Hodgson 2002, 2003; Hodgson and Knudsen 2006; Stoelhorst 2005a,b; Stoelhorst and Hensgens 2006).ⁱ

Economists use the term evolution in a variety of ways. Some theories are called evolutionary simply because they deal with change over time, while others are specifically based on biological metaphors and analogies. Nelson and Winter's (1982) evolutionary

economics belongs to the latter category. One of their achievements is that they ground their evolutionary theory more firmly in Darwinian principles than their predecessors in economics (Hodgson 1993). This is illustrated in the way in which Nelson (1995) describes the general principles of evolutionary theory:

‘The general concept of evolutionary theory ... involves the following elements. The focus of attention is on a variable or set of them that is changing over time and the theoretical quest is for understanding of the dynamic process behind the observed change ... The theory proposes that the variable or system in question is subject to somewhat random variation or perturbation, and also that there are mechanisms that systematically winnow on that variation. Much of the predictive power of that theory rests with its specification of the systematic selection forces. It is presumed that there are strong inertial tendencies preserving what has survived the selection process’ (p.54)

But there is the possibility of a third category of evolutionary theory in economics. Such theory would go beyond the analogical use of evolutionary principles and start from the recognition of ontological similarities between all complex open systems. The label ‘Generalized Darwinism’ captures the notion that the development over time of any open complex system can be understood in terms of the same principles that are at the core of Darwin’s theory of natural selection (e.g. Plotkin 1994; Cziko 1995; Dennett 1995). The universality of Darwin’s theory stems from its specification of a general, substrate neutral, algorithm to explain evolution (Dennett 1995). This algorithm consists of three meta-mechanisms: variation, selection and retention (Campbell 1965; 1974; Plotkin 1994), and a Darwinian explanation of evolution consists of specifying the nature of these three mechanisms for the domain that is being studied (cf. Hodgson and Knudsen 2006, Stoelhorst 2005b).

The triumvirate of variation, selection and retention is implicit in Nelson’s specification of the general concept of evolutionary theory above, yet Nelson and Winter have been reluctant to admit to more than the use of a Darwinian analogy (Hodgson 2003; Nelson 2006). This reluctance seems to stem from an understandable fear to get stuck in ‘notions that, while salient in biological evolution, seem irrelevant or wrong-headed when applied to economics’ (Nelson 1995, p.54).ⁱⁱ Therefore, it ‘seems more fruitful to start with a general notion of evolution’ (ibid.). But this is exactly what Generalized Darwinism is about: to abstract from the specific mechanisms of biological evolution, and specify the general principles of evolution as they apply across entirely different domains.

This paper is premised on the idea that something can be gained from developing more fully specified Darwinian accounts of economic phenomena.ⁱⁱⁱ While Nelson's general concept of evolution above goes some way towards specifying what the general principles of evolution are, his description does not qualify as a fully developed Darwinian framework. First, whereas he puts emphasis on the need to *specify* 'systematic selection forces', he makes allowance for the mere *assumption* of the existence of mechanisms for variation and retention. Generalized Darwinism calls for the specification of *all three* mechanisms. The second way in which Nelson steers clear of an explicitly Darwinian account is by not specifying what evolution is about. From the vantage point of Generalized Darwinism, his phrase 'understanding the dynamic process behind the observed change' is unnecessarily vague. Darwinism is about explaining *adaptive* change, *variety*, and the accumulation of *design* (Stoelhorst 2005b). To say that when mechanisms of variation, selection and retention are present 'evolution will occur', means saying that (1) the systems in question will become adapted to their local environment, (2) that variety between systems will develop from common origins, and (3) that design, or adaptive complexity, will accumulate without the necessary interference of an (omniscient) designer. It is by explicitly recognizing these *explananda* that evolutionary theory can move beyond the truism of survivor selection.

3. Darwinism and the evolutionary theory of the firm

Evolutionary theories of economic organization typically focus on how markets select efficient firms. While not perfect (Knudsen 2002), our understanding of how such economic selection works is fairly well developed (Nelson and Winter 1982). But a firm is both an economic and a social entity and merely asking how economic selection works would deny the inherently social nature of economic organization. The idea that a firm is both an economic and a social entity has a long history in management studies (Barnard 1938), but most economic theory abstracts from the social dimension of economic organization. Nelson and Winter's (1982) work is an exception in the sense that part II of their book (chapters 3-5) offer an elaborate discussion of the behavioral principles on which firms operate. However, they do not offer a fully developed theory of the firm.

There is an interesting parallel between the work of Nelson and Winter and that of Darwin. In his book on the universal applicability of Darwinian principles, Dennett (1995) starts by pointing out that Darwin developed his theory by 'starting in the middle'. Despite choosing the title 'The Origin of Species', Darwin *assumed* the existence of many different

species, and from that mid-stage point in biological evolution proposed that natural selection could explain both the variety of these species and their adaptation to their specific natural environments. Nelson and Winter's evolutionary theory similarly starts in the middle. Their primary concern is to account for economic change, and their way of addressing this phenomenon is to assume the existence of firms and competitive markets. But a theory of the firm should ideally explain the existence of firms, as well as their internal organization and the differences between them (Holmstrom and Tirole 1989; Foss 1996). Nelson and Winter's theory of economic change offers an elegant theory of why firms are different (see also Nelson 1991), but it does not explain why firms exist and gives a rather simplified account of their internal organization.

It is with respect to this last point, the way in which the internal organization of the firm is treated, that we find a fundamental tension in Nelson and Winter's work. In *An Evolutionary Theory of Economic Change* they explicitly state that it is their aim to develop a theory of economic change that is based on realistic behavioral assumptions. And part II of their book not only sets out to present a behaviorally realistic view of what goes on inside firms, but also succeeds in doing so. Unfortunately, this realism is lost in the rest of the book, which is aimed at modeling different aspects of economic growth. In part III-VI of the book, the elaborate discussions of the inner workings of the firm in part II are essentially collapsed into the notion of routines.^{iv} This is shorthand for the idea that firms routinize their behavior in the quest for economic success, and an essential part of an explanation of economic growth in terms of a variation-selection-retention algorithm operating on a population of firms. However, in putting so much of the explanatory burden of their models on this notion, Nelson and Winter veer away from their own agenda with respect to building theory on realistic behavioral assumptions. In essence, the notion of routines abstracts from individual behavior. This is most obvious when considering how Nelson and Winter model variation. In their models variation results from higher-level search routines that induce change in lower-level operating routines. In such a conceptualization, the individual is absent from any consideration of organizational change, and variations in individual behavior as a source of variation within firms are lost in an infinite regress of different levels of routines operating on each other (cf. Winter 2003).

In his broad review of evolutionary theorizing, Nelson quite rightly takes the position that theories of socio-cultural evolution have 'not as yet tried to come to grips with the dynamics of change in modern industrial societies' (1995, p.60).^v He goes on to argue that

evolutionary theorists that work in these traditions 'have by and large assumed that selection mechanisms are individualistic, transmission mechanisms are person to person, and that 'memes' like genes are carried by individuals. Yet these perceptions seem quite inadequate for analysis of how science or modern technology evolves, or forms of business organization, or law' (1995, p.61). It is with this latter position that the current paper takes issue.

The position that is taken here is that there is a need to build theories of economic organization from the bottom up. There are three reasons for doing so that will be further developed in the remaining sections of the paper. First, the behavior of individuals is the historical linking pin between biological and cultural evolution. Individual behavior is therefore an essential part of any explanation of why socio-economic institutions such as the firm exist in the first place. Second, abstracting from individual behavior is an unfortunate way of circumventing the problem of agency. Firms do not behave as such, only their employees do. In other words, in addition to being the historical linking pin in an explanation of why firms exist, individual behavior is also the ontological linking pin in explanations of how the internal organization of firms affects their performance in the market. It follows from the two previous points that a theory of the firm that wants to explain why firms exist, why they are different, and how they are organized, needs to build on an understanding of how individual behavior relates to the nature and performance of firms. Note also that such an understanding is in line with Nelson and Winter's own insistence on theories that take a behaviorally realistic view of economic organization. The third reason for advocating the development of a theory of economic organization that reasons from the bottom up is simply that it can now be done. As will be demonstrated below, Generalized Darwinism offers a general framework that can make the necessary connections between selection of individual behaviors within socio-economic contexts such as the firm on the one hand, and selection between socio-economic groups such as the firm on the other. Our current understanding of Darwinism makes it possible to take up the legacy of Nelson and Winter's view of the firm and further develop it in ways that are consistent with their original agenda.

4. Individual behavior as historical linking pin

Evolutionary theories of biological, social, economic and cultural phenomena abound. But what is often lost in this melee of theorizing is that there is an undeniable historical connection between the different phenomena that these theories address. In addition to teasing out the general principles of evolution, Generalized Darwinism also posits that all design in

our world is the result of an evolutionary process, and that the common origins of all adaptive complexity can be traced back along evolutionary pathways, all the way to the emergence of life in the primeval soup (cf. Dennett 1995). Witt (2003, 2004) has suggested a similar idea in evolutionary economics. His 'ontological continuity hypothesis' states that there are historical links and ontological similarities between production in nature and in the economy.^{vi} These historical links are lost in theories of economic organization that start in the middle by assuming the existence of firms, and while this may not be much of a sacrifice when explaining industrial change or economic growth, a theory of the firm as a socio-economic institution has much to gain from taking them seriously.

Dennett's (1995) discussion of evolution as a cumulative design process shows how Darwin's theory of natural selection does away with the necessity to invoke an omniscient designer to explain adaptive complexity. Darwin's theory explains how the complex designs of living organisms could arise from simple beginnings through a mindless algorithm of variation, selection and retention. In the case of biological evolution, this algorithm works through random variation in the genotype (which codes for the design of organisms), and selective retention of phenotypic behavior that is successful in securing scarce resources from the environment. This selective retention takes place through a generational filter: the genes of organisms that are unsuccessful in the competition for survival and mates are lost for the next round. Dennett goes on to show that, when suitably abstracted from their specific manifestation in biology, the principles of variation, selection and retention can also explain cultural evolution. But he also makes another point: that biological and cultural evolution can not only both be understood as processes in which useful design variations accumulate from the bottom up, but that they should ultimately be seen as part of one and the same process.

This view of evolution as a process in which change percolates from the bottom up through selective filters and results in ever increasing forms of adaptive complexity is as much a part of Generalized Darwinism as the variation-selection-retention algorithm itself. It establishes the historical primacy of selection at the level of individual organisms over the evolution of such cultural entities as the modern firm. In doing so, it also raises some fundamental questions. How is it that one and the same evolutionary process has produced both living organisms and cultural phenomena? Or, in terms of what concerns us here: how has the selection of individuals pursuing their own interest resulted in the existence of such social entities as the firm? In other words, how are biological and cultural evolution related, and how does the existence and nature of the firm fit within this scheme?

This brings us to the notion of ‘major transitions’ in the evolutionary process (Maynard-Smith and Szathmary 1997). Biological evolution is essentially the result of differential success in two separate biological realms. Organisms engage in matter-energy transfer processes to survive and they reproduce. The evolutionary biologist and paleontologist Eldredge (1995) refers to the behavior of organisms related to matter-energy transfer as ‘economic’. Biological evolution thus hinges on two types of behavior: ‘economic’ and ‘reproductive’. During the billions of years of biological evolution, the process of variation, selection and retention has hit on many viable designs to exploit the available matter and energy, as well as on different ways to reproduce these designs. Some of the designs that the process of biological evolution has hit on have been particularly ‘good tricks’ that have fundamentally transformed the process of evolution itself. These particular design tricks are the so-called major transitions in the evolutionary process.^{vii} Dennett (1995) calls them ‘cranes’ to illustrate how the mindless process of evolution can lift itself to new levels of complexity.

The nature of such major transitions can help us understand the place of the firm in the overall process of the evolution of adaptive complexity. All major transitions share three features: they (1) involve an increased division of labor, that (2) is made possible by a new way of transmitting information, and (3) they result in the emergence of an additional level of selection (Maynard Smith and Szathmary, 1997). For instance, in the case of the transition from single celled life to multi-cellular organisms, the division of labor takes the form of cell differentiation. This can only work if there is a way to coordinate the behavior of the specialized cells for the benefit of the whole organism, as well as a way of passing on the information about how to do this to the next generation. The solution of this problem in biological evolution needs to be understood in terms of a multi-level selection logic that explains how a viable multi-cellular system can emerge in the face of competition for scarce resources among individual cells that pursue their own interest (Maynard Smith and Szathmary 1997; Sober and Wilson 1998). As soon as multi-cellular organisms emerge, there is an additional level of selection to consider: selection between organisms. But the emergence of this new level of selection depends on the way in which the design of the organism overcomes the problem of the competition between individual cells. In all major transitions, there is the real problem that selection at the lower level of organization will disrupt integration at the higher level. Any increase in adaptive complexity must therefore be

understood in terms of how it solves the conflict of interest at the level of selection that preceded it.

This logic also needs to be applied to explain the transition to social organization. While in multi-cellular life there is division of labor between the cells within an organism, social organization makes use of division of labor between organisms within a group. Social organization thus takes the principle of coordinating specialist tasks to a higher level of complexity and introduces the additional level of selection: that of the group. We have here a very general principle in the design of adaptive complexity that was introduced to economics by Adam Smith's discussion of the pin factory. The division of labor enables specialization and efficiency gains, but comes with a problem of coordination that needs to be overcome by the design of the system. Note that social organization can emerge through genetic mechanisms alone, as it has done in social insects such as ants and bees. But it can take on yet another level of complexity if cultural transmission systems that make use of (symbolic) language to pass down information about successful designs are in place. Learning by imitation and language allowed humans to pass on information through time by way of another mechanism than genetic reproduction. This has resulted in a level of social organization that is unique in the animal kingdom: we are the only species that is able to sustain cooperation in large groups of individuals that are not genetically related (Bowles and Gintis 2003; Fehr and Fischbacher 2003). Note that this unique human ability has all the characteristics of a major transition. There is a marked increase in the division of labor that is made possible by a new way of transmitting information (symbolic language) and that gives rise to additional levels of selection.

Modern firms are an example of these new levels of selection. In essence, firms are a social solution to the economic problem of securing scarce resources that individuals face. This solution is made possible by cultural transmission mechanisms that allow individuals to coordinate their behaviors and keep competition between them from undermining the functional integrity of the firm as a whole. In so doing, the existence of firms introduces an additional level of selection in terms of the competition for scarce resources between them. This between-group level of selection has its own emergent properties and is a bona fide target for the development of theories about what happens at this additional level of analysis. But a view that takes the ontological continuity of all evolutionary processes seriously would call for an understanding of what happens at this level of analysis in terms of how firms are

able to coordinate the behavior of individuals in ways that channel within-group competition to the benefit of their performance in between-group competition (cf. Campbell 1994).

5. Individual behavior as ontological linking pin

The previous section made a point of the historical primacy of individual selection over group selection and pointed out that the functional integrity of a system at a level above the individual needs to be explained in terms of how it channels competition between individuals for the benefit of the group as a whole. This section develops a second reason for the need to explicitly build theories of socio-economic organization on an understanding of how they channel individual behaviors. This second reason is that a proper treatment of agency would see individual behaviors as the ontological linking pin in an evolutionary explanation of how the behavior of groups evolves.^{viii}

Problems with agency in evolutionary theory come in two forms: one that is general to all evolutionary theory and another that is specific to theories at the level of groups such as the firm. As Nelson (1995) states, much of the predictive power of an evolutionary theory rests with its specification of systematic selection forces. The archetypal examples are the ways in which the natural environment selects organisms in biology and the ways in which markets select firms in economics. But what do we mean when we say that ‘the environment selects’? This phrase seems to impute agency to the environment. This directs our attention away from the agency that really matters in understanding selection. To understand selection, we need to recognize that the relevant agents are the systems competing for scarce resources. What is selected is the system’s relative ability to secure scarce resources from the environment. Selection, then, is about winnowing the ways in which systems interact with their environments.

Selection works on open systems that need resources from their environment to survive. Living organisms need energy to overcome the second law of thermodynamics, and firms need to generate income to pay their suppliers, employees and owners. If these resources are not secured, the system simply cannot maintain its functional integrity. Selection pressure exists to the degree that the resources that the system needs for survival are scarce. It follows that what is selected is the system’s relative ability to secure scarce resources from the environment. That the relevant agency is not in the environment but in the system that is being selected can be seen when considering natural selection. In the case of natural selection, the environment does not actively promote successful behaviors. Instead, the less successful

organisms are weeded out. This doesn't happen by any positive act from the environment, but simply as the result of the organisms coming up short in the competition for resources. In that sense, the term 'natural selection' is a misleading metaphor. Darwin adopted the term to show how natural selection could have similar effects as artificial selection, but in doing so gave us a term that can be easily misinterpreted. While the nature of artificial selection shows that agency can be part of the selection mechanism, this is not necessarily the case and is secondary to the logic of evolution.

To be able to specify the agency around which evolution revolves, let us refer to the way in which a system interacts with its environment as the system's *behavior*. Underlying a system's behavior is the way in which the components of a system interact. Let us refer to this as the system's *design*. The design of a system underwrites its behavioral repertoire in the sense that it both enables and constrains the possible ways in which the system can interact with its environment. The notions of an open complex system's 'behavior' and 'design' allow us to specify more fully how selection works. Selection weeds out the designs of systems that are unsuccessful in securing sufficient scarce resources from the environment to survive. Or in shorthand, selection propagates designs that allow for successful behavior. As a corollary, evolution can be understood as a process in which the ways in which systems interact with their environment change over time so that (1) individual systems become adapted to their local environment, (2) variety between systems increases, and (3) design principles that underlie behavior that works accumulate. The mechanisms that drive this process are the introduction of variation in the behavior of individual systems, selective pressure from scarce resources, and retention of the principles of successful behavior in the systems' design.

The central role of interaction with the environment, or 'behavior', in the evolutionary logic points to a further problem with the notion of agency in evolutionary theories at levels above the individual. A social group such as the firm does not behave as such. It is the firm's employees that behave, and the 'behavior' of a firm can only be understood as the coordinated behavior of its employees. The way in which social entities such as the firm interact with their environments is simply an extension of the behavior of their members, and the notion of agency should therefore be reserved for the level of analysis where it belongs: that of the individual. We can, of course, use the notion of 'the behavior of the firm' as shorthand in analyses at the level of competition between firms. But, and this is essential, we cannot say anything that is empirically meaningful about how the behaviors of firms evolve over time without explicitly referring to individual behavior. To explain how firms change the way they

interact with their environment and how they adapt to changing circumstances (or fail to do so), the evolutionary algorithm requires a specification of the mechanism of variation. And individual agency is quite simply the only source of variation in how firms behave. It is the new CEO, the enterprising manager, the innovative engineer, or the pro-active employee that are the sources of behavioral variations on which selection works.

6. Socio-economic fitness and the evolution of individual behavior

The previous two sections each developed a fundamental reason to develop evolutionary theories of socio-economic organization from the bottom-up. The historical and ontological primacy of individual behavior calls for the development of theories of economic organization that build on an evolutionary understanding of individual behavior. But can the evolution of individual behavior be understood in Darwinian terms? Evolutionary theory in biology distinguishes between phylogenetic (evolutionary) and ontogenetic (developmental) processes. Darwinism is generally seen as pertinent to phylogenetic processes only. The reason for this is that it is not clear how the population logic that is at the heart of the Darwinian algorithm applies to ontogenetic processes. In phylogenetic processes, the generational filter of natural selection weeds out the genes of those individuals in the population that come up short in the competition for resources and mates. In biology, individual behaviors are selected, the genes that code for successful behaviors are retained, and populations evolve. It would indeed seem that this population logic is lost when we consider how individuals adapt their behavior during their lifetime. But this is not necessarily so.

The result of the Darwinian algorithm is that organisms become adapted to their environment. Fitness is a measure of how well an individual organism is adapted to its local environment. The fitness of all organisms is in large part the result of the accumulation of adaptations that have been passed on through genetic mechanisms. In other words, their level of fitness is the result of an evolutionary process that has taken place before their lifetime. But many organisms also have an ability to adapt during their lifetime. While obviously constrained by the adaptations that have been passed down through genetic mechanisms, they have an additional ability to evolve successful ways of interacting with their environments through what we call learning. There are different types of learning, which range in sophistication from such simple forms as operant learning, through learning by imitation, to

conscious reasoning and formal instruction. Organisms that possess the ability to learn thus have a second type of mechanism at their disposal to increase their fitness.

In essence, learning is an ontogenetic process, but in modeling its nature the population logic of Darwinism can nevertheless be preserved. This can be seen when we consider how learning leads to an increase in adaptive fit. For this to happen, organisms need to be able to vary their behavior and selectively retain the behaviors that work. Consider the genetic endowment of an organism as an enabler of, and constraint on, its possible behaviors. Seen in this way, each organism has a set of possible behaviors. Learning during an organism's lifetime can then be understood as a way of selecting those behaviors that work under specific environmental conditions. At the most rudimentary level, this may take the form of selecting from a given set of behaviors. But in higher animals with more complex behaviors, it may also involve adding possible behaviors during the organism's lifetime. In each case the Darwinian logic still applies.^{ix} Learning can be understood as the selective retention of specific behaviors in an individual's set of possible behaviors.

Let us refer to an organism's set of possible behaviors as its 'behavioral repertoire'. With this notion the population logic is preserved. To flesh out a Darwinian explanation of learning we furthermore need to specify mechanisms of variation, selection and retention. Let us start by retention. The central question here is what codes for the learned behaviors of an organism. The answer must be found in the neural system, where behavioral dispositions are stored. Next, consider variation. Here the question is how variations in behaviors are introduced. Again, the answer must be found in the neural system where behavioral reactions to environmental stimuli are triggered.^x On this interpretation, it is easy to render learning in Darwinian terms similar to those that apply to phylogenetic evolution: individual behaviors are selected, the neural connections that code for successful behaviors are retained, and the repertoire of behaviors evolves. In Darwinian terms, learning is the differential propagation of behavioral dispositions.

This leaves us with the task to specify mechanisms of selection. Selection refers to what leads to the differential propagation of behaviors, so that the fitness of individual organisms is increased. This brings us back to our main concern of understanding the evolution of socio-economic behavior. Such an understanding requires a definition of socio-economic fitness. Such a definition is most easily given by separating social from economic fitness. Let us define economic fitness as the ability to secure the resources necessary for survival from the natural environment. Let us define reproductive fitness as the organism's ability to pass on its

genes in the reproductive game. Together, these two types of fitness are what drive biological evolution. But when social organization emerges as a solution to the economic problem, and especially when such social organization hinges on more advanced forms of learning, a third form of fitness becomes relevant that we may refer to as social fitness. Let us define social fitness as the organism's ability to secure resources from the social environment. This third type of fitness is especially relevant when the social environment involves scarce resources other than food and mating opportunities. A Darwinian explanation of individual learning needs to show that such socially scarce resources exist.

7. The mechanisms of socio-economic selection

The previous section has shown how individual learning can be understood in a way that preserves the population logic needed for the Darwinian algorithm to apply. But a Darwinian explanation of changes in socio-economic behavior also needs to be clear about the nature of socio-economic selection pressures, and this in turn requires the specification of socio-economic resources that may be scarce. In modern society, money and status are obvious examples of such resources. Modern humans still face the economic and reproductive problem, but the selection pressures of the natural environment have in large part been replaced by selection pressures from our socio-cultural environment that put a premium on an individual's ability to secure money and status. Even though there may be a strong relationship between a person's ability to earn money and achieve social status on the one hand, and his or her ability to secure food resources and create mating opportunities on the other, the type of behavior that leads to success in a socio-economic environment is in many ways different from the type of behavior that would lead to success in the natural world. Complex forms of social organization and highly developed learning abilities thus give rise to a type of selection environment that is fundamentally different from the natural environment that shaped the behavior of our early ancestors.

Positing money and social status as the scarce resources in socio-economic environments opens up the possibility to unravel the nature of the selection pressures that individuals face in such environments. Table 1 presents a first attempt at this essential task for an evolutionary theory of socio-economic change.

Table1: The sources of socio-economic selection pressure

	Economic	Social		
<i>Scarce Resource</i>	Money	Status		
		Group membership	Power	Authority
<i>Selection pressure</i>	Market	Social network	Dominance hierarchy	Expert opinion
<i>Selection Mechanism</i>	Price	Peer pressure	Enforcement	Rules
<i>Instinct</i>	Survival Status	Belonging	Submission	Docility

It proposes that the coordination of individual behavior involves four types of socio-economic selection pressure. The sources of these pressures are markets, social networks, dominance hierarchies, and expert opinions. These four selection mechanisms should be understood as *idealtypen*, in the sense that the specific ways in which social institutions such as the firm coordinate individual behavior will typically involve a mix of the selection pressures associated with each of them.

Let us consider each of the elements of this table in turn. In keeping with the point of departure of the paper, the first distinction in the table is between the ‘economic’ and ‘social’ aspects of socio-economic organization. The second column of the paper captures the traditional concern of economic theory in Darwinian terms by summarizing how market exchange leads to selection pressures on behavior. Money is the scarce resource, and the market exerts selection pressures through the price mechanism. Individuals respond to these selection pressures because of two evolved genetic dispositions, or instincts: their survival instincts and their status consciousness make them look for ways to secure the necessary resources from the environment to survive and establish their status, and in modern environments securing money has become a proxy for meeting both these needs.

But individuals meet their needs in a social context, and economic selection by the market is not the only selection pressure they face. The rest of the table presents an attempt to capture the way in which the social aspect of socio-economic organization leads to selection pressures on individual behavior. The pertinent ‘resource’ in social contexts is status, and money is not the only source of status. The table distinguishes between three additional

sources of status: group membership, power, and authority. Status can become a source of selection pressure when it is scarce. For instance, individuals can derive status from their membership of a group, especially when such membership is more or less exclusive. But group membership also comes with selection pressures on individual behavior from the group as a social network. Within a social network, peer pressure will make certain behaviors more successful than others. Individuals respond to such pressures because their 'tribal instincts' (Richerson and Boyd 2005) make them susceptible to identifying with the group. People have a need to 'belong', and in wanting to belong they will have to adapt their behavior to what is expected from members of the group.

While group membership is a widespread phenomenon in social organization, so are dominance hierarchies within groups. Individuals can derive status from their position in the hierarchy. Note that the source of such status is inherently scarce: the number of high-ranked individuals is limited by definition. Note also that such status is strongly correlated with access to other scarce resources (be it food, money, or mating opportunities). In fact, the status of dominant individuals is directly related to their power to control scarce resources. But the existence of dominance hierarchies within groups is also a source of selection pressures on the behavior of individuals. Given the existence of a dominance hierarchy, certain behaviors will be more successful than others. Higher placed individuals can literally enforce certain behaviors among lower placed individuals. Individuals respond to such pressure because of an evolved instinct to submit to power they cannot overcome (Buss 2004).

Although the previous two social selection mechanisms may have taken on particularly sophisticated forms in human societies, they are in fact widespread in nature. The third mechanism is not. Deriving status from authority requires language and symbolic culture. Whereas status as a result of hierarchical power rests on the ability to enforce control of resources, status as a result of authority rests on knowledge claims. These knowledge claims may take the form of metaphysical claims on the truth (epistemological claims), functional claims on what works (pragmatic claims), appreciative claims on what is worthwhile (esthetic claims), and moral claims on what is good (ethical claims). Such claims are what experts derive their status from. But to the degree that expert opinions are accepted, they also become a source of selection pressure on individual behaviors. Expert opinions establish rules, and specific individual behaviors will be more or less successful given the nature of these rules. Individuals respond to the selection pressures established by expert rules because of an

evolved instinct that Simon (1990) has called docility: the tendency to learn vicariously by accepting the opinion of others.

8. The firm as a socio-economic selection environment

This paper has argued for the need to build theories of socio-economic organization by applying Generalized Darwinism from the bottom-up. Individual behavior should be the starting point of evolutionary theories in economics for both historical and ontological reasons. The paper has furthermore argued that the evolution of individual behavior can be understood in Darwinian terms. Despite its ontogenetic nature, the population logic of Darwinism can be preserved by modeling individual learning as the selective retention of genetically transmitted and culturally learned behavioral dispositions in contexts of scarce economic and social resources. But what are the implications of such an approach for theories of socio-economic organization? Let us consider the contours of a Darwinian theory of the firm that reasons from the bottom up.

Such a theory of the firm would take the behaviors of individuals as its starting point. It would distinguish 'ultimate' and 'proximate' explanations of individual behavior. Ultimate explanations of behavior are given in phylogenetic (evolutionary) terms and take the form of statements about the evolved genetic dispositions (instincts) that drive human behavior. This is the domain of evolutionary psychology, which is rich in findings about universal drivers of human behavior that would allow us to build theories on behavioral assumptions that go beyond bounded rationality and opportunism. Possible examples of such behavioral assumptions are status consciousness, tribal instincts, submission and docility. Proximate explanations are given in ontogenetic (learning) terms and take the form of statements about the evolved behavioral repertoires that drive the behavior of specific individuals. The evolution of behavioral repertoires can be understood as the result of the interplay between genetic dispositions, mental schemes grounded in evolving neural connections, and the specific socio-economic selection pressures that an individual faces.

A firm can then first and foremost be understood as a source of such socio-economic selection pressures. Individuals become members of a firm to meet their socio-economic needs, but in doing so need to adapt their behavior to the specific socio-economic context of the firm. From the point of view of the individual employee, behavior is successful if it helps secure scarce economic (money) and social (status) resources. Both the scarcity of economic resources and social status can be seen to exert selection pressure on the behavior of

employees. This is, for instance, clear from how membership of a firm needs to be secured: employment opportunities are scarce, and employment at certain firms confers more status than employment at others. Moreover, once individuals have become members of a firm, their productive tasks are governed by market mechanisms, reciprocal relationships with peers, authoritative relationships within the context of the hierarchy, and rules established by experts. From the point of view of individuals, these aspects of socio-economic organization represent the selection environment to which they have to adapt. Given the nature of pressures from the market, from peers, from higher placed individuals, and from organizational rules (e.g. promotion criteria) certain individual behaviors will be more successful in securing money and status than others.

In other words, a Darwinian view of the firm from the bottom up would first consider the firm as a selection environment within which individuals compete for economic and social resources. But the existence of firms also introduces an additional level of analysis with its own emergent properties. Just as there is competition for resources between individuals within firms, so there is competition for resources between firms. In this competition, the success of firms depends in large part on their selection of employees and on how well they are able to coordinate the behaviors of their employees towards the goal of securing scarce resources from the environment. The success of such coordination, in turn, depends on the same four mechanisms as discussed above. Firms coordinate the behaviors of their employees through the interplay of price mechanisms, peer pressure, hierarchical enforcement, and organizational rules. Together, these four mechanisms constitute the building blocks of the 'design' of the firm that enables its 'behavior' in interacting with the environment.

On this view of the firm, the question of the socio-economic selection of individual behaviors and the question of the internal organization of the firm collapse into one. From the point of view of the individual employees, the internal organization constitutes the socio-economic selection environment in which they compete for scarce economic and social resources. From the point of view of the firm, its internal organization constitutes a way to retain individual behaviors that contribute to the success of the system as a whole. From the point of view of the individual employee, behavior is successful if it helps secure scarce money and status. From the point of view of the firm, the behavior of individual employees should contribute to its ability to secure scarce resources from its environment in the competition with other firms. The internal organization, or 'design', of a firm can thus be seen as the essential linking pin in a multi-level view of socio-economic organization. In essence,

the firm as a unit of socio-economic organization links within-group competition between individuals to between-group competition between firms (cf. Campbell 1994).

Applying Darwinism from the bottom up can help answer the two questions of a theory of the firm that Nelson and Winter did not address: why do firms exist and how are they organized? Generalized Darwinism shows that questions about the existence of the firm and its internal organization need to be framed in a multi-level selection framework that allows us to understand how the interaction between within-group competition and between-group competition plays out. In answering the question 'why do firms exist', rather than looking for an answer in a comparison of the firm with the market, a Darwinian approach would take a historical perspective and look at how firms first originated and subsequently evolved as a form of economic organization (Stoelhorst, 2005c). As argued in this paper, firms can be seen as a social solution to the economic problem of securing the resources necessary for survival that makes use of cultural transmission mechanisms. The modern firm is, of course, a relatively recent solution to the economic problem, and has been preceded by a host of other social solutions that also made use of cultural transmission. This shows that the firm can only be understood as an accumulation of social design principles that work in relation to the broader socio-economic selection environment in which modern humans deal with the economic problem. Moreover, this broader environment has evolved a number of 'cultural cranes', such as property rights, that have made firms viable. Ultimately, the question 'why do firms exist?' can only be answered by taking into account the historical process by which the design principles of modern societies have evolved.

This brings us to the second question: how are firms organized? Firms are one of the ways in which humans are able to achieve large-scale coordination among individuals that are not genetically related. This ability is unique in the animal kingdom and represents a major transition in the accumulation of adaptive complexity. All major transitions require an explanation of how the new level of selection overcomes competition at the lower level of selection. From a Darwinian perspective, then, questions about the internal organization of the firm have to be answered in terms of an explanation of how firms channel within group competition for resources in a way that allows the group as a whole to be successful in the competition for resources with other groups. This perspective opens up possibilities to unravel the internal organization of the firm in terms of the design principles that create a social selection environment that results in the successful coordination of individual behavior towards a common economic goal. The firm's internal organization is a way to preserve

behaviors that work in light of this goal. In other words, in Darwinian terms, the ultimate causes of the firm's behavior can be found in the accumulation of design principles to channel within group competition in order to coordinate human behavior to deal with the economic problem. The proximate causes for a firm's behavior need to be found in a more detailed understanding of the relationship between the specific design principles found in firms on the one hand, and the specific selection pressures to which they are subjected in their local environments on the other. Such a perspective would combine an interest in universal design principles to achieve large-scale cooperation that play on behavioral dispositions that have been genetically transmitted with an interest in design principles that are specific to the cultural and legal idiosyncrasies of different institutional environments.

9. Conclusion

This paper has explored how Generalized Darwinism can be used to further evolutionary theories of socio-economic organization. Generalized Darwinism holds that the evolution of all open complex systems can be understood in terms of the Darwinian variation-selection-retention algorithm. This algorithm explains how open complex systems become adapted to their local environment, how the variety between them can be traced back to common origins, and how adaptive complexity, or design, accumulates. These explananda also point to the historical and ontological continuity of all evolutionary processes as an essential premise of Generalized Darwinism. The ontological continuity of all evolutionary processes means that Generalized Darwinism should be applied 'from the bottom-up'. The evolution of individual behavior is both the historical and ontological linking pin between biological and cultural evolution and an essential component of understanding why and how such forms of social organization as the modern firm work.

The paper has argued that the theory of socio-economic organization in Nelson and Winter (1982) represents an advance over earlier evolutionary theories in economics in its use of Darwinism, but that it does not yet offer a fully developed theory of the firm. Our current understanding of Darwinism makes it possible to take up the legacy of Nelson and Winter's view of the firm and further develop it in ways that are consistent with their original research agenda. Applications of Generalized Darwinism hold the promise of a third wave of theory development that will strengthen the ontological foundations of evolutionary theory in economics, add to the behavioral realism of our theories of socio-economic organization, and

put within reach an evolutionary theory of the firm that can explain why firms exist, why and how they are different, and how they are organized.

In contrast to extant theory, an evolutionary theory of the firm that applies Generalized Darwinism from the bottom-up would link up with theories of biological and cultural evolution and give individual behavior a central place in modeling competition between firms. The paper has shown that, despite its largely ontogenetic character, the evolution of individual behavior can be understood in Darwinian terms. Such an understanding would preserve the population logic of Darwinism by seeing learning during an individual's lifetime in terms of the evolution of a behavioral repertoire. This evolution takes place as the result of feeding back the results of environmental interactions in a socio-economic context in which an individual faces selection pressures from markets, social groups, hierarchical relations, and expert opinions.

On such a view of the socio-economic selection of individual behavior the firm can be seen as a social solution to the economic problem of securing scarce resources that makes use of socio-economic selection pressures to retain behaviors that work. From a Darwinian perspective, the existence of such a solution needs to first and foremost be understood in terms of how firms channel competition for scarce resources within them in ways that make them successful in the competition for scarce resources with other firms. On this view, the internal organization of a firm can be seen as both a source of socio-economic selection pressures on individual behavior, and as an enabler of its success in securing scarce resources in the competition with other firms. Both the existence of firms and the nature of their internal organization need an explanation in terms of a multi-level selection perspective that links within-group competition to between-group competition. Applying Generalized Darwinism from the bottom up allows us to develop such a perspective in terms of the interplay between universal genetic dispositions, specific mental maps of individuals, and culturally evolved socio-economic selection mechanisms.

Notes

10. References

- Barnard, Chester I. (1938), The Functions of the Executive, Cambridge, MA: Harvard University Press.
- Becker, Markus C. and Nathalie Lazaric (2003), 'The influence of knowledge on the replication of routines', Economie appliquée, 61 (3), 65-94.
- Bowles, Samuel and Herbert Gintis (2003), 'The Origins of Human Cooperation', in: Peter Hammerstein (ed.), The Genetic and Cultural Origins of Cooperation, Cambridge, MA: MIT Press, pp. 429-444.
- Buss, David M. (2004), Evolutionary Psychology: The New Science of the Mind, Boston: Pearson Education, Inc.
- Campbell, Donald T. (1965), 'Variation and Selective Retention in Socio-Cultural Evolution', in: H.R. Barringer, G.I. Blanksten, and R.W. Mack (eds), Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory, Cambridge, MA: Shenkman, pp. 29-49.
- Campbell, Donald T. (1974), 'Evolutionary Epistemology', in: P.A. Schilpp (ed.), The Philosophy of Karl Popper, Vol. 14, I & II, The Library of Living Philosophers, LaSalle, Ill: Open Court Publishing, 14-I, pp. 413-463.
- Campbell, Donald T. (1994), 'How Individual and Face-to-Face Group Selection Undermine Firm Selection in Organizational Evolution', in Joel A. Baum and Jitendra V. Singh (eds), Evolutionary Dynamics of Organizations, Oxford: Oxford University Press, pp. 23-38.
- Cziko, Gary (1995), Without Miracles: Universal Selection Theory and the Second Darwinian Revolution, Cambridge, MA: MIT Press.
- Dawkins, Richard (1983), 'Generalized Darwinism ', in D.S. Bendall (ed.), Evolution from Molecules to Man, Cambridge, Cambridge University Press, pp. 403-425.
- Dennett, Daniel C. (1995), Darwin's Dangerous Idea: Evolution and the Meanings of Life, London: Penguin Books.
- Eldredge, Niles (1995), Reinventing Darwin: The Great Evolutionary Debate, New York: John Wiley & Sons.
- Fehr, Ernst and Urs Fischbacher (2003), 'The Nature of Human Altruism', Nature, 425, 785-791
- Foss, Nicolai J. (1996), 'Knowledge-based approaches to the theory of the firm: Some critical comments', Organization Science, 7 (5), 470-476.
- Gould, Stephen Jay (1997), 'Evolution the Pleasures of Pluralism', The New York Review of Books, June 26.

- Hodgson, Geoffrey M. (1993), Economics and Evolution: Bringing Life Back Into Economics, Cambridge, UK and Ann Arbor, MI: Polity Press and University of Michigan Press.
- Hodgson, Geoffrey M. (2001), 'Is Social Evolution Lamarckian or Darwinian?', in John Laurent and John Nightingale (eds): Darwinism and Evolutionary Economics, Cheltenham: Edward Elgar, pp. 87-118.
- Hodgson, Geoffrey M. (2002), 'Darwinism in Economics: From Analogy to Ontology', Journal of Evolutionary Economics, 12 (3), 259-281.
- Hodgson, Geoffrey M. (2003), 'The Mystery of the Routine: The Darwinian Destiny of An Evolutionary Theory of Economic Change', Revue Economique, 54 (2), 355-84.
- Hodgson, Geoffrey M. (2004), The Evolution of Institutional Economics: Agency, Structure and Darwinism, Routledge, London.
- Hodgson, Geoffrey M. and Thorbjørn Knudsen (2006), Why we Need a Generalized Darwinism And Why a Generalized Darwinism is Not Enough, Journal of Economic Behavior and Organization, 61 (1), 1-19.
- Holmstrom, B.R. & J. Tirole (1989), 'The Theory of the Firm', in: R. Schmalensee R. and R.D. Smilig (eds), Handbook of Industrial Organization, Amsterdam: North Holland, pp. 61-133.
- Klaes M (2004) 'Ontological Issues in Evolutionary Economics', Journal of Economic Methodology, 11 (2): 121-124
- Knudsen, Thorbjørn (2001), 'Nesting Lamarckism within Darwinian Explanations: Necessity in Economics and Possibility in Biology?', in John Laurent and John Nightingale (eds.): Darwinism and Evolutionary Economics, Cheltenham: Edward Elgar, pp. 121-159.
- Knudsen, Thorbjørn (2002), 'Economic Selection Theory', Journal of Evolutionary Economics, 12, 443-470.
- Laland, Kevin N. and Gillian R. Brown (2002), Sense and Nonsense: Evolutionary Perspectives on Human Behaviour, Oxford: Oxford University Press.
- Maynard Smith, John and Eors Szathmary (1997), The Major Transitions in Evolution, Oxford: Oxford University Press.
- Nelson, Richard R (2006), 'Evolutionary Social Science and Universal Darwinism', Journal of Evolutionary Economics, 16 (5), 491-510.
- Nelson, Richard R (1991), 'Why do Firms Differ, and How does it Matter?', Strategic Management Journal, 12, 61-74.
- Nelson, Richard R. (1995), 'Recent Evolutionary Theorizing About Economic Change', Journal of Economic Literature, 33, 48-90.

- Nelson, Richard R. and Sidney G. Winter (1982), An Evolutionary Theory of Economic Change, Cambridge, MA: Harvard University Press.
- Penrose, Edith (1952), 'Biological Analogies in the Theory of the Firm', American Economic Review, 42 (5), 804-819.
- Plotkin, Henry C. (1994), Darwin Machines and the Nature of Knowledge, Harmondsworth: Penguin.
- Richerson, Peter J. and Robert Boyd (2005), Not By Genes Alone: How Culture Transformed Human Evolution, Chicago: The University of Chicago Press.
- Simon, Herbert A. (1990), 'A Mechanism for Social Selection and Successful Altruism', Science, 250, 1665-1668.
- Skinner, B.F. (1981), 'Selection By Consequences', Science, 213, 501-504.
- Sober, Elliot and David Sloan Wilson (1998), Unto Others: The Evolution and Psychology of Unselfish Behavior, Cambridge, Ma: Harvard University Press.
- Stoelhorst, J.W. (2005a), The Naturalist View of Universal Darwinism : An Application to the Evolutionary Theory of the Firm, in J. Finch & M. Orillard, Complexity and the Economy. Cheltenham: Edward Elgar, 127-147. Reprinted in Hodgson, G.M. (2007), *The Evolution of Economic Institutions: A Critical Reader*. Cheltenham: Edward Elgar Publishers.
- Stoelhorst, J.W. (2005b), The Explanatory Logic and Ontological Commitments of Generalized Darwinism, Working paper, University of Amsterdam.
- Stoelhorst, J.W. (2005c) Why Do Firms Exist? Towards an Evolutionary Theory of the Firm, Working paper, University of Amsterdam.
- Stoelhorst, J.W. and Robert Hensgens (2006), On the Application of Darwinism to Economics: From Generalization to Middle-range Theories, Working paper, University of Amsterdam
- Vromen J.J. (2007), Generalized Darwinism in evolutionary Economics: The Devil Is In the Details, Working paper, Erasmus University Rotterdam.
- Winter, Sidney G. (2003), 'Understanding Dynamic Capabilities', Strategic Management Journal, 24, 991-995.
- Witt, Ulrich (1999), 'Bioeconomics as Economics From a Darwinian Perspective', Journal of Bioeconomics, 1, 19-34.
- Witt, Ulrich (2003), The Evolving Economy: Essays On the Evolutionary Approach to Economics, Cheltenham: Edgar Elgar.
- Witt, Ulrich (2004), 'On the proper interpretation of "evolution" in economics and its implications for production theory', Journal of Economic Methodology, 11 (2), 125-146

Witt, Ulrich (2006), 'Evolutionary Concepts in Economics and Biology', Journal of Evolutionary Economics, 16 (5), 473-476.

ⁱ While discussions of the possibility to develop ontological foundations for evolutionary economics on the basis of Darwinism originally referred to ‘Universal Darwinism’ (Hodgson 2002, Stoelhorst 2005a), it has now become customary to use the term ‘Generalized Darwinism’ (Hodgson and Knudsen 2006; Stoelhorst 2005b; Stoelhorst and Hensgens 2006). This term has the advantage of steering clear of Dawkin’s (1983) original use of the term Universal Darwinism for the claim that all life anywhere in the universe would have evolved by way of Darwinian principles. This is a claim within the context of biological theory, whereas the claim here is that core Darwinian principles apply outside biology.

ⁱⁱ This fear is exacerbated by a long tradition of influential critiques of the use of evolutionary theory in the social sciences. An influential critique within economics is Penrose (1952), while Gould (e.g. 1997) is among the natural scientists that would rather confine evolutionary theory to biology. The central argument against the use of an evolutionary view in the social sciences in Penrose and elsewhere is that social evolution is ‘Lamarckian’. However, this does not in any way invalidate the usefulness of the Darwinian framework for developing theory in the social sciences (Hodgson 2001; Knudsen 2001).

ⁱⁱⁱ There is an ongoing discussion of the value of this premise: see for instance the special issues of *Journal of Economic Methodology* (Klaes 2004) and *Journal of Evolutionary Economics* (Witt 2006), as well as Stoelhorst (2005b), Stoelhorst and Hensgens (2006); Vromen (2007).

^{iv} For a critical evaluation of the notion of routines and the analogy of ‘routines as genes’ see Becker and Lazaric (2002), Hodgson (2003) and Stoelhorst (2005a).

^v The reference is to theories of evolution such as sociobiology, evolutionary psychology, gene-culture co-evolution and memetics. For a balanced overview see Laland and Brown (2002).

^{vi} It is interesting to note that while Witt seems to be on par with this part of Generalized Darwinism, he is skeptical about the generality of the Darwinian algorithm of variation, selection and retention (Witt 1999; 2003).

^{vii} Maynard Smith and Szathmary (1997, p.6) present a tentative list of the major transitions in the evolution of complexity, which includes the origin of chromosomes, the origin of the genetic code, the origin of eukaryotes, the origin of sex, the origin of multicellular organisms, the origin of social groups, and the origin of language.

^{viii} Note that what follows is *not* meant to endorse either methodological individualism or methodological collectivism. Both individuals and groups are here seen as units of selection with their own emergent properties that are not fully reducible to lower levels of analysis (viz. genes and individuals). For a discussion of these issues from a Darwinian perspective see Hodgson (2004, chapter 2). What is argued here is that only individuals are endowed with *agency* in any sense that is meaningful to the social sciences. However, the collective behavior of a group of individuals has its own emergent properties, and these properties will typically need to be understood to achieve satisfactory explanations at the level of groups of individuals such as firms. In other words, the claim for only one level of agency does not reduce to a claim for methodological individualism.

^{ix} For the application of Darwinian principles to different types of learning see for instance Skinner (1981) on operant learning and Campbell (1974) on conscious learning. See also Plotkin (1994) for a more general discussion of learning in Darwinian terms.

^x Although an additional point of interest is how intentional reasoning can play a role in directing behavioral variations. More generally, the human ability to build mental models of the environment is an important part of evolving successful behaviors: this both allows adaptability to a wider variety of environments, and a faster way of learning by feeding back the consequences of behaviors into changes to the internal models of the environment.