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REGULAR ARTICLE

Evolutionary developmental economics: how to generalize Darwinism fruitfully to help comprehend economic change

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Abstract Darwinism is shown possible to generalize fruitfully to help comprehend economic change by drawing on evolutionary developmental biology ("evo–devo")—its recent version, less concerned with replication of genes than with genomic instructing of development of organisms. The result is a conceptual model with multilevel applications, generalizing development as instructed self-organizing with inputs from environments, and evolution as experimental search for instructions making the development successful. Its economic interpretation suggests to unite several existing fields into *evolutionary developmental economics*, where economic change can be studied comprehensively as development instructed by actual institutional rules, intertwined with the evolution of these rules.

Keywords Instructed development · Evolution of instructions · Multilevel evolution · Evolution of institutional rules · Development of economies

JEL Classification A10 · D02 · K10 · O10 · P50 · Z10

1 Introduction

There is a broad agreement that no version of Darwinian evolutionary biology is directly applicable to the evolution of human economies and societies. But evolutionary economists still disagree on whether or not *some* generalization of *some* version of Darwinism might nevertheless be helpful. These

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disagreements perhaps most clearly appear in the recent conflict between the generalization of Darwinism elaborated by Hodgson (2002, 2004), Knudsen (2004), and Hodgson and Knudsen (2006a), and the Continuity Hypothesis advocated by Witt (2003, 2004) and Cordes (2006, 2007)—let me refer to the two as HKGD and CH, respectively. While HKGD extracts from biological Darwinism certain notions and principles that its authors claim also to apply to socioeconomic evolution, CH considers Darwinism able to explain the origins of the human cognitive abilities on which this evolution builds, but insists that Darwinism has nothing to do with this evolution itself.

This paper can roughly be situated by its agreements and disagreements with these two sides. It agrees with HKGD that biological evolution and socioeconomic evolution do follow certain common principles that can be regarded as Darwinian, but disagrees with it about what these principles are. And it agrees with CH that socioeconomic evolution is a continuation of the biological one, and that it is indeed not Darwinian in the sense of HKGD, but shows that it does follow certain principles that can be considered Darwinian, provided Darwinism is generalized more suitably than by HKGD.

Rather than criticizing existing generalizations of Darwinism, however, the main purpose of this paper is to suggest one of its own, and illustrate how useful to economists and other social scientists this might be. Its main novelty is to generalize one of the latest versions of Darwinism–the evolutionary developmental biology ("evo–devo") following Carroll (2005) and Carroll et al. (2008). Compared to the standard neo-Darwinian synthesis, the basis of previous generalizations, this version extends attention in three directions: (1) from genes to entire genomes, (2) from how genomes replicate to how they instruct, with uses of inputs from environments, the forming and development of organisms; and (3) from fully developed organisms to the entire developmental process.

All of this makes Darwinism easier to generalize for the needs of social scientists. Extension (1) makes it unnecessary to search for an exact socioeconomic correspondent to a single gene. This is a great relief, as no such search has been very successful, and one may doubt that it might ever be. Instead, evolutionary social scientists only need to realize the prime importance of genomic instructions, but may think of them in broader terms than those of genes coding for proteins—now known not to be the only important parts of genomes (see e.g. Mattick 2004).

Extension (2) allows principles of Darwinism to apply to socioeconomic change without replicating. The change must only use some evolving instructions that guide, at each stage of their evolution, some developmental process. This also makes it clear that the main products of evolution are instructions, whereas replicating is only one special way of their storing over time—obligatory in biological evolution, where the storing must rely on short-lived organisms. For evolutionary social scientists, this is another relief, as much of socioeconomic change takes place without replicating. More often than not, economies and societies form, develop, evolve, further develop, evolve, or possibly fall, as childless singles.[1]

Extension (iii) makes it clear that development is an inseparable but distinct companion of evolution, with plenty of room for all the phenomena that are undeniably part of the forming and functioning of organisms, yet difficult to accommodate within evolution itself–such as cooperation, altruism, and self-organization. In economics, as shown below, the logic of this extension may help to interconnect evolutionary, institutional, and development economics into a single well-ordered field of *evo–devo economics*, where all the important parts of economic change have their well-defined and clearly interrelated places.

All three extensions converge on an important point: the central role of instructions. These form the link between evolution and development, and provide the main reference for distinguishing the two. In a first approximation, the distinction may roughly be put as follows: *Evolution produces instructions for guiding development.*

Attention to instructions also leads to a new promising direction for analysis, starting with the logically obvious, but so far little exploited principle: *all uses of instructions require pre-existing instructions.* It is from this principle that an interesting constraint on what evolution can, and what it cannot, achieve will be deduced.

Emphatically, however, the central role of genomic and other instructions has nothing to do with genetic determinism. In addition to involving also other parts of genomes than genes, it fully admits the importance of inputs from environments. It will only lead to the conclusion, deduced from the basic logic of information processing, that genomic instructions are primary: the inputs must initially be prepared and are ultimately limited by them. Thus, without determining what exact features an organism will actually develop, its genome will nevertheless be found to set strict limits to what these features might, in the most ideal environments, possibly become. In other words, each genome will be seen to imply a certain developmental potential that environments can more or less actualize, but never expand. But this may perhaps be described as "genomic limitism," not "genetic determinism."

[1] The emphasis on replicating is an important reason why HKGD is of so little use in the social sciences. In this respect, Campbell's (1965) early generalization of Darwinism in terms of "variation, selection, and retention" is wiser: the biology-loaded notions of "inheritance" and "replication" are there carefully avoided. This makes it hard to understand why Hodgson and Knudsen insist on building on these notions, and even misquote Campbell as if he also used them. Hodgson (2004), for instance, contains two such misquotes: "variation, inheritance, and selection" and "replication, selection, and variety-creation." Both moreover ignore Campbell's sound logic with which he puts "selection" before "retention"—as, logically, whatever is retained must have first been selected—and put instead "replication" and "inheritance" before "selection."

To be as concise as possible, the present generalization of Darwinism will be given the form of a conceptual agent-based model. This will provide it with a solid micro-basis and establish a well-defined link to methodological individualism in the social sciences. That HKGD has no clear micro-basis appears to be another reason, in addition to its misplaced focus on replicating, why it is so short of meaningful socioeconomic applications.

Concerning such applications, the present generalization has an inbuilt advantage. In contrast to HKGD, which stems from the highly abstract spheres of ontology and philosophy of biology, this one was taking shape during inquiries into the more mundane issues of comparative economics, economic reforms, and transformation policies (Pelikan 1988, 1992, 2003a). While it is thus guaranteed applicable at least to these issues, this paper will illustrate that its economic applicability is much broader.

Emphatically, generalizing Darwinism is not claimed to be the only way to understand economic change. That this understanding may also be sought with purely economic tools is fully admitted. The choice is free, depending on what one hopes to find with these tools, and how much interested one is to learn new things from other disciplines. This paper is addressed to those economists who are interested in such learning.

The rest of the paper is organized as follows. The general agent-based model is described in Part 2, its possible economic applications, including a rough outline of the new field of evolutionary developmental economics, are discussed in Part 3, and its possible usefulness for other social sciences is briefly noted in a concluding comment.

2 The origins of successful complex agents: a general evo–devo model

2.1 The overall plan

The main task of the model is to depict the processes by which given basic agents (b-agents) in given environments can form, develop and operate a complex agent (C-agent) successful in these environments. While dealing with only one level of such processes, the model is recursively applicable to many of their levels, both biological and socioeconomic—including cells that form and operate organisms, and individuals who form and operate economies and societies.

With one important exception, what needs to be kept in mind about the agents and the environments may be summarized as follows:

The given b-agents may be heterogeneous, of different abilities and behaviors.

The environments of each b-agent include parts of the common environments and some of the other agents.

Each C-agent is a network of b-agents, which play there possibly different roles, and thus interact with each other and with the environments in possibly different ways.

The environments test the performance ("fitness") of the C-agents according to non-specified success criteria. These may, but need not, be those of natural selection, and the environments may, but need not, include competition and/or cooperation with other agents.

The b-agents' behaviors are of two dimensions: (1) *associative*, which they use to self-organize into, and find their roles within, a certain network, and thereby form their C-agent; and (2) *operational*, which they use to operate in the roles found, and thus enable the C-agent to operate and perform. The network may also aggregate their associative behaviors, and thus enable the entire C-agent to behave associatively in relation to other agents.[2]

An agent's behaviors may be more or less goal-oriented (purposeful, intentional), more or less responsive to inputs from the environments and other agents, and more or less learning from these inputs and adapting to them.

That the model is reductionist, but not naively so, deserves emphasis. No C-agent is reduced to a "simple sum" of its b-agents. What a C-agent is and does also depends on the network into which its b-agents have self-organized. It is thanks to this network that the C-agent's behaviors may be more complex than the behaviors of any of them. For instance, the C-agent may pursue objectives, conduct trial-and-error searches, learn, and develop self-awareness—while none of its b-agents may be able to do any of that.

Moreover, the network may in return influence the b-agents' behaviors—although, emphatically, only within the limits of their intrinsic abilities to allow it. It is only that no C-agent is allowed to fall as a holistic mystery from the sky, but each is required to originate with some b-agents forming its initial network. Only then can the network start to influence, under the constraint of their intrinsic malleability, the b-agents' behaviors, while they may respond by helping the network, some possibly more than others, develop and evolve.

2.2 Instructions and the ultimate constraint on their uses

The important exception that needs more than a brief mention in a summary, is that all behaviors of all agents are guided by instructions, arranged into more or less complex programs. This also means that all features of an agent's behaviors—including the above-mentioned intentionality, responsiveness to inputs, and learning—need corresponding instructions for their realization.

[2]Distinguishing the two dimensions of agents' behaviors, and considering both, appears to be the only way to clarity about the link between self-organization and Darwinism. That most authors deal with only one of these dimensions, while leaving aside the other, may well be why this link has not yet been fully clarified. For instance, most economists limit attention to how economic agents operate within an already organized economy, while most of the authors studying self-organizing—such as Camazine et al. (2001), or Doursat (2008)—limit attention to the architecture of the networks that given self-organizing agents will form, without studying how these agents and the entire network will then operate.

With this link between agents and instructions, it is possible to make the above distinction between evolution and development more precise: *Evolution produces instructions for the development of a C-agent by guiding the self-organizing and operating of its b-agents.*

But to get it right, the term "instruction" must be understood more broadly than in computer programming. An instruction may prescribe a certain operation, but it may also mean a constraint ("negative rule," "rule-of-the-game") that only specifies a more or less broad variety of permissible actions. Instructions-constraints may thus be combined with each other by logical intersection, each excluding a more or less different subset of an agent's feasible actions, and then combined with instructions-for-operations, which lead the agent to take a specific action within the remaining subset.

Illustrations can be found in games and chemistry. In a game, both its general rules and the specific ways of playing it are seen to consist of instructions. In chemical reactions, instructions are seen in the valences that guide atoms to form molecules with certain atoms, and not others.

It is also important to realize that programmed behaviors need not be mechanistic, purposeless, deterministic and uncreative—as many social scientists used to believe. For this, it suffices to consider advances in two disciplines: in computer programming, which can make computers behave purposefully, search, learn, innovate and be "aware" of their activities; and in neurophysiology, which makes it increasingly clear that all human thinking and behaviors are governed by what may be understood as programs in human brains.

An important kind of instructions that are commonly used in computer programming and appear widespread in brains are those for generating and using what may be called "random signals." These need not be random in the absolute sense that they would lack definite causes, but only in the sense that they are uncorrelated with the problems to be solved. They are important for avoiding deadlocks in decision-making with incomplete information, and for conducting trial-and-error searches, both in brains and in nature.

The main result of studying the agents' instructions is the finding of an important ultimate constraint. This follows from the principle that all uses of instructions require pre-existing instructions, applied to the fact that an agent's actual instructions can only be of three origins: (1) initial endowment; (2) received from environments; (3) elaborated by own learning. The principle implies that acquiring new instructions—be it from environments or by own learning—also requires pre-existing instructions. While these may also be partly received and/or learned, also this required pre-existing instructions. The constraint, easy to deduce by simple recursive reasoning, is: *For each agent, the development of its actual instructions must start with, and is ultimately constrained by, its initial instructions*.

A minor complication is that "initial" is relative. In part, it is relative to the agent considered. Thus, many initial instructions of a C-agent may be younger than those of its b-agents. The b-agents may have obtained them later, for the specific forming of that C-agent, with the help and under the constraint of their older initial instructions.

In part, what is "initial" may also depend on our choice of $t = 0$, the beginning of our inquiry. The agent considered may have started its development earlier, from some truly initial instructions, so that its initial instructions at the chosen $t = 0$ also include all the other instructions that it has received and/or learnt in the meantime, with the help and under the constraint of the truly initial instructions. For instance, when considering a young person starting a school, the initial instructions that limit what the school might possibly teach her include both her inborn talents and the ways in which these talents have been developed, or inhibited, by her education and experiences up to that time.

Interestingly, the ultimate constraint suffices to refute the not so long ago widespread belief that a human individual is a blank slate ("tabula rasa"), on which anything can be written by society.[3] It also helps to settle the still lasting debate whether it is a person's genome ("nature"), or her experiences and education ("nurture"), that determine her cognitive abilities (intelligence, rationality). While both are now widely recognized to matter, how exactly they cooperate is still disputed. The constraint makes it clear that "nature" determines a certain development potential, which "nurture" can more or less actualize, but not expand. The cognitive abilities are thus no simple sums of "talents *plus* experiences and education," where more of the latter could compensate for less of the former. Quite to the contrary, more of the latter, to be properly interpreted and used, requires *more* of the former.[4]

The key implication is that a certain minimum of an agent's instructions must always be initial, embedded in its internal set-up ("hardware"). For some agents, these instructions may be so simple that they are all the instructions that the agents may ever possess. Abilities to obtain additional instructions—from other agents, or by own learning, or both—require more complex initial instructions. The greater these abilities are to be, the more complex initial instructions are required.

All this implies that b-agents can be classified into two categories: *programmable*, able to receive and follow additional instructions, and *non-programmable*, limited to their initial instructions, plus possibly those that the initial ones are programmed to develop with time. This classification will be important for understanding the possibilities of evolution.

2.3 How the given b-agents may form, develop and operate a successful C-agent

The given environments are assumed moderately hospitable, to allow some, but not all, of the feasible C-agents that the given b-agents might possibly form

[3] A more extensive refutation of this belief is in Pinker (2001). What may be helping today's social scientists to see its absurdity is their growing use of computers. This makes it indeed crystal-clear even to the most non-technical of them that there are no ways of instructing and informing an empty box.

[4] This largely agrees with Ridley (2003), with the exception of the title: instead of "Nature via Nurture," more logical here appears to be "Nurture via Nature."

to be successful ("fit"). Clearly, if the environments were less hospitable, no evolution and development could take place, and if they were more hospitable, so that all of the feasible C-agents could succeed, there would be no interesting problem to study.

In such moderately hospitable environments, the given b-agents need suitable instructions, able to guide them to form, develop and operate one of the successful C-agents, and steer clear of all of the unsuccessful ones. To visualize how they may proceed, recall the two dimensions of their behaviors, for which they need the corresponding two dimensions of instructions. The associative ones guide their self-organizing to form a certain network, where each finds a certain position, while the operational ones guide their acting and interacting in the positions found. But the two dimensions need not be sharply separated in time. Stages of self-organizing and operating may overlap or alternate with each other.

The instructed self-organizing, by which the b-agents form and develop their C-agent, proceeds by their selectively establishing, following their associative instructions, certain connections with certain neighbors, while refusing other connections and other neighbors. Their instructions may not be fully informative, but may require uses of random signals for trial-and-error searches, during which connections can be made, unmade and re-made. In some cases no stable C-agent may ever form. For a successful C-agent, however, the development must converge to a stable network, or at least to a stable envelope of networks, within which the actual one may vary in function of states of environments.

The self-organizing may be classified into different types, in which different b-agents play more or less different and more or less differently important roles. The types may roughly be divided into "homogenous" and "diversified," these into "decentralized" and "hierarchical," and these into "multicenter" or "centralized."

The common feature of all hierarchical self-organizing is that some b-agents are there leading organizers, associatively more active and more selective than others—such as enzymes in the development of organisms, or entrepreneurs in the development of economies. Different mixes of cooperation with competition may be used for their selection. But this is only one special kind of competition that may take place as part of the development of a C-agent. A suitable label for it is therefore "developmental."

Which type of self-organizing will actually take place depends again on the b-agents' instructions. Thus, how cooperative or competitive the self-organizing will be depends on their instructions for choosing between cooperative and competitive behaviors, possibly in response to inputs from environments and other agents. Whether or not the self-organizing will be hierarchical depends on whether the agents are homogenous or heterogeneous. Hierarchies most likely arise if they heterogeneous, but may also arise if they are homogeneous and highly competitive. Then, however, it is possible to put in doubt their homogeneity, and admit that their abilities may differ in hidden, difficult to observe ways that only competition can reveal.

Whether or not the resulting C-agent will succeed at its environmental performance tests most directly depends on its operating, which is an aggregate of its b-agents' operating. But, as the ways of the aggregating are determined by the network into which the b-agents have self-organized, the C-agent's success also depends, less directly but not less importantly, on their associating.

To clearly see that the C-agent's success depends indeed on both, consider the two reasons why it might fail: (1) its b-agents' operating could make it successful, but only if they were put into a suitable network, into which they are unable to self-organize themselves; (2) they are able to self-organize into a network where other, more suitably operating b-agents could make it successful, but are unable to do so there themselves.

The crucial problem of development can be put as follows: *How to make the b-agents adjust their associating to their operating abilities, to prevent their network both from overtaxing these abilities and from leaving them too underexploited?* Clearly, if overtaxed, the C-agent would fail because of the b-agents' operating errors, and if too underexploited, it could only succeed in easy environments, but fail in more difficult ones—although in many of these it might still succeed, had only its b-agents self-organized into a more suitable network that would exploit their operating abilities more efficiently.

Much like self-organizing, networks can also be classified into different types, where different b-agents occupy more or less different and more or less differently important operating positions. The types may also be divided into "homogenous" and "diversified," these into "decentralized" and "hierarchical," and these into "multicenter" and "centralized." Hierarchical networks also make some b-agents leading—such as brains in organisms and managers in firms. But these are leading operators, which may differ from leading organizers, while the type of the network may also differ from the type of the self-organizing that produced it. For instance, a multicenter ontogeny may produce an organism with a central nervous system, while centralized entrepreneurship may produce a decentralized firm.

The operating of networks may also use different mixes of cooperation with competition, but this is another kind of competition, suitably denoted as "operational," different from the earlier considered developmental one. A clear economic example is the price competition among established firms, different from the Schumpeterian developmental competition for the establishment, growth, and survival of firms.

2.4 Evolution as the search for, and producer of, needed instructions

Two points should be now reasonably clear: (1) what the b-agents must do to form, develop and operate a successful C-agent, and (2) that for doing all this they need suitable instructions. The next question is: how can such suitable instructions be obtained?

In principle, as noted, the answer is: by evolution. But this cannot help all b-agents. If they are non-programmable, they have no room for any additional instructions that evolution might produce. They may form, develop and operate a C-agent only as pre-programmed by their initial instructions, and may thus succeed only if these instructions happen to be suitable. Let me say that such agents constitute a "self-assembling puzzle."

Importantly, the puzzle need not be limited to a single solution. The instructions may admit certain inputs from environment, and thus lead to different solutions in function of these inputs. But they must then pre-program the variants, the admissible inputs, and the function.

Evolution may only help b-agents that are programmable, with sufficiently complex initial instructions that admit a certain variety of additional instructions—somewhat like a complex hardware that admits a certain variety of software. Let me say that such agents constitute a "programmable construction set."

The admissible variety of additional instructions is the window within which evolution can work and to which it is limited. Success is possible only if this variety includes some suitable instructions, and if evolution proceeds in ways that can sooner or later find them.

As the admissible variety of additional instruction is determined by the b-agents' initial instructions, their relation to evolution can be summarized as follows: *Given b-agents in need of suitable additional instructions, the possibilities of evolution to help them are constrained by their initial instructions.*

Note well that in this evolution, the b-agents are given and only their C-agents are in question. It will be the task of the following section to consider that the b-agents may be C-agents of a lower level with initial instructions produced by a lower-level evolution. As a first step to understanding this complication, think of ants and humans. Biological evolution has produced the initial instructions for both, but socioeconomic evolution may only work with humans. Ants constitute socially non-programmable self-assembling puzzles, which may form, develop and operate successful societies only if their biologically evolved initial instructions prove suitable even for this purpose. In contrast, thanks to their more complex initial instructions, humans constitute programmable constructions sets with both a large room and an urgent need for additional instructions from socioeconomic evolution.

All types of evolution must use random signals, random in the above-mentioned sense: they may have deterministic causes, but they lack information on what instructions may be suitable. Without this information, the only way to success is a trial-and-error search, in which random signals are needed for triggering the trials.

Such a search may vividly be described in Campbell's (1965) classical terms of "variety, selection and retention." Random signals may be said to choose instructions from a *variety* of possible instructions; the b-agents use them to try to form, develop and operate corresponding C-agents, and these are tested by the environments. If the C-agents succeed, the instructions are *selected* and *retained*, if not, they are rejected.

That in the present model, evolution select and retains instructions, and not C-agents, deserves emphasis. The performance ("fitness") of C-agents is important, but only as a proxy through which their instructions take part in evolutionary competition. This is the third kind of competition, reserved to instructions, which must be distinguished from the earlier noted developmental and operational kinds among the b-agents within their C-agent.

The present model thus disagrees with the old but still widespread view of evolution as selection of organisms, but is fully in line with the modern view that the main products of evolution are genes and genomes. It also agrees, although with a qualification, with Dawkins's (1976) argument that in Darwinian evolution the units of selection are genes and not organisms. Since genes are special cases of instructions and organisms are special cases of C-agents, the agreement is with the exclusion from evolutionary selection of the latter. The qualification is that the units are not limited to single genes, but admitted to include unions of several genes and sequences of non-genic DNA.

For evolution to proceed, at least some of the b-agents must possess, in addition to their instructions for associating and operating, also instructions for making and spreading, with the help of random signals, trials with new instructions—such as a genomic mutation, or an institutional change. Each new trial typically originates in a single b-agent, from which it may spread by lateral communication and/or by inter-generational transmission (inheritance).

Biological evolution mostly uses the latter way. The b-agents (cells) of a C-agent (organism) are there usually offspring of the cell in which a new trial originated. But lateral communication is not entirely absent: in some populations of bacteria, a gene that one of them happens to find to provide defense against an antibioticum may rapidly spread to many of its neighbors. In socioeconomic evolution, new instructions spread both laterally, among the actually present individuals, and from one generation to the next.

The present model admits that the evolutionary trial-and-error searches may proceed both in parallel, involving many different short-lived C-agents, as in the evolution of life, and in a time series using a few long-lived C-agents, as in the evolution of economies and societies. Moreover, to be applicable to socioeconomic evolution, it also admits that past trials may produce relevant information that affects the probabilities of future trials. As long as the relevant information is not complete, however, some random signals are still needed, although the trials themselves then become probabilistic, rather than entirely random. That this means to admit elements of Lamarckism does not seem to be a problem. Following Nelson and Winter (1982)—with the notable, but for me difficult to understand exception of Hodgson and Knudsen (2006b)—most of evolutionary economists appear to agree that in this sense, socioeconomic evolution is indeed partly Lamarckian.

2.5 Levels of evolution vs. levels of development

The basic difference between evolution and development should now be clear, but a few points may need additional clarifications. The reason is that several key terms—in particular randomness, competition and selection—make sense in the context of both, but in different meanings. Much confusion has been caused by not distinguishing the two. The distinctions that are most important to realize may be summarized as follows.

Trials generated with the help of random signals play important roles in all evolution and in some development. But the former consist of tentative instructions, and the latter of tentative self-organizing of b-agents during the development of their C-agent guided by its actual instructions. In biology, this is the difference between mutations of genomes, and the possibly tentative attempts of cells to find their places in their organism during the genomically guided ontogeny. In economics, as considered in more detail below, this is the difference between changes of institutional rules, and attempts of entrepreneurs to form firms and introduce technological innovations under the actual institutional rules.

The main difference between the evolutionary and the developmental kinds of competition and selection is, as noted, that the former take place among instructions and the latter among b-agents. This difference is particularly important for the issue of cooperation. As clarified below, developmental competition may be replaced by cooperation to a larger extent than evolutionary competition.

A tricky issue that may appear to challenge the present model is the one of epigenetics, concerning inherited changes in features of organisms caused by mechanisms other than changes in DNA. As this issue is of little interest to economists, let me just mention the key to coping with it. This is to further extend the biological meaning of the term "instructions" beyond genes and genomes to the non-DNA factors that may also help to govern the gene expression. An organism's instructions can then be seen to form hierarchies, where higher-level instructions help govern the uses of lower-level instructions. While many of these levels may consist of DNA itself, what epigenetics points out is that they may also include some non-DNA factors. But in the present model, these are also instructions.

A particularly tricky issue is the one of multilevel evolution and multilevel selection. This one evolutionary economists need to understand, while not even biologists appear to be entirely clear about it. What allows the present one-level model to help is that it can embrace several levels by recursive applications. Except for what is defined as the lowest and the highest levels, it allows b-agents to be modeled as C-agents of a lower level and their initial instructions as products of some lower-level evolution, and C-agents as b-agents of a higher level which, thanks to their initial instructions, are more or less able to form, operate and develop C-agents of a higher level. The help comes from its four elementary, but often neglected conceptual distinctions: (1) between evolution and development; (2) between instructions and agents, (3) between initial and additional instructions; and (4) between self-assembling puzzles and programmable construction sets. What these distinctions help to clarify can be summarized as follows.

There may be more levels of development than of evolution. This is because evolution needs programmable construction sets, whereas development may also take place with self-assembling puzzles. Some levels of development may therefore lack evolution, while one level of evolution may produce instructions for several levels of development.

As an example, think again of ants and humans. In both cases, their biologically evolved genomic instructions suffice for several levels of development—from proteins through cells to individuals. Each of these levels can be understood as a self-assembling puzzle with possibly several solutions, as directly or indirectly programmed by the genomes. Ultimately, however, ants are genomically programmed to constitute socially non-programmable self-assembling puzzles, so that no higher-level evolution can take place. In contrast, humans are programmed to constitute socially programmable constructions sets, for which a higher-level evolution is both possible and necessary. Perhaps the schematic Fig. 1 may help to visualize this apparently complicated situation.

For clarity on multilevel selection, the main help comes from the distinction between the evolutionary selection of instructions and the developmental selection of b-agents for positions within their C-agent. This makes it possible to see the key dependence of the latter on the outcomes of the former. As the instructions selected by evolution guide the development of the C-agent, they also determine what competition and selection of its b-agents, if any, this development will employ. As development may have more levels than evolution, developmental selection may also have more levels than evolutionary selection. In nearly all biology, the former may have many levels, but the latter only one: the evolutionary selection of genomic instructions.

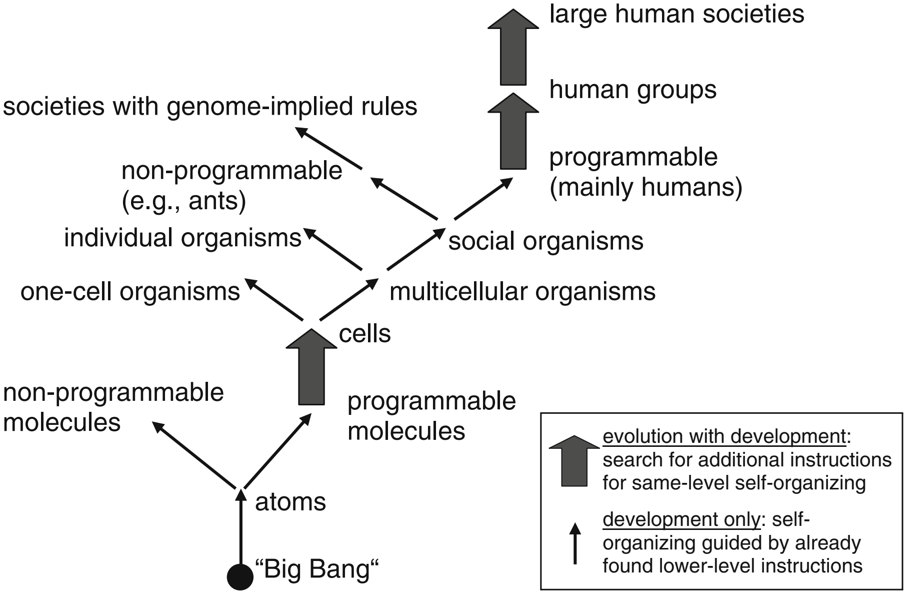

Fig. 1 A schematic survey of levels of evolution and levels of development

Evolutionary selection that has more levels, as in the case of humans, raises a new question: which instructions will be rejected, if the highest-level C-agent—such as a national economy—fails its performance tests? The first victims will always be the highest-level additional instructions. Their fault is not to lead the highest-level b-agents (= the next-to-the-highest-level C-agents) to make the highest-level C-agent successful. But this is may not be the end of the story. It may also be the fault of the b-agents' initial instructions not to make enough room for evolution that could find in time suitable highest-level additional instructions. Next victims may therefore be the b-agents' initial instructions.

Another new question is: how do the different levels of evolutionary selection influence each other? Important examples of such influences can be found in the literature on gene–culture co-evolution concerned with links between socioeconomic evolution and the biological evolution of human genomes (for a recent account, see Laland et al. 2010). The general principle can be summarized as follows. To recall, the instructions of the b-agents forming a C-agent consist of two parts: (1) their initial instructions, and (2) the additional instructions for this forming. Each part has its own level of evolution, which may at first be independent. But once the C-agent is formed, it may internally modify the success criteria for its b-agents, and thus modify the evolution of their individual instructions. These in turn may influence its further development and performance, and through it the evolution of the additional instructions. For more on this question, see Section 3.2 below.

2.6 Cooperation, altruism, and group selection

These three often debated notions have two things in common: their roles in evolution are still far from clear, and Darwinism has been claimed unable to accommodate them. To show that the present evo–devo model can both accommodate them and clarify a few points about them is therefore a strong argument in its favor—and a nice way to wrap up Part I.

The main problem with these notions is that they are used in different meanings, not always properly distinguished from each other. The model need not do much more than bring the relevant distinctions to light, and most of the missing clarity immediately appears.

The two possible meanings of cooperation and altruism are: (1) among instructions, (2) among the b-agents of C-agent. The conceivable third meaning, among free C-agents, need not be considered separately. Cooperating or altruistically interacting C-agents may formally be defined as b-agents of a higher-level C-agent, and thus included in meaning (2).

Cooperation is admitted in both meanings, but in meaning (1) only among instructions specialized in *different types* of b-agents' activities. Such instructions must indeed cooperate to guide all the different actions that b-agents must take to develop and operate a successful C-agent. But *alternative* instructions specialized in the same type of b-agents' activities may only compete: in each C-agent, only one can rule. As noted, their competition uses their C-agents as interposed heroes, whose performance success imply their evolutionary success.

Cooperation (2) is accommodated without restrictions, and admitted to mix with competition in many ways and degrees. How much, or how little, the b-agents will cooperate depends on their instructions of both dimensions. Their operational instructions are responsible for how cooperative each of them will be in response to the conditions they face within the C-agent's network, such as the incentives for cooperating vs. those for defecting. Their associative instructions are responsible for the network, and thereby for the conditions.

But, how cooperative the b-agents will be made by their instructions is only one side of the story. The other side is, how cooperative they must be to allow their C-agent to succeed. This depends in part on the distribution of their abilities, and in part on the severity of their environments. If these are severe and they are heterogeneous, the C-agent will need to develop efficient hierarchies, which will require a certain minimum of competition among them for leading positions. But if they are homogenous, no competition is needed: all of their permutations are equally good. As all competition is costly, success in severe environments will on the contrary require a maximum of cooperation.

The problem for evolution is how to make the two sides meet—that is, how to find suitable instructions that would make the b-agents combine cooperation with competition as required for their C-agent's success. As explained, a solution may exist only if the b-agents constitute either a self-assembling puzzle, with all the needed instructions already produced by their lower-level evolution, as in the case of ants, or a programmable construction set with instructions that would allow a higher-level evolution to find in time some suitable instructions of the higher level, as we must hope is the case of humans.

While there are many features that altruism shares with cooperation, there is also an important difference: cooperation is admitted in both meanings, but altruism only in meaning (2). In other words, both agents and some instructions may cooperate, but only agents may be altruistic to each other. The only relation to altruism instructions may have is that, to make their C-agent successful, they may have to prescribe much of altruism (2) for its b-agents. But they are always selfish in the sense in which Dawkins (1976) shows genes to be selfish.

Altruism (2) is not only admitted, but recognized to be often necessary for a C-agent's success—and thereby for its b-agents' success, to the extent to which this depends on the C-agent's success. The instructions may prescribe altruism directly, as for ants, or conditionally, as for humans, but no agent can be altruistic without instructions for it.

Altruism (2) thus raises similar problem for evolution as cooperation (2): how to endow the b-agents with instructions that would make them as altruistic as required for their C-agent's success. There are also similar conditions for a solution to exist: the b-agents must constitute either a self-assembling puzzle, with all the needed instructions already evolved, or a suitably programmable construction set, allowing a higher-level evolution to produce them.

A particularly important factor, on which the actual level of altruism strongly depends, is the C-agent's defense against selfish b-agents—such as cancer cells in an organism, or free-riders in a society—realized by the b-agents' self-organizing. Obviously, it will be easier to attain the required level of altruism if selfishness is punished and eliminated rather than tolerated and rewarded. Taking such a defense into account qualifies and extends the propositions by which Wilson and Wilson (2007) summarize their argument: "Selfishness beats altruism within groups. Altruistic groups beat selfish groups." The qualification is that selfishness beats altruism only in groups without an effective anti-selfishness defense. The extension is that altruistic groups with such a defense beat altruistic groups without it.

To clarify the issue of group selection, the first step is to understand "groups" as C-agents and specify their b-agents. The key distinctions are: (1) between free C-agents and subordinate C-agents that are b-agents of a larger C-agent; and (2) between fully instructed b-agents, constituting a self-assembling puzzle, and b-agents in need of additional instructions, constituting a programmable construction set.

In general, as the model excludes evolutionary selection of agents, it also excludes evolutionary selection of groups as such. Evolution can only select instructions that enable given individuals (b-agents) to form, develop and operate successful groups (C-agents), but not the groups themselves. In the two-level case, however, the model admits *developmental* selection of lower-level groups (subordinate C-agents) for positions within the higher-level group (larger C-agent)—such as selection of firms for positions within the national economy.

The evolutionary selection concerning groups is thus limited to their instructions, but admitted to have several levels. There is always the level selecting the initial instructions of the group members (the lowest-level b-agents). For groups of organisms, this is the level of phylogeny, selecting the organisms' genomes. These genomes determine what groups, if any, the organisms will be able to form, develop and operate. For fully instructed organisms, like ants, this is the only level. Only for organisms that have genomically provided room for additional instructions may evolutionary selection concerning groups (but not *of* groups!) have more than one level. It is such organisms that the rest of this paper is about.

3 Evolutionary developmental economics

3.1 A simple evo–devo model of economic change

To build an evo–devo model specialized in economic change, the notions of the general model must first be given a clear economic meaning. To convey the main ideas, it suffices to include agents of three levels: individuals, economic organizations, and economies. Individuals are b-agents of the lowest level. The organizations—understood very broadly to include households, firms, governments agencies, and markets[5]—are C-agents for individuals and b-agents for economies. These are the C-agents of the highest level: their b-agents may be individuals, or organizations, or both.

The corresponding instructions are of four levels, starting with human genomes. These provide a large, but not unlimited room for three levels of additional instructions with the corresponding three levels of socioeconomic evolution. In the short run, human genomes may be viewed as stabilized outcomes of purely biological evolution and natural selection. In the long run, however, they must be admitted to continue to evolve, and their selection to be increasingly artificial rather than natural, shaped in a feedback fashion by the very economies and societies that they have made possible to form and develop.

The three levels of additional instructions are termed "cultural," "organizational," and "national." The cultural level contains the first additional instructions that individuals receive during their education, before they enter into what may be defined as their "economic life." In economic analysis, the cultural and the genomic instructions may often be considered together as sources of individual preferences, values and cognitive abilities ("rationality")—in part for individual decisions, and in part for the understanding and respecting of social rules.

The instructions of the organizational and national levels, the domain proper of economic analysis, are termed "institutional rules." They may be visualized as "the rules of the game" that constrain and shape the acting and interacting of individuals within the corresponding organization or economy. Such rules may be formal, produced by specified rule-makers, and/or informal, consisting of widely imitated contributions of anonymous institutional innovators.[6]

In no economic C-agent—neither in a firm, nor in an economy—do its institutional rules fully determine how it will develop and perform. There nearly always leave a large room for their different interpretations by different individuals in different environments. Yet they do specify many of the C-agent's features—such as the form of corporate governance for a firm, or the extent of government policies for an economy. They thus also indicate where, in the popular classification of economies into different types of capitalism, welfarism, etatism, and socialism, the economy may best be placed. Last but

[5] Why markets are counted as organizations is that they, too, may be viewed as C-agents containing networks of b-agents. They may also be ascribed objectives—such as seeking equilibrium prices—even if these may not be the objectives of any of their participants, and may never be fully attained.

[6] The term "institutional rules" means what North (1990) defined as "institutions." While I like North's word-economizing terminology and also used it in Pelikan (2003a, b), it has proved to have a major flaw: not even after twenty years has it been generally adopted. Many economists continue to call "institutions" also large organizations, and some even such disparate things as routines, money, and languages. It is this continuing ambiguity of the term "instructions" that induced me to return to the longer term I used in Pelikan (1988, 1992).

not the least, they constitute a crucial constraint on the C-agent's performance and development: they imply a limit to what the firm or the economy might ever achieve in the most favorable environments.

Like genomes in evo–devo biology, institutional rules constitute the interface between economic evolution and economic development: they are the products of the former and instructions for the latter. Each of their levels has its own level of evolution, with its more or less random trials, criteria of selection, and methods of retention. Why the trials, despite their origins in human minds, are at least partly random—in the sense of being only imperfectly correlated with their future success—is that humans, including the most advanced institutional economists, are still far from able to foresee all of their important effects. While some learning of these effects has been going on—which is why socioeconomic evolution is partly Lamarckian—this learning is still far from eliminating all randomness.

A novelty is that the selection criteria are double: external and internal. To succeed in their evolution, the institutional rules of a C-agent must both enable it to be efficient enough to pass its environmental performance test, and gain sufficient approval of its b-agents not to be internally rejected. The difficulty of achieving both may be illustrated by the still numerous national economies where economically efficient institutional rules cannot obtain the needed political support, whereas the politically popular ones are ruinous.

Retention typically uses written documents for formal institutional rules, and states of minds, maintained by verbal and non-verbal communication, for the informal ones.

As economic evolution only concerns institutional rules, the entry and exist of firms together with changes in technologies and industries are parts of development, shaped and constrained by the so far evolved institutional rules. This disagrees with Nelson and Winter (1982), who label such changes as "evolutionary," but agrees with Schumpeter (1934/1912), who calls his theory for dealing with them "of economic development."

In this simplified version, the model includes two levels of developmental competition and selection: (1) of individuals for positions within organizations and/or the economy, such as those of managers, leading investors, and policymakers; and (2) of organizations for positions within the economy, such as those of firms on markets. The success criteria usually require efficiency in the uses of scarce resources—including technologies, innovations, and human capital. But they may even more importantly depend on the economy's institutional rules—such as the competition law, the bankruptcy law, and the conditions for obtaining government subsidies. It depends on these rules how the success of individuals and organizations will be correlated with the success of the economy. If the rules allow the correlation to be weak or negative, they will pay for it by failing in their own evolution.

Why so many studies of economic development are improperly labeled "evolutionary" may be that the difference between the two is more difficult to see in economics than in biology. First, economic development is usually more experimental than ontogeny. Like evolution, it also extensively uses tentative trials, elimination of errors, and selection of successes. It is indeed in these terms that Schumpeter's notion of "creative destruction" may be described. Second, the speeds of the two differ much less in economics than in biology. There, phylogeny is so much slower than ontogeny that hardly anyone may fail to see the difference. In economics, in contrast, institutional rules sometimes change as often as networks of firms and markets, which makes the two more difficult to disentangle.

The possible similarity of speeds has two other consequences. First, institutional rules that change after a relatively short period of economic development may not have had enough time to demonstrate their full development potential. Second, new institutional rules cannot start from scratch, but must build on the possibly wrongly developed economy left to them by their predecessors. Much of the previous development may have first to be undone before the development under their guidance may start taking off.[7]

But there *is* a simple way to clarity: specify the C-agent and distinguish its institutional rules from the network of its b-agents. The trial-and-error changes of the rules are evolution, and those of the network, instructed by the so far evolved rules, are development.

3.2 Levels of economic evolution vs. levels of economic development

If economic evolution has more than one level, the way to clarity is slightly more complicated. More levels of evolution mean more levels of development, and this creates a maze of effects through which the different levels may interrelate. In principle, this maze should be possible to understand by interpreting in economic terms Section 2.5 above. But an explicitly economic map may nevertheless be useful.

To draw such a map, start from the top: consider an economy and identify the effects of its institutional rules on its performance. Distinguish their *agent-coordination* effects from *agent-quality* effects, and divide these into *ex post* and *ex ante* branches.

The agent-coordination effects concern the economy's *actual* agents—both organizations and individuals. They shape the agents' choice sets, incentives, and information exchanges. It is these effects, and especially those on transaction costs, that most of modern institutional analysis has been about.

The less explored, but not less important agent-quality effects are on the agents' internal instructions—that is, the institutional rules of organizations, and the cultural-genomic instructions of individuals. Because of them, the economy's institutional rules also affect the agents' cognitive abilities, preferences and values. The ex-post branch do so through its effects on the suc-

[7] This consequence is clearly illustrated by the J-curve growth of the economies of Central and Eastern Europe after the transformation of their institutional rules from the failed trials with forms of socialism to new trials with forms of capitalism.

cess criteria of the developmental selection, which influences the qualities of the b-agents promoted to leading positions. The institutional rules with such effects include competition law, bankruptcy law, patent law, tax law, and the conditions for obtaining government subsidies. The success of b-agents in this developmental selection implies the success of their instructions in the economy's internal evolutionary selection.

The ex ante branch intervenes in the agents' internal instructions directly. It restricts the permissible variety of these instructions at the outset, and thus also reduces the room for their evolutionary selection. Examples include the corporate law that restricts the variety of forms of corporate governance of firms, and the social and religious norms that restrict the variety of individual choice procedures. If the restrictions happen to be targeted correctly, they help the evolution succeed faster, but if not, they doom it to fail. If the restrictions are so strong that they prescribe the agents' internal instructions in all relevant detail, they close this evolution. There is then only one level of evolution—the one of the economy's rules.

In general, the economy's rules constrain all of its agents, whether these are members of organizations or not. An organization's members are moreover constrained by the organization's internal institutional rules. Like the economy's rules, these may also be formal and/or informal, and also responsible for the organization's performance via member-coordination and member-quality, ex post and ex ante. But their responsibility is only partial. Much of the responsibility stays with the economy's rules: these constrain the permissible variety of the organization's rules, and possibly strongly influence its success criteria.

Finally, the map must also show how all these levels are constrained by the individual instructions produced by the gene-culture co-evolution. This makes it necessary also to put into it instructions for what may be termed "rule-making" and "rule-following." The former constrain the variety of the institutional rules that the individuals may potentially imagine and economic evolution might consequently try. The latter constrain the sub-variety of these trials that the individuals may actually follow. The larger the potential variety, the more likely it contains some actual successes, but also the longer the expected time for finding any of them.

For a deeper insight, it is necessary to leave pure economics and try to separate cultural instructions from the genomic ones. It may be that human genomes endow people with too much fantasy, implying a too broad potential variety of institutional rules that people could imagine and be willing to try, where successes are too rare and therefore too difficult to find. Cultural instructions may then be understood as helping economic evolution by ex ante narrowing this enormous potential variety. But they carry the same risk as the institutional rules with ex-ante agent-quality effects: they may help only if they happen to be targeted correctly—that is, if the narrowed potential variety is not entirely outside the successful sub-variety. Otherwise far from helping, they are the main obstacle to the success of economic evolution, and hence an error of cultural evolution.

Economists may play an important role in cultures where knowledge is valued more than blind faith and superstition. They may reduce the above risk by building and teaching reasonable theories of institutional rules that can effectively predict, if not which rules can succeed, at least which ones are bound to fail. While much of the risk then reappears in the evolution of theories, which also must proceed by trials and errors—or, in Popper's (1963) words, by conjectures and refutations—the advantage is that such errors are usually less costly.

3.3 Two rough examples

A map cannot solve problems, it may only help to organize the search for their solutions. But this may still be useful. If the problems are complex, with many different parts where their solution may hide, a good map of all the parts may even be necessary not to overlook it.

Details must be left to another occasion. For a rough idea, consider some of the often overlooked points that the map brings to light in two hotly debated issues: (1) the growth and development of poor economies; (2) multiculturalism in developed economies.

In issue (1), the map turns more attention than usual from availability of resources to institutional rules. These were for a long time entirely neglected, as if the growth of an economy only depended on how much resources it possessed or was given in foreign aid. Since the beginning of the 1990's, development economists have been increasingly recognizing that institutional rules also matter, but not much more than other growth factors. The map points out that they do matter much more. They imply a certain development potential that a lack of resources may leave unfulfilled, but no surplus of resources can exceed—much like a lack of nutrition may prevent a mouse embryo from developing, but no nutrition, however abundant, can make it grow into an elephant.

More specifically, the map calls attention to some of the effects and limitations of institutional rules that their usual analysis has been leaving aside. While this analysis has been preoccupied with their coordination effects at the economy level, the map also brings to light their agent-quality effects and the limitations stemming from the cultural-genomic instructions of individuals. It is these effects and limitations that appear to hold the keys to the old puzzle of why some economies continue to perform poorly even when endowed with the same formal institutional rules that make other economies prosper.

For issue (2), it must first be realized that cultures are much more than instructions relevant to economic behaviors. In Dawkins's (1976) terms, a culture may be described as a set of "memes"—meaning "units of cultural ideas, symbols or practices, which can be transmitted from one mind to another." The memes with instructions relevant to economic behaviors—such as those concerning respect for property rights, sense of fairness, business ethics, propensities for lying and corruption, ways of solving conflicts, and trust—constitute only a subset of this set. The memes from the remaining subset—such as those concerning costumes, food, music, dances, and rituals—may suitably be denoted as "ornamental".

Admittedly, the precise divide between the two subsets may not be entirely clear, and may have to be shifted in the light of new discoveries. For instance, some memes that at first appear purely ornamental may turn out to have significant effect on economic outcomes—such as food diets that may turn out to affect health and longevity, or religious rituals that may turn out to harm production. Where precisely to draw the boundary is therefore to some extent an open question that calls for further inquiry.

But once the boundary is at least roughly identified, the answer to issue (2) becomes clear. A developed economy may unlimitedly accommodate ornamental multiculturalism, but must set strict limits to the economically relevant one—under the threat of undermining its own development. It must protect the institutional rules and values on which its development fundamentally depends against contamination by any of the economically relevant memes that have been hindering the development of other economies.[8]

All this modifies the usual valuation of the labor imported into a rich country from a poor country. In addition to the usually considered labor quantity, it calls attention to the risks of import of economically relevant memes which may be the prime causes of the poor country's poverty—such as low respect for property rights, rules of honor that foster wasteful conflicts, soft constraints on corruption and hard constraints on education opportunities for women, which both waste their talents and lower the quality of education of their children.

The difficult question is, what civilized policies can defend developed economies against imports of economically detrimental memes. To steer clear of all forms of racism and fascism, a minimum requirement is that they must welcome ornamental multiculturalism and adopt strictly individualistic approach to immigrants, not to discriminate against the many of them who are keen to learn and adopt the economically successful memes of the host country. But the exact form of such civilized defense policies is far from clear.

Interestingly, the division of a culture between ornamental memes and memes with economically relevant instructions formally corresponds to the division of a genome between non-instructing DNA and DNA with ontogenetically relevant instructions, namely genes and the non-genic DNA coding for RNA regulators. Whereas all memes and all DNA segments may replicate, only some carry instructions for the corresponding b-agents on how to form, develop and operate a successful C-agent. In both biology and economics, much still remains to be learned about the exact position of the divide, which may be found somewhat different than initially believed. To recall, the biological divide was first believed neatly to separate genes from non-genic

[8]Some of the best explanations of what rules and values lead to economic development can be found in North and Thomas (1973) and Rosenberg and Birdzell (1986).

DNA, which was called "junk"–before parts of the "junk" were discovered to contain important instructions for the regulation of gene expression.

The division between the two kinds of memes also calls for a correction of Dawkins's argument. By itself, as just demonstrated, the term "meme" is useful, but the argument that memes logically correspond to genes is faulty. According to their definition, they only share with genes the abilities to replicate, but not necessarily those to instruct, which Dawkins is leaving aside. Memes may therefore correspond to any segments of DNA, of which only some are genes. But, as genes are now known not to be the only relevant parts of genomes, it is no longer very interesting to look for exact socioeconomic correspondents just to them.

3.4 Evolutionary developmental economics: a rough outline of a new field

The main potential contribution of the evo–devo generalization of Darwinism appears to be methodological. By interrelating several areas studied by different specialized fields, the above map offers a solid support through which the fields may orderly be interconnected into a single field of evo–devo economics. It is only in such a broad field that economic change can be studied comprehensively, without missing any of its important aspects.

This field may be here only very roughly and very tentatively outlined. The map suggests to structure it into three main areas: (1) the evolution of institutional rules; (2) the development of economies; (3) the behaviors of individuals.

Each area can be seen to contain several topics. In area (1) they include: (1.1) the evolution proper, which includes (1.1.1) the evolution of formal law and (1.1.2) the evolution of informal socio-cultural norms; (1.2) the properties of the institutional rules evolved, which include (1.2.1) their coordination effects and (1.2.2) their agent-quality effects. Moreover, each of these topics may concern entire economies, or organizations within economies.

The topics of area (2) include: (2.1) macroeconomic performance and growth; (2.2) the development of markets, firms and industries; (2.3) the development of technologies; (2.4) the effects of government policies and the development of government bureaucracies.

The topics of area (3) include: (3.1) bounded rationality; (3.2) human learning with its cultural and genomic limitations; (3.3) the differences in these boundaries and limitations across individuals and across cultures.

The verb "include" means that the list of the topics is only rough and incomplete. It is also only roughly and incompletely that the different fields can be identified. Many of them do not clearly define the scope of their specialization, and several of them overlap, studying basically the same topics under different names, without communicating with each other. The list may perhaps best be seen as a public announcement of topics related to economic change, addressed to all the specialist who already understand, or seek to understand, some of these topics, to come forward and join, be it only part-time, the new broad field.

There are many fields from which competent volunteers might come, but three appear particularly promising: (1) the new institutional economics that studies institutional change in the spirit of Douglass North; (2) the "evolutionary" economics (that, as noted, should be renamed to "developmental") that studies the development of markets, firms and technologies in the spirit of Joseph Schumpeter, Richard Nelson and Sidney Winter, and (3) the relatively new field of behavioral economics with its old roots in the works on bounded rationality by Herbert Simon.

To succeed, the specialists in one field must search for what may be interesting about their topics to the specialists in the other fields. In other words, they must be willing to collaborate by trying to answer each other's questions—rather than enclose themselves, as many of them now appear to do, in separate chapels.

Examples of what behavioral economists will be asked about by others are (1) the variety of alternative institutional rules that humans may be able to invent and adopt, (2) the bounds of human rationality and the inequalities of their distribution in society; (3) the limits of adaptability of human preferences and values.

Institutional economists will mainly be asked about (1) the evolution of institutional rules and the possibilities of influencing it by reform policies; (2) the effects of different institutional rules on development processes, including the so far little explored effects on agent qualities.

What the Schumpeterian developmental economists will mainly be asked about is how the development of firms, industries and technologies depends (1) on the prevailing institutional rules, and (2) on the unequal abilities of the individuals involved, as implied and limited by their cultural-genomic endowments.[9]

All this is only a very rough outline of how the field of evo–devo economics may be built. But not much more can be said about it in a short paper. To build it properly must be expected to take a long time and require close cooperation of many different specialists.

4 Concluding comment

The evo–devo generalization of Darwinism was here only applied to economic change, which is only a part of change of entire societies. This raises the

[9] A particularly weak link on which much work will have to be done is the one between Schumpeterian economists and new institutional economists. Still only few of the former take into account institutional rules, and most of the latter only study the static effects of institutional rules on incentives and transaction costs. My earlier attempts to interconnect the two fields are in Pelikan (1992, 2003b)—although then I was still following Schumpeterian economists by calling the processes they study "evolution," as opposed to the present finding that it is more proper to call these processes, in agreement with Schumpeter himself, "development."

question of how this part interrelates with the other parts–such as political change, cultural change, and the above-mentioned gene-culture co-evolution. My conjecture is that the generalization can help answer also this question. But showing it must be left to another occasion or to other in generalizing Darwinism interested social scientists.

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References

Camazine S, Deneubourg J-L, Franks NR, Sneyd J, Theraulaz G, Bonabeau E (2001) Self-organization in biological systems. Princeton University Press, Princeton

Campbell DT (1965) Variation, selection and retention in sociocultural evolution. In: Barringer HR, Blanksten GI, Mack RW (eds) Social change in developing areas: a reinterpretation of evolutionary theory. Schenkman, Cambridge. Reprinted 1969 in General Systems 14: 69–85

Carroll SB (2005) Endless forms most beautiful: the new science of evo devo. Norton, New York

Carroll SB, Prud'homme B, Gompel N (2008) Regulating evolution. Sci Am 298(5):38–43

Cordes C (2006) Darwinism in economics: from analogy to continuity. J Evol Econ 16:529–541

Cordes C (2007) Can a generalized darwinism be criticized? A rejoinder to Geoffrey Hodgson. J Econ Issues 41:277–281

Dawkins R (1976) The selfish gene. Paladin, London

Doursat R (2008) Organically grown architectures: creating decentralized, autonomous systems by embryomorphic engineering. In Würtz RP (ed) Organic computing. Springer, Heidelberg

Hodgson GM (2002) Darwinism in economics: from analogy to ontology. J Evol Econ 12:259–281

Hodgson GM (2004) Darwinism, causality and the social sciences. J Econ Methodol 11:175–194

Hodgson GM, Knudsen T (2006a) Why we need a generalized Darwinism, and why generalized Darwinism is not enough. J Econ Behav Organ 61:1–19

Hodgson GM, Knudsen T (2006b) Dismantling Lamarckism: why descriptions of socio-economic evolution as Lamarckian are misleading. J Evol Econ 16:343–366

Knudsen T (2004) General selection theory and economic evolution: the Price Equation and the replicator/agent distinction. J Econ Methodol 11:147–173

Laland KN, Odling-Smee J, Myles S (2010) How culture shaped the human genome: bringing genetics and the human sciences together. Nat Rev Genet 11:137–148

Mattick JS (2004) The hidden genetic program of complex organisms. Sci Am 291(4):30–37

Nelson RR, Winter SG (1982) An evolutionary theory of economic change. Harvard University Press, Cambridge

North DC (1990) Institutions, institutional change, and economic performance. Cambridge University Press, Cambridge

North DC, Thomas RP (1973) The rise of the western world. Cambridge University Press, Cambridge

Pelikan P (1988) Can the imperfect innovation system of capitalism be outperformed. In: Dosi G et al (eds) Technical change and economic theory. Pinter, London

Pelikan P (1992) The dynamics of economic systems, or how to transform a failed socialist economy. J Evol Econ 2:39–63; reprinted in H.J. Wagener, ed., On the theory and policy of systemic change, Physica-Verlag: Heidelberg, and Springer, New York

Pelikan P (2003a) Why economic policies require comprehensive evolutionary analysis. In: Pelikan P, Wegner G (eds) The evolutionary analysis of economic policy. Edward Elgar, Cheltenham

Pelikan P (2003b) Bringing institutions into evolutionary economics: another view with links to changes in physical and social technologies. J Evol Econ 13:237–258
Pinker S (2001) The blank slate: the modern denial of human nature. Penguin, London
Popper K (1963) Conjectures and refutation. Routledge, London
Ridley M (2003) Nature via nurture: genes, experience, & what makes us human. HarperCollins, New York
Rosenberg N, Birdzell LE (1986) How the west grew rich. Basic Books, New York
Schumpeter JA (1912/1934) The theory of economic development. Harvard University Press, Cambridge
Wilson DS, Wilson EO (2007) Rethinking the theoretical foundation of sociobioogy. Q Rev Biol 82:327–348
Witt U (2003) The evolving economy: essays on the evolutionary approach to economics. Edward Elgar, Cheltenham
Witt U (2004) On the proper interpretation of 'Evolution' in economics and its implications for production theory. J Econ Methodol 11:125–146