# The Challenge of Evo-Devo: Implications for evolutionary economists[1]

I am interested more in the fly's back than the bristles on its back, and more in its eye than its eye color (E.E. Just)

**Abstract** Usually evolutionary economists equate evolutionary theory with modern Darwinism. However the rise of evolutionary developmental biology (Evo-Devo) puts into question the monopoly of Darwinism in evolutionary biology. The major divergences between the two paradigms in evolutionary biology are drawn in the analysis of three trade-offs: population vs. typological thinking, creative role of natural selection vs. internal (inherent) change, and microevolution vs. macroevolution. It is argued here that the Evo-Devo breakthrough helps to better understand the limits to Darwinism in the social realm and design the contours of an alternative paradigm in evolutionary economics privileging structural macroevolution and what Schumpeter called "change from within".

**Keywords** Evolutionary Economics · Evo-Devo · Darwinism · Macroevolution · Structural explanations

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## 1 Introduction

In modern evolutionary economics the notion of evolutionary theory refers to evolutionary biology, and the latter is usually equated with Darwinism (e.g. Wilson and Gowdy 2013). Most of the debate focuses on which version or application of Darwinism might be more productive in social sciences. The status of Darwinism as the unique evolutionary theory in modern biology is never called into question. Still, over the last two decades Darwinian approaches no longer

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have the monopoly on evolutionary biology. Evolutionary developmental biology, dumped Evo-Devo, established itself as an alternative paradigm in explaining biological evolution. With a few exceptions (Knottenbauer 2009; Pelikan 2011; Schwessinger 2013; Martin and Sunley 2014) evolutionary economists and social scientists in general tend to downplay the importance of Evo-Devo for both biological and social theory. The main objective of the present paper is to outline the fundamental differences between Darwinism and Evo-Devo, and to explain why those differences are important for evolutionary economists.

Before presenting the whole argument a short introduction to the different approaches in evolutionary biology seems necessary. Darwin's theory focuses on the creative role of selection (Gould 2002, p. 139; Godfrey-Smith 2012, p. 2162). "Creative" means that the scope of natural selection is not limited to the elimination of the unfit. Such a negative role would imply that another force was behind the creation of the fit. Above all, Darwinian natural selection is a positive force capable of fostering the fit though the gradual accumulation of incremental novelties. This becomes possible thanks to the existence of never-ending cycles of "copious", "small in extent" and "undirected" variation in all species. Variation is the self-rejuvenating resource for natural selection. The development of Mendelian genetics in the first decades of the twentieth century finally confirmed the logical presuppositions for variation required by natural selection to perform its creative role. Furthermore, it provided the mechanisms of inheritance that were lacking in Darwin's theory. The integration of Darwin's theory with population genetics was dubbed Neo-Darwinian or Modern Synthesis.

The Evo-Devo approach offers an alternative account of evolution by questioning some of the most fundamental assumptions held by modern Darwinism. In the neo-Darwinian framework changes in genotypes are "automatically" reflected in the phenotypes of adult organisms. This means that ontogenesis, the developmental process starting from the fertilized egg and continuing to the adult form, is not considered important; it can be "black-boxed" by evolutionary accounts. The Evo-Devo researchers reject the assumption that the developmental process of individual organisms is far too idiosyncratic to be scientifically studied. They suggest that beneath the apparent chaos of individual narratives there lie stable patterns or types of ontogenetic development. Furthermore, the study of the above developmental types is crucial

for understanding how important novelties or radical innovations are achieved at the adult stage of development. The above working hypothesis also explains the meaning of the term "evolutionary developmental biology". Ontogenetic development instead of being a kind of background noise in evolutionary theory thus becomes the sine qua non condition for studying evolution.

A second controversial assumption returns to Darwin and refers to the level of evolutionary forces. Darwin's credo was that changes at the micro-level (populations, species) were capable of explaining the totality of evolution. Striking morphological or physiological homologies between extremely different species were considered by him as simple evidence of a common ancestor in the remote past. Even now, Darwinians still think that inter-species structures or "body plans" (Baupläne) are merely fictitious or mystical entities. Supposedly such a postulate was confirmed by the enormous success of population genetics. However, this kind of validation was more or less artificial. Given that experimentation in population genetics presupposes interbreeding organisms, by definition it precludes the research for genes at the inter-species level. Beginning in the 1990s the breakthrough of developmental genetics has led to revolutionary discoveries about the existence of body-building (master, regulatory) genes shared by either the whole animal kingdom, or by an entire phylum, or even among different phyla (Carroll 2005, 2008; Davidson 2006; Erwin and Davidson 2009; Shubin et al. 2009). The theoretical and philosophical importance of the above discoveries should certainly not be underestimated. They showed that body plans or structural homologies are not mystical entities but rather the most important *explananda* of modern evolutionary theory. This also implies, as we will be discussed in the main text, that macro-evolutionary mechanisms are fundamentally different from the micro-evolutionary ones.

It must be noted, however, that the success of developmental genetics is seen by many Evo-Devo researchers as but a first step towards the explanation of origin and evolution of forms (e.g. Hall 2000, 2012; Gilbert 2003; Callebaut, Müller and Neuman 2007). According to these versions of Evo-Devo, between the genes and the organism other levels of organization intercede, namely cells, tissues and organs. Their interaction, as well the interaction of the organism with its environment, plays a critical role in the expression of genes and the direction

the whole developmental process takes. However, in what follows, the debates between the "gene-centric" and the "organismic systems" or "epigenetic" approaches of Evo-Devo will not be taken in account. This is justified by the fact that the focus of the present paper is not the internal divisions within Evo-Devo but the major trade-offs between modern Darwinism and Evo-Devo.

The plan of the paper reinforces the above choice. The second section, that ensues, seeks to shed light on the main divergences between modern Darwinism and Evo-Devo. The presentation of the divergences between the two paradigms in evolutionary biology proceeds by the analysis of three trade-offs: population vs. typological thinking, natural selection vs. internal (inherent) change, and micro-evolution vs. macro-evolution. The third section builds on the analysis of the second one. It takes the three oppositions as givens and asks what evolutionary economists can learn from each trade-off, and the Evo-Devo paradigm as a whole. In a nutshell, the argument is that typological thinking, structural-internal change and macroevolution design the contours of an alternative paradigm in evolutionary economics. The latter is not something to be invented from scratch in the future. It already exists in the heterodox legacies of *structural macroevolution* put forward by thinkers like Marx, Schumpeter, Keynes, Galbraith, and Minsky but has been censured within the Darwinian-based version of evolutionary economics. Finally, the fourth section provides concluding remarks and caveats.

## 2 In what way is Evo-Devo's big picture different from the Darwinian one?

At the most abstract level, the differences between Modern Darwinism and Evo-Devo are not all that new. In the history of biology the most notorious precursors are considered to be the French biologists Geoffroy Saint Hillaire and Cuvier from the first decades of the nineteenth century. Geoffroy based his "*Unity of Type*" theory on the existence of structural similarities or homologies between species that seemed *not* to be adaptations to functional needs. In the other camp, Cuvier's "*Conditions of Existence*" principle stipulated that the morphology of organisms reflects the interrelated functions that assure *adaptation* to their environment[2].

[2] Note that by "conditions of existence" Cuvier "did not only designate adaptation to external environment, but also coordination of parts by and for the pursuit of proper function" (Gould, 2002, p.

Darwin followed up on Cuvier's functionalism. For him, adaptation to the conditions of existence is the only force operating in evolution. Therefore the *Unity of Type* is an outcome of the *Conditions of Existence*, and anatomical similarities across species are merely evidence of the adaptations originally evolved in their common descent (Darwin 1859, p. 206). This is also the position taken by many Darwinians on the subject even today (e.g. Lewens 2009). It is worth noting that Evo-Devo does not reject the explanatory power of 'conditions of existence.' As it will be made clear in the next paragraphs, Evo-Devo recognizes the need to integrate both frameworks, but it gives the dominant role to the "unity of type" explanations.

In conclusion, the opposition 'conditions of existence vs. unity of type' is exactly the same as the trade-off "function (adaptation) vs. form (structure)". Darwinian orthodoxy (e.g. Breidbach and Ghiselin 2007) usually considers two other oppositions to be similar to the previous ones, namely 'science vs. creationism' and "materialism vs. idealism". The first assimilation is erroneous. It is well known that the creationist cause has also been defended through functionalist-adaptationist frameworks. The second assimilation contains a grain of truth, especially regarding the past, when most structuralist thinkers in biology were idealists. But, as the case of Evo-Devo demonstrates, this is neither logically necessary nor verifiably true.

**2.1 Population vs. typological thinking**

What demarcates Darwinism from other biological theories based on conditions of existence, like Lamarckism for example, is the interplay between variation and selection. The key-role of variation (diversity) in the Darwinian framework was clearly articulated a century after the publication of Darwin's *Origins*. In 1959 Ernest Mayr, a major proponent of the neo-Darwinian Synthesis, claimed that 'Darwin introduced a new way of thinking into the scientific literature, "population thinking."' (Mayr, 1959/1976, p. 27). According to Mayr, the former scientific way was the typological thinking that had its roots in Plato's idealistic philosophy, where reality was the blurry reflection of perfect Ideas or Forms (types). Echoing Plato, modern "typologists" focused their attention on ideal types or statistical means and considered variation an

294, note). In general, the debate presented here between Geoffroy and Cuvier is oversimplified. For a more detailed account, see Gould (2002), pp. 291-312.

accidental phenomenon. On the contrary, "populationists" privileged the diversity of individuals, "or any kind of organic entities" within populations. In a nutshell: "For the typologist, the type (eidos) is real and the variation an illusion, while for the populationist the type (average) is an abstraction and only variation is real" (p. 28)[3].

Some years later, David Hull (1965) pushed Mayr's point even further by claiming that Darwin had put an end to 'two thousand years of stasis' in biological systematics and in Western science and philosophy more generally speaking. Such statements reflected the euphoria created by the unconditional domination of the neo-Darwinian Synthesis. What was for Darwin a major difficulty for his framework has been transformed in Modern Synthesis to an arrogant dismissal of all pre-Darwinian thinkers in biology. Over the last years a revisionist history of biology has evolved that refutes the claim that biologists before Darwin were mired in Plato's idealism or in Aristotle's essentialism (e.g. Winsor 2006; Amundson 2005)[4]. Nevertheless, the denigration of past thinkers does not mean that Mayr was wrong about the originality of population thinking and its key-role in Darwinism. Actually the real opposition was not between static and evolutionary approaches but between *two forms of evolutionary thinking*, the variational and the developmental (transformational). R. Lewontin, who with S.J. Gould revolted against the excesses of Modern Synthesis, emphasized the importance of the Darwinian framework in more precise terms:

> There are two basic dynamic forms for evolving systems. One is *transformational*, in which the collection of objects evolves because every individual element in the collection undergoes a similar transformation. (…) Most physical systems and social institutions evolve transformationally, and it was characteristic of pre-Darwinian evolutionary theories that they, too, were transformational (…) The alternative evolutionary dynamic, unique as far as we know to the organic world, and uniquely understood by Darwin, is *variational* evolution... Variational evolution occurs by the change of frequency of different variants, rather than by a set of developmental transformations of every individual (Lewontin 2001, pp. 53-4).

[3] What Mayr means here by "real" has no ontological component: being real is to dispose of explanatory power or "causal efficacy" (Sober, 1980, p. 371).

[4] Wagner (2007, p. 151) summarizes very aptly this turn in the history of biology with the following rhetorical question: "Was everyone before Darwin an idiot?"

Lewontin's trade-off between variational and transformational evolution corresponds to Mayr's juxtaposition of population and typological thinking. By definition, the study of transformational (developmental) evolution requires the use of typological thinking, whereas population thinking is the appropriate method for studying variational evolution. The question in this second part of the paper is whether population thinking or variational evolution can ultimately account for the evolution of life in earth.

The existence of apparent or phenotypic homologies in the structure of a broad range of animals offers an opportunity to test the scope of population thinking. One possible answer is that structural and morphological similarities reflect the existence of a common ancestor and therefore the selection pressures that determined it. Nevertheless, given that the creation of fundamental phenotypic similarities goes back to the Cambrian period - ca. 530 million years ago- (e.g. De Robertis 2008), it is difficult to explain how variation and selection forces have been inert for such a long lapse of time. This is a rather self-defeating strategy that opens the door to non-Darwinian explanations. A more promising alternative is to presume a similarity of environments and therefore of functional demands. In this case the phenotypic homologies observed would be nothing more than evidence of similar selection pressures and subsequent adaptations. What could be detrimental to this explanation is the existence of "deep homologies", that is to say, of homologous genes across different kingdoms and phyla. Mayr was reassuring:

> Much that has been learned about gene physiology makes it evident that the search for homologous genes is quite futile except in very close relatives. If there is only one efficient solution for a certain functional demand, very different gene complexes will come up with the same solution, no matter how different the pathway by which it is achieved. The saying "Many roads lead to Rome" is as true as in daily affairs (Mayr 1963, p. 609).

Mayr applied his conjecture to address one of the major difficulties of variational evolution, the creation of complex organs (radical novelties) like the eyes. Von Salvini-Plawen and Mayr (1977) claimed that eyes would have been invented independently between forty and sixty-five different times. The rest of the story is more or less familiar. The rise of developmental genetics in the 1990s refuted Mayr's conjectures. The general concept is that the existence of body-building (master, regulatory) genes, also called Hox genes, which are common to all the

animals. The most famous example is the Pax-6 gene that determines the creation of eyes in vertebrates and has its counterpart in all the animal kingdom. The now well-established fact that the same genes are behind the formation of eyes in humans, flies and squids has shaken the faith of modern Darwinians in the monopoly of population thinking in evolutionary biology. This also explains the hasty identification of Evo-Devo with developmental genetics. Organismic systems theories lead to similar conclusions. However, developmental genetics challenged Modern Synthesis on its own turf.

**2.2 Natural selection vs. internal change**

In all Darwinian versions adaptation to the conditions of existence takes place mainly, or exclusively[5], through natural selection. Copious, small, and non-directed (random) variation provides the boundary condition for the dominant role of the natural selection mechanism in the evolution of life. This also implies that external causes (the environment of organisms) command the main explanatory power, whereas changes coming from within the organism are 'random' regarding the challenges presented by environment conditions.

The key-role of natural selection in explaining evolution evinces at least two limitations. The first, and minor one, concerns the internal consistency of adaptations. Natural selection can guarantee that if there is a particular functional need, the environment will "select" the variant that best corresponds to it. But, it cannot guarantee that the successful adaptations to the selection pressures will be integrated in the organism. Taking the example of Darwin's finches, who can guarantee that longer beaks will be harmoniously integrated into the head of finches, or even that the rest of head will be able to sustain the new longer beaks (Gerhart and Kirchner 2007, p. 8588)? Natural selection can determine *ceteris paribus* which trait corresponds to the environmental conditions but can hardly ensure the co-ordination or the co-evolution of different traits into a well-integrated whole. In other words, natural selection can

[5] The exclusive role of natural selection in evolution characterizes the "hardening of the Modern Synthesis" (Gould 2002) and is labelled "adaptationism" (Orzack and Forber 2010). This debate is however beyond the scope of this paper. We don't need the excesses of Modern Synthesis to prove there are limits to the explanatory power of natural selection put forward by the Evo-Devo.

allow for incremental improvements in a given structure, but it cannot provide the internal coherency or the logic of the structure. But an organism without internal consistency is a hopeless monster, and the latter is not adaptive to any environment. This limitation is not something new in the relevant literature. Lewontin made it clear that adaptation through natural selection presupposes the quasi-independence of traits or characters: "If character correlations are unbreakable, or nearly so, then no single aspect of the phenotype (…) could ever develop without totally altering the rest of the organism in generally non-adaptive ways" (Levins and Lewontin 1985, p. 64). Yet even today many Darwinian scholars tend to underestimate the importance of the "quasi-independence of characters" condition and therefore to postulate that evolution is a *ceteris paribus* story[6].

The *ceteris paribus* postulate becomes even more problematic in the case of radical innovations or novelties shared by different species or/and phylla. The most classical examples of such innovations are the eyes and the tetrapod limbs. It has been remarked many times that Darwin's *magnum opus* is about everything but *Origins*. In fact, in Darwin's framework of gradual evolution the question of origins does not make sense. Continuous cycles of variation and selection don't require origins. Mayr's speculations about the genesis of the eyes through the slow-moving convergence of different evolutionary pathways corresponding to similar functional needs are typical of Darwinian thinking. Still, the story as a whole is not very plausible. The creation of complex organs or structures implying all variety of detailed complementarities between their constituent parts can hardly be coordinated by gradual genetic variation and natural selection. The latter can successfully explain the adaptations of eyes of each species in different environmental conditions but not the creation of the eye itself in the entire animal kingdom. Stated more plainly, the hopeful contingencies or 'contrivances' needed for the creation of complex organs are so extensive that only an extremely high degree of chance could provide them.

[6] In Evo-Devo the decomposability of complex structures into simpler ones is called modularity. Note, however, that modularity concerns the quasi-independence of structures and not of simple traits: "Modules are generally distinguished by their greater internal (intramodule) than external (intermodule) integration, by their repetitiveness and by their persistence and reuse" (Müller 2007, p. 944).

Evo-Devo scholarship reassures us that such a miraculous accumulation of hopeful contrivances is not necessary. Thus, it is not a surprise that the study of novelties has been the hottest subject on the Evo-Devo agenda. (Müller and Newman 2005; Shubin, Tabin and Carroll 2009; Hall and Kerney 2012, …). As already stressed in the Introduction, behind the complex structures or body plans of organic life there are "causal-mechanistic" explanations that are independent of the statistical explanations of modern selection-based theories. The gene-centered version of Evo-Devo gives priority to the existence of body-building or master (networks of) genes that control the developmental trajectories of the different body parts. The organismic systems version prioritizes the physico-chemical and self-organizational properties of cells, tissues and organs. Other versions (e.g. Gerhart and Kirchner 2007) combine both mechanisms and demonstrate how small changes in the master genes of bones can initiate – through self-regulating mechanisms - the required changes in cells, muscles and nerves. Therefore, in the creation of novelties like the bird's wing, very little genetic change is needed to produce large phenotypic differences.

The debate continues as do the synthetic propositions. What is important for the purposes of the present paper is the common denominator shared by the above versions of Evo-Devo. This is aptly resumed by G. Muller in the following passage:

> (E)vo-devo introduces a shift in emphasis regarding the role of natural selection in phenotypic evolution. Whereas in Modern Synthesis framework the burden of explanation rests on the action of selection, with genetic variation representing the necessary boundary condition, the evo-devo framework assigns much of the explanatory weight to … development, with natural selection providing the boundary condition. (…) Thus, evo-devo moves the focus of evolutionary explanation from the external and contingent to the internal and inherent (Müller 2007, p. 947).

We find here, in more specific terms, the aforementioned trade-off between population thinking ("the external and the contingent") and typological thinking ("the internal and the inherent"). Yet, as it is also obvious in the Müller's citation, the framework of population thinking or variational evolution is not rejected by Evo-Devo researchers as being obsolete. All of them, albeit to different degrees, integrate natural selection mechanisms in their

evolutionary accounts. Still, the primary role is reserved for internal and inherent change[7]. That's why they insist on the difference between their own "causal-mechanistic" approach and the 'statistical' approach advocated by Modern Synthesis.

### 2.3 Microevolution vs. macroevolution

The opposition between typological and population thinking is also intimately connected to the dichotomy between macroscopic (top-down) and microscopic (bottom-up) approaches. Darwinian population thinking implies that processes within species (micro-level) may explain structural similarities/differences within the higher taxa (macro-level). In other words, macroevolution can be extrapolated from microevolution. Obviously, if higher groups possessed their own emergent properties, as different kinds of "typologists", "structuralists", "essentialists" presumed, then Darwinian mechanisms would not be able to provide an explanation for the most important aspect of evolution. On the contrary, in this case the top-down (macroscopic) approach would be a necessary complement to the analysis at the micro level.

The fact remains that for Darwin, micro-reductionism[8] was the only solution that would honour his scientific-materialist point of view. A scientific approach in biology needed empirical evidence. And the latter could only result from the careful study of the evolution of individual variants within single species or populations. After Darwin, the rise of population genetics in the beginning of the 20th century took it a step further by shifting the focus from Darwinian

[7] For most Evo-Devo scholars, natural selection mainly intervenes to "elaborate" and "refine" (Müller 2010, p. 323) the morphological structures (body plans) developed by internal change. However, In Carroll's version (e.g. Carroll 2005, pp. 286-91), natural selection has a far more important role: it also checks for the viability of the different morphological structures in force. Note also that, in spite of their emphasis on inherent change, all the Evo-Devo authors insist on the importance of environment for evolution and the creation of novelties. Still, the influence of environment has a Lamarckian flavour: it induces changes in developmental genes or systems without necessarily passing through natural selection mechanisms.

[8] Usually, in economics the notion of micro-reductionism goes hand in hand with a version of methodological individualism. Obviously, this is not the case with population thinking and Darwinian biology. Here micro-reductionism means to extrapolate the properties of higher levels of organization from the lower levels. Regarding the complex status of individuals in Darwinian population thinking see Sober (1980, pp. 371-2).

phenotypes (individual organisms) to individual genotypes[9]. During the middle of the 20th century, the advance of population genetics coincided with the domination of positivism in the philosophy of science. Positivism's condemnation of "unobservables" as mystical entities met with Modern Synthesis' proscription of autonomous macro-evolutionary entities (e.g. Baupläne) and causal properties. Some discontented followers of Modern Synthesis, like the palaeontologist G.G. Simpson, made very cautionary statements about the pertinence of extrapolating macroevolution from micro-evolution: "if the two (i.e. micro- and macro-evolution) proved to be basically different, the innumerable studies of micro-evolution would become relatively unimportant and would have minor value in the study of evolution as a whole" (Simpson 1944, p. 97). Nevertheless, for the era that saw the calcifying of Modern Synthesis and the simultaneous rise of positivism**,** such cautionary statements sounded like nonsense.

Today, things are quite different. Certainly, some scholars remain faithful to the tough micro-reductionist standard set by Modern Synthesis (e.g. Grafen 2009). However, other Darwinian scholars try to deal with the existence of different levels of evolution through the notion of "multilevel selection". This notion, on the one hand acknowledges the existence of different levels of evolution, and on the other reduces them to Darwinian selection mechanisms. In fact, turning macro-evolution into a simulacrum of micro-evolution is the only solution for integrating macro-evolution into the Darwinian paradigm. As one of the major proponents of the multilevel selection approach contends: Multilevel selection "falls squarely within the paradigm of microevolution, population genetics models, and an emphasis on adaptation and natural selection models established by the Modern Synthesis" (D.S. Wilson 2010, p. 88)[10].

[9] Dawkins' slogan presuming that genetically speaking, "individuals and groups are like clouds in the sky or dust-storms in the desert" expresses in the most extreme way the new genetic micro-reductionism that prevailed in the golden era of Modern Synthesis.

[10] For many years the expansion of selection to higher levels was (incorrectly) labeled "macroevolution". The misnomer makes the discussion susceptible to confusion. Note that the notion of macroevolution used here (see mainly Amundson 2005) has nothing to do with the idea of "species selection" put forward by Gould (2002, chapter 8) and his colleagues. For example, some evolutionary economists (e.g. Bergh and Gowdy 2003) convincingly argued that the possibility of selection between groups challenges

The difference Evo-Devo makes is that it shows how the macroevolutionary properties of higher taxa are substantially different from the microevolutionary mechanisms explored by the Darwinian paradigm (Amundson 2005; Erwin 2010). Perhaps nothing better explains this radical change of perspective than the prophetic reaction - during the 1930s - of the embryologist E.E. Just to the rise of neo-Darwinian Synthesis: "I am interested more in the fly's back than the bristles on its back, and more in its eye than its eye color" (reported inter alia in Amundson 2005, p. 182). E.E. Just's first assertion was that the developmental mechanisms governing the creation of the eye *in general* are substantially different from the micro-evolutionary mechanisms explaining the ubiquity of variation in eyes. The second claim was that mechanisms explain the fundamental structures of organisms, whereas Darwinian adaptation is accountable for the minutiae of their characteristics. In other words, typological thinking, internal change and macroevolution come first in the explanatory agenda of biology and, then follow population thinking, external change and microevolution. Contemporary Evo-Devo, as it has already been stated, presents many different nuances as to the overdetermination of micro-mechanisms by macro-mechanisms. Still, it completely endorses Just's premise about the relative autonomy of macroevolutionary processes.

It should also be noticed that the idea of a unique macro-level is oversimplified. Macro-level properties are also hierarchized. Davidson and Erwin (2006) and Erwin and Davidson (2009) provide a comprehensive account distinguishing four levels within the Gene Regulatory Networks (GRNs) that determine the course of animal development. At the highest level there are the 'kernels' of the GRN that have remained unchanged from the Cambrian period and are common to all the members of a phylum or a super-phylum. Modifying the kernel implies destroying the organism. As a result, kernels are immune to change. Peripheral changes are detected at the lowest level, which account for the speciation processes that preoccupy Darwinian scholarship. Therefore, at the lowest or the micro level, developmental elements complete natural selection mechanisms. Changes in the intermediate levels ("plug-ins" and "switches") are responsible for the creation of taxa positioned between species and phyla.

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the individualistic postulates of neoclassical economics. Nevertheless, their common denominator that group selection puts into question the microfoundations project of mainstream economics disregards that group, or multilevel, selection is but a simulacrum of Darwinian microevolution.

Major differences in body plans morphology are related to these intermediate levels. Yet such major differences are beyond the spectrum of the Darwinian microscopic approaches.

In a nutshell, Evo-Devo's fundamental *explanandum* is more the development of shared forms or body plans in higher taxa (macroevolution) than the evolution of individual traits within single populations or species (microevolution). The Darwinian scholar explains the beak size of a single species of bird by the availability of different types of seeds. The Evo-Devo scholar asks what the developmental mechanisms of beaks (in general) consist of and how changes in beaks are functionally integrated with the rest of the head. Note, however, that the above difference does not prevent Evo-Devo researchers from contributing substantially to the micro-level. The most famous example is the re-examination of Galapagos finches and the discovery of the developmental mechanisms that permit the extension of their beaks (e.g. Abzhanov et al. 2004). Still, at the micro level, Evo-Devo, even though it limits the creative role of natural selection, can be perceived as a complement both to Darwin's thought (West-Eberhard 2008; Brakefield 2011) and even to neo-Darwinian Synthesis (Minelli 2010). By definition, if a top-down approach is valid, it will also make important contributions to the micro level. Hence, what really makes the difference is the relative autonomy of macro-level causal mechanisms[11].

An important problem of interpretation regarding the meaning of macro and micro stems from the stubborn tendency of some Darwinian scholars to understand Evo-Devo as a research program dedicated to the study of individual entities and not to the developmental processes *common to a whole phylum or even to a whole kingdom*. If this was true, the Evo-Devo could be apprehended as an individualistic and reductionist approach vis-à-vis the population-level perspective of Darwinism. Such misinterpretation reflects the neo-Darwinian black-boxing of developmental processes to "proximate" causes not having a real impact on evolution. Even philosophers like Ariew (2003, p. 561), who tried to reformulate Mayr's

[11] Within evolutionary economics Pelican (2011) sees Evo-Devo not as an alternative paradigm but as a complement leading to a more consistent generalization of Darwinism. Significantly, his objective is to provide "a solid micro-basis" and to establish "a well-defined link to methodological individualism in the social sciences". (p. 344).

problematic distinction between ultimate and proximate causes, echoed the same understated view of developmental processes:

> Proximate causes of individual life histories vary between individuals in population (…) So, after tracing out proximate causes for every individual in a population, there is something left over to explain, namely what some of these disparate life histories have *in common* that set them apart from their conspecifics. Evolutionary explanations identify these commonalties in terms of statistical properties of an evolving *population*. Hence, evolutionary explanations differ *in kind* from proximate explanations. Evolutionary explanations are statistical, they range over the ensemble of individuals, taken as a class. Proximate explanations are individual-level causal explanations ranging over individual life histories.

Obviously, it is extremely difficult to find an Evo-Devo version that could assert itself as a study of the developmental processes governing individuals or singular entities. As already illustrated in the paper, Evo-Devo focuses *on what species and populations have in common and not on what is specific to the individual entities belonging to the same population or species*.

Finally, it should be noted that the above misinterpretation is far from neutral. Darwinian scholars after having denounced for decades structuralist-developmental ideas as a case of intellectual madness, they are now compelled to capitulate and to recognize their cogency. The only way they can preserve their faith in Darwinian orthodoxy is to scale down the Evo-Devo revolution to the level of the individual. In this case, the Evo-Devo findings would be a simple refinement of Darwinian population thinking and natural selection. As Breidbach and Ghiselin put it so astutely (2007, p. 169): “At any rate, the suggestion that Darwinism is somehow incompatible with embryology makes no more sense than the notion that it is incompatible with genetics”.

### 2.4 Taking stock of the discussion so far

An instructive way to summarize the previous discussion is to invoke Lewontin’s distinction between transformational (developmental) and variational evolution. Darwin’s revolutionary idea was to make variational evolution the fundamental mechanism of biology. Evo-Devo has challenged the monopoly of variational evolution by focusing on the developmental mechanisms operating in the organic world. In the final analysis, all the oppositions presented

in this section refer to the fundamental trade-off between developmental and variational evolution.

**Table 1: Variational vs. Developmental evolution**

| **Variational evolution** | **Developmental evolution** |
|---|---|
| Conditions of Existence | Unity of Type |
| Function (Adaptation) | Structure (Form) |
| Population Thinking | Typological Thinking |
| External and Contingent Mechanisms | Internal and Inherent Mechanisms |
| Statistical (Probabilistic) Explanations | Mechanistic Explanations |
| Microevolution (bottom-up) | Macroevolution (top-down) |

Table 1 summarizes the oppositions presented in our discussion. The first two, conditions of existence vs. unity of type and functionalism vs. structuralism, are more general and belong to the history of biology. Therefore, no special place was reserved for these oppositions. The rest concerns the current state of the debate, and have been examined more extensively in paragraphs 2.1, 2.2 and 2.3. It is also worth recalling that at the micro level the two opposing approaches can constructively be combined to provide a more comprehensive understanding of the evolution of single species or populations. Where the gap seems difficult to bridge is at the macro level.

## 3 What can evolutionary economists learn from the Evo-Devo revolution?

The general message of Evo-Devo for evolutionary economists should be more or less clear by now. The main contribution of evolutionary economics has been to introduce into the science of economics the variational approach borrowed from Darwinian biology. The objective was to break with the mechanistic and ahistorical approach of neoclassical economics, inspired by classical physics. Still, the rise of Evo-Devo shows that even in nature the role of transformational evolution is fairly important. For the remainder of this paper the oppositions

developed in the previous section will be explored with special emphasis on the ontology of economic and social realms.

Before elaborating the whole argument, a clarification is needed regarding the use of the term evolutionary economics in the present article. The term refers to a massive literature including quite divergent approaches. It should be clear, however, that what follows could not cover all the field of evolutionary economics. It will be contented instead to a small bundle of contributions that seem more important for the economy of the discussion. In a nutshell, priority will be given to *productive* applications of Darwinism in economics. Overarching programmes preaching for the existence of *general principles of evolution* governing both the biological and social field will only indirectly be taken in account.

To be more precise, one can distinguish three main waves of Darwinian thinking in contemporary economics. The first wave was inaugurated by Nelson and Winter (1982). It has produced a very important literature on innovation, corporate and industrial dynamics and the related public policies. Yet, as we will see in the third section, it has a rather limited contribution to macroeconomic theory. The main feature of this first wave is that it uses Darwinian concepts as *analogies or metaphors*. Instead, the second wave launched by Hodgson and his allies (Hodgson 2002, Hodgson et al. 2008) has argued for the existence of ontological communalities between the biological and the social realm. Hodgson coined the term *Generalized Darwinism* to distantiate this current from the fundamentalist strand of *Universal Darwinism* initiated by Dawkins. Nevertheless, the main inspiration of Generalised Darwinism still comes from the now obsolete hardening of Modern Synthesis (Callebaut 2011a,b; Liagouras 2013). Most importantly, the successive refinement of the Generalized Darwinism has rarely resulted in productive applications in the study of the social realm. The most known application, the evolution of traffic conventions (Hodgson and Knudsen 2004), will be taken in account in the discussion about the qualitative differences between conventions and social structures (section 3.2). Instead, more attention will be paid to U. Witt's alternative to Generalized Darwinism - the so-called "continuity hypothesis" - that generated more productive applications.

The third wave of Darwinian economics is more recent (e.g. Wilson and Gowdy 2013). Although this new version of Universal or Generalized Darwinism adopts Lewontin and Gould's revolt against the excesses of Modern Synthesis, it is based on two of its most controversial features. First, it reproduces Mayr's distinction between ultimate and proximate causes: Darwin's variational evolution provides the ultimate causes of evolution, whereas developmental and molecular biology are condemned to deal with the proximate causes[12]. Second, it follows the research programme of evolutionary psychology regarding the quest for human nature by enriching it with the approach of behavioural-experimental economics. A first problem is that both, Mayr's ultimate-proximate causation and evolutionary psychology, are now discredited by contemporary Darwinian scholarship (e.g. Laland et al. 2011, Callebaut 2011a,b). A more important concern has to do with how an 'empirically inaccessible' (Plotkin 2008, p. 153) theory on the formation of human nature could result in an evolutionary theory of the modern economy and society we live in[13]. Certainly, the scholars working along this line of thought anticipate that such an ambitious task is totally possible. However, it is too early to judge the productive potential of this third wave of Darwinism in evolutionary economics. Therefore, the third wave of Darwinism in evolutionary economics will not be considered in the discussion that follows.

### 3.1 Is population thinking the only game in the social sciences?

There are two ways of talking about the limits to an approach, more specifically population thinking. The first one means that the approach is incomplete in general, whereas the second one signifies that it is appropriate for some fields and inappropriate for others. The word

[12] This strand of literature tries to temperate Mayr's distinction by referring to Tinbergen's four causes but the outcome is really demanding. Regarding the drawbacks of Mayr's distinction, the misinterpretation of Tinbergen, the conflation between Mayr's backward-looking and population genetics' forward-looking causation, and the chaos that has resulted, see Liagouras (2016).

[13] For example, Stoelhorst and Richerson (2013, p. S52) explain that the "detailed phylogeny of the path by which tribal-scale human organizations evolved into the large-scale organizations of modern complex societies" is "beyond the scope" of their paper. Witt and Schwessinger (2013) provide a very condensed account of the aforementioned phylogenetic path. Still, as they acknowledge, what remained in capitalism from the initial egalitarian endowment is just "footprints".

"limits" is used here in the latter sense. There are at least two broad areas where population thinking proved to be a valuable approach in economics: the analysis of firm and market competition and the study of consumers' preferences.

On the supply side, Nelson and Winter's (1982) seminal book paved the way to major developments in the study of firm and industrial dynamics. Neo-Schumpeterian scholars (e.g. Metcalfe 1994; Saviotti 1996; Andersen 1994) used population thinking to provide an alternative to the standard neoclassical analysis of firm and market competition. Taking seriously the variety of firms in the marketplace, or more generally the heterogeneity of agents in transactions, instead of postulating a representative firm (agent), proved to be a big step towards more realistic microeconomics. The same applies to the modelling of market competition as a process and not as a stationary state. Furthermore, the integration of the Schumpeterian theme of innovation (Dosi 1988), and consequently of the differential innovative-absorptive capacity of firms, gave impetus to important theoretical and empirical research.

In sum, the neo-Schumpeterian approach stands a success story on the supply-side, boosted by the rise of the competitiveness imperative in the global economy. More recently, population thinking has been useful in theorizing the demand side, and in particular the dynamics of consumer behaviour. The objective here is to open another black box of standard neoclassical theory, consumers' preferences, by underlining the importance of social interactions in consumption choices (e.g. Buenstorf and Cordes 2008; Witt 2010). The growing interest of the evolutionary on the demand side seems relevant on two accounts, at least. First, it allows for the analysis of changing patterns of consumption within an "affluent" economy where consumer goods and services have an important symbolic component. Second, it enables the exploration of the possibility that sustainable consumption behaviours can be diffused in a modern consumerist society.

Perhaps there are, or there will be, other important applications of population thinking in economics. Yet the above examples suffice to show the potential of this biology-based approach in economics. The question remains whether the success of population thinking in modern evolutionary economics means that typological thinking is obsolete in the study of the

economic and social realms. If one accepts that the only possible form of typological thinking is that of standard microeconomic theory, then the answer might be yes[14]. But this is far from true at least in the above two cases. From an internal point of view, the productive application of population thinking in the social realm cannot bypass the questions of behaviour mechanisms, and especially of learning and imitation processes in humans (Sugden 2001; Vromen 2009). This necessarily implies a typological theory about human behaviour informed by cognitive, behavioural, social, and neuropsychological factors. Witt (2010) provides an outstanding example of recognising how population-based dynamics needs to be grounded in the cognitive and behavioural endowment of a representative individual (see also Witt 2001). From an external point of view, which is more consistent with the Evo-Devo perspective, the rejection of typological thinking conflates the ahistorical version of typological thinking in neoclassical theory with the study of historically-bounded social *structures* or systems in non-mainstream approaches. What follows is a synopsis outlining three well-known examples of typological thinking at the firm level. The question of the irreducibility of macroeconomic properties will be treated later.

The first and most famous example comes from Adam Smith's pin manufacture. It is rather clear that Smith does not underestimate the enormous diversity in the organization of production that reigns in the late eighteenth century. But, behind the chaotic variety of firms, he distinguishes a kernel of shared principles that assure the dynamism of capitalist production: the intra-firm division of labour. There is no need to search very far to find the high-tech firms of his era where this kernel of organization principles is located. The latter can be found even in the modest manufacture of pins that he gives us a tour of. Certainly, after the *Wealth of Nations* the advent of two industrial revolutions will substantially transform the organization of production. But, all these important transformations build on the initial "body plan" analysed by Smith.

[14] Note that the representative firm of standard neoclassical theory is actually more alive in textbooks than in research. Population thinking is already used by neoclassical scholars when they analyze "competitive selection" in markets (e.g. Jovanovic 1982). Evolutionary game theory is another area where population thinking and neoclassical scholarship converge (Friedman 1998). See also the intriguing comparison, in formal terms, between Walras and Darwin in Joonsten (2006).

Another well-known example stems from the work of Alfred Chandler, and especially his *Visible Hand* (Chandler 1977). Chandler as a business historian is focused on evolution. Nevertheless, Chandler's notion of evolution has little to do with the notion of evolution implied by population thinking. Here we have a *transformational* or *structural* evolution from the traditional family firm to the modern multiunit enterprise. Chandler knows that for each firm structure he analyzes there is an immense variety of individual enterprises and that variety really matters in market competition. The cases-studies he uses to advance his argument are indicative of the great variety existent. But underneath the apparent ubiquity of diversity in firm organization, there are some structural features that are common to most of the enterprises. As in the case of Evo-Devo, those common structures are not phantoms or mere figments of our imagination. Studying them is extremely important for understanding economic reality. Hence, typological thinking is an appropriate tool for studying the structures that constrain the populational phenomena. Without reference to specific structures, even populational explanations that implicitly make the assumption of a capitalist system are destined to conflate competition between Smithian firms with competition in the *Visible Hand* era.

A third, less famous example but one that is more pertinent for our times, can be found in Lazonick and O'Sullivan's (2000) analysis of the maximization of shareholder value. The authors by studying the US economy bring to light some major contradictions of the financialisation that would become apparent after the 2008 crisis. But before coming to the question of contradictions the two authors examine the causes of the transition from the Chandlerian firms applying the principle of "retain and invest" to the contemporary finance-led corporations that go by the principle of "downsize and distribute". Significantly the title of their first section is "*The origins of the "shareholder value*"" (p. 14). But this is not the kind of origin that can be explored through population thinking. The transition from "retain and invest" to "downsize and distribute" is explained by the interplay of structural transformations like the excessive expansion of corporations through mergers and acquisitions, the rise of new international competitors applying decentralized and more innovative methods of production, the ascent of institutional investors, the deregulation movement in the banking sector, and so

forth. As in the Evo-Devo framework, structural explanations of change are qualitatively different from populational mechanisms. They correspond to what Charles Tilly (1984) called "big structures" and "large processes".

Certainly, the proponents of a Darwinian social science would have great difficulty accepting that structural explanations are different in kind from population thinking mechanisms. They could argue that the important literature analyzing the evolution of conventions and rules is able to supply sufficient explanations for structural or developmental change. This is a transposition of the classical Darwinian micro-reductionism from biology to the social sciences. The evolution of a *trait* in a population or a species is supposed to adequately explain, by extrapolation, the evolution of the *structures* shared by higher taxa, or even the entire animal kingdom. However, in the same way that a body plan is not just a huge pile of traits subject to selection mechanisms, a social structure is characterized by the internal logic that organizes a multitude of conventions and rules into a coherent whole. Hence, whatever the value or the limits of the literature on the evolution of single conventions and rules may be, the latter says too little about the inner workings and the transformation of social structures. Social structures change when their internal logic or organizing principles are transformed and not because one or some of their conventions and rules are subject to gradual evolution. That's why populational accounts address the emergence of isolated conventions and rules and not the rise of complex structures like the representative corporation of finance-led capitalism[15].

Finally, it must be noted that in the case of structural evolution there exist *important differences* between biology (Evo-Devo) and the social sciences. First, the deep-seated structures underlying the phenotypic homologies or stylized facts cannot be explored experimentally. We can proceed through abstraction, and build theoretical models but we will never encounter anything like homeotic genes or organismic systems. Second, given that structures are human products, they are subject to significant changes. So mechanistic explanations about the logic of a social structure are time and space bounded (Bhaskar 1978;

[15] This results in the following important difference which will not be developed here. The inner workings of single conventions or rules are quite limpid and hence they don't need special examination. The focus of analysis concerns mainly their emergence and persistence. On the contrary, the inner workings of a complex social structure are of primary importance (Liagouras 2015).

Lawson 1997). Third, even within a given time and space frame there are no pure structures. For example, Chandler's "modern" business enterprise was dominant in the US for several decades, but never came close to occupying the totality of production. Even though the above specificities of social structures, and perhaps others, are extremely important, they cannot be treated within the confines of the present article.

### 3.2 Are selection mechanisms sufficient means for explaining the emergence of complex social structures?

The previous discussion about the autonomy of structural explanations vis-à-vis populational mechanisms contradicts one of the more fundamental postulates of Darwinian biologists and evolutionary social scientists. The sympathy of the latter for Darwinian population thinking is hardly coincidental. It corresponds to a more general philosophical attitude that assumes it's possible to explain the emergence of complex social structures from the interaction between "individuals". This tradition spans the range from Hume's conventions and Adam Smith's invisible hand to Schelling's focal points (saliences), Hayek's and Sugden's conceptions of spontaneous order, and evolutionary game theory's equilibria. Darwin's notion of natural selection revolutionised our way of understanding the living world, but it certainly did not come from out of the blue. It clearly belongs to the long philosophical tradition of spontaneous order, widespread and considered an absolute truth in English-speaking countries. As Hayek (1988, p. 24) put it: "Darwin's work was preceded by decades, indeed by a century, of research concerning the rise of highly complex spontaneous orders through a process of evolution". In the same way, the neo-Darwinian postulate that body plans or structures are but occult metaphysical entities is symptomatic of the same reductionist program in philosophy.

As we have seen, Evo-Devo opposes the monopoly of this tradition in evolutionary biology by questioning the creative role of natural selection. It demonstrates that the formation and evolution of complex structures cannot be guaranteed by selection mechanisms. On the contrary, the latter operate within the limits provided by structures. If this is true regarding the formation and subsequent evolution of body plans in biology, what does it imply for social

structures? Once again, the problem with selectionist explanations in the social sciences is not that they are false but that they explain emergence as a very special case of social order.

For example, it has already been pointed out that consumption patterns can be analyzed through population thinking and selection mechanisms. One way is to think that the formation of consumption trends in an "affluent" society closely resembles the spontaneous emergence of conventions. Hence, spontaneous order processes can effectively analyze the competition between goods and services in the same sector, or within a population sharing the same lifestyle. But they would face serious difficulties in explaining the formation of interlocking complementarities within a model of consumption like the "American way of life" in the past or an environment-friendly pattern of consumption in the future. And, above all, it would be inadequate for examining the rise of consumerism in the modern economy, which ultimately accompanies the rise of capitalism. In his *Protestant Ethic and the Spirit of Capitalism* Weber (2003 [1905], p. 60) admirably defined the " ideal type" of pre-capitalist man:

> (T)he opportunity of earning more was less attractive than of working less. He did not ask: how much can I earn a day if I do as much work as possible? but: how much must I work to earn the wage … which I earned before and which takes care of my traditional needs? …. A man does not 'by nature' wish to earn more and more money, but simply to live as he is accustomed to live and to earn as much as is necessary for that purpose.

From Weber's long-run perspective, evolutionary and neoclassical economics are not really that different. Both are contingent on individuals having insatiable needs or wants. By postulating or deducing that man strives to consume more, they endow their individuals with the spirit (or the structure) of capitalism[16]. Taking the structure as a given is a legitimate hypothesis to study consumption dynamics within capitalism in general or a specific era of it. But trying to explain the emergence of the structure itself, as Weber did, is no less legitimate an objective. Furthermore, as Pagano (2011) argued**,** selection mechanisms are more apt to explain

[16] Similar concerns apply to the alternative theory of consumption put forward by Nelson and Consoli (2010).Their approach very adequately describes consumers' behaviour in the everyday life of a capitalist economy. But their realistic picture of *homo oeconomicus* presumes social structures are a given. On this point see Hédoin (2012) who, taking as example Avner Greif's game-theoretic explorations of late medieval economies, shows that micro-explanations implicitly presuppose macro-structures.

structural inertia than structural change. A capitalist pattern of behaviour would have no chance in a pre-capitalist society. It would have been rejected by the community, if not severely punished. We have here an example of what is called a stabilizing or purifying selection[17].

The transition from pre-capitalist to capitalist man requires collateral changes in all spheres of social life that would somehow be aligned to produce a new "spirit". This is very similar to the question posed by Evo-Devo scholars studying novelty: How the changes in developmental genes, cells and tissues are coordinated to produce a new structure? This is also the question that was "black-boxed" by neo-Darwinian Synthesis. Even though the emergence of the new structure could not possibly be designed or known a priori, it is dependent on macro-variables that seem arcane compared to variational evolution. We need only mention some of the explanations offered for the rise of capitalism: the Protestant ethic, the Enlightenment, the Renaissance, the weak influence of political institutions on the economy, the enclosures, and so forth. What all explanations attempt to do is to find which social sphere is the most critical for the consolidation of the new structure. This is such a complex question that it risks never being solved. Social scientists studying novelties will never have at their disposal the experimental evidence their Evo-Devo colleagues have at hand. Nor will they ever be able to build a model for the major transitional processes within the social realm. It remains however that in both cases the study of the emergence of new structures (novelties) refers to explanations that are substantially different from population thinking or selection models. Selection processes between similar commodities, firms, institutions can hardly be equated with the transition from one social system to another.

Usually social theorists inspired by Darwinian biology pass over the unsuitability of selection models for the study of structural change (and stasis) via a twofold reductionist movement. First, they collapse the different spheres of the social realm (economy, social stratification, politics, law, ...) to the cultural realm. The standard argument in favour of this

[17] Buenstorf and Cordes (2008) present a model of cultural evolution that challenges "the vision of a permanent transition toward sustainability" on the grounds that green consumption patterns "are not self-reinforcing and cannot be 'locked-in' permanently" (p. 646). Actually, what their model shows is that within a consumerist culture, animated by "apparently insatiable human desires", selection forces act against the transition to an environment-friendly model of consumption.

cultural-cognitive reductionism is that society resides primarily in the minds of individuals. Second, they reduce culture to *a population* of antagonistic variants (beliefs, opinions, norms, tastes, …), after which they study the selection processes operating amidst them[18]. Let us put aside the question of cultural reductionism that characterises the majority of spontaneous order approaches and focus on the second reduction. This could be an interesting framework for studying incremental changes within a specific (democratic) society. There exists a variety of beliefs about what society should be, and selection processes pick up the "winners" within. Politicians assure the implementation of the outcome because they are constrained to uphold the hegemonic beliefs in civil society if they want to be elected. In turn, the experience with a changed society affects how individuals think about what it should be, and so forth. Hence, we can see here the classical Darwinian scheme of a self-rejuvenating cycle of variation and selection (retention) and of gradual-continuous evolution appropriately adapted to the study of the social realm.

Nevertheless, the above framework is of little help when we want to study culture not as a simple collection of competing beliefs but as a structured whole (Fracchia and Lewontin 1999, p. 71). When Weber thinks about the origins (and perspectives) of the "Spirit of Capitalism", he does just that. His reflections refer not to occult metaphysical entities (spirits) but to the very conditions of selection processes in modernity. The same "holistic" inquiry into culture can even be found in Veblen, who while striving to build evolutionary economics had the tendency to reduce society to culture or shared habits of thought. In his approach**,** institutions form "a more or less organic whole" (Veblen 1899, p. 53) animated by a single "cultural scheme". The savage, barbarian, handicraft and machine eras are the major cultural schemes that marked the history of humankind. Significantly enough, in Veblen's most elaborate account of the transition from one cultural scheme to another (Veblen 1914) there is no reference to selection mechanisms. Change is inherent, or as Schumpeter used to say "change from within".

[18] Godfrey Smith (2009, ch. 8, 2012) argues that most of the so-called Darwinian models of culture are simply populational and not Darwinian. But this question is beyond the scope of the present paper.

Finally, the fact that the principles underlying social structures or cultural schemes are historically bounded implies that in the social realm change is internal in the more strict sense of the term: it emanates/issues from the successes, the contradictions or the implosion of the anterior system and not from universal developmental laws. Searching for non-trivial universal laws in the evolution of humankind would amount to compiling a "philosophy of history" in disguise. The only non-trivial "laws" that one could hope to encounter in the study of social evolution refer to the workings or the developmental dynamics of historically bounded structures.

### 3.3 Can macroeconomic properties be extrapolated from micro- or meso-evolutionary processes?

The trade-off between micro and macro-evolutionary processes has already been anticipated in the earlier discussion about the limitations of selectionist models. Weber's spirit of capitalism and Veblen's cultural schemes operate at the macro level. They presuppose that the macro level has emergent properties that make it irreducible to micro-evolutionary processes. What follows is an attempt to make explicit what was implicit in the previous discussion by focusing on the issue of evolutionary macroeconomics, or growth models. The main question is whether the revolution in evolutionary microeconomics[19] that was sparked by Nelson and Winter (1982) is also able to produce a macroeconomic alternative to the mainstream.

The essence of Nelson and Winter's position on the subject of the link between microeconomics and macroeconomics was already announced in a seminal paper published in 1974 (Nelson and Winter 1974). The authors' starting point is the "sharp inconsistency" between the "micro studies of technological change" and the neoclassical assumptions (maximizing firms, equilibrium) underpinning Solow's model of growth. They show that an evolutionary model of industrial dynamics (diversity of firms, innovation efforts, selection processes, disequilibrium) can generate – through simulation – the data used by Solow as well as his estimations on the Cobb-Douglas production function of American economy. The striking

[19] Note that in evolutionary accounts of industrial dynamics, populations usually consist of firms and/or routines rather than individuals. Therefore, micro-evolutionary processes do not imply the adoption of methodological individualism. For more on this point see Vromen (2010).

similarity between their simulations and Solow's estimations – and especially his measure of technical change –permits them to conclude with all the redundancy of neoclassical assumptions: "If this is the sort of result that represents 'success' for neoclassical theory, then the world clearly does not have to be very neoclassical for such success to occur" (898,9).

It remains that Nelson and Winter's argument presents some major weaknesses. First of all, their macroeconomic model consists in an extrapolation from competition processes with a single industry. This can be seen as another form of "composition fallacy" because an important aspect of economic growth is the linkages between different industries and not the simple addition of intra-industry competition processes. Second, the model is not very convincing in its critique of neoclassical theory. If alternative (evolutionary) micro-foundations yield the same macroeconomic properties as standard neoclassical microeconomics, why not opt for the simpler ones? Occam's razor implies that we should prefer the basic calculus of standard microeconomic theory to the Markov processes and the simulations of evolutionary theory.

Third, Nelson and Winter's model is even less convincing from a heterodox point of view. In sum, its disequilibrium microeconomics results in Solow's equilibrated growth path. Certainly Nelson and Winter are fully conscious that their model follows Say's law and therefore is "immune to Keynesian difficulties" (896). But they seem to minimize the problem by noting that Keynesian difficulties refer to short-term adjustment and not to long-term growth dynamics of capitalist economies. This reflects the neoclassical postulate that claims shocks have no significant long-term consequences[20]. One could add that the relegation of demand to short-term dynamics also overlooks its importance for long-term growth in the post-Keynesian scholarship. Nevertheless, the underestimation of post-Keynesian literature in a neo-Schumpeterian model of growth is more or less understandable. What *is* more controversial is the contrast between Schumpeter's "gales of creative destruction" and the equilibrated path generated from Nelson and Winter's simulations. Such a contrast can be explained by the authors' endeavour to revive the Schumpeterian legacy by providing a formal framework at the

[20] Recently Foster (2011, p. 13) nicely resumed Keynes' point in evolutionary parlance: "in the short period, variations in financial flows are important and, if too many firms slip out of their basins of attraction because of a negative aggregate shock, this can impact upon long period, non-equilibrium trajectories, leading to positive feedback and sustained underemployment of resources".

micro-meso level. There is no doubt that their project led to a revolution in micro and meso economics. But the price to be paid was rather high. The extrapolation of the macro level relationships from neo-Shumpeterian microeconomics ultimately detracted from Schumpeter's macro-evolutionary theory.

Most of the above critiques can be seen as extremely harsh, even out of place. In fact, it does not make sense to ask of an initial and simplified model, whose main purpose is to challenge the monopoly of neoclassical micro-foundations, to solve all the problems mentioned above. Nevertheless, those criticisms present the advantage of setting an agenda of issues to be tackled by future research in evolutionary macroeconomics. So, the real question is how evolutionary scholarship has dealt with the aforementioned shortcomings over the four decades that followed the publication of Nelson and Winter's seminal paper on evolutionary theories of economic growth. In order to provide an answer to this question we refer to two well-known and recent contributions: An analytical model developed by Metcalfe, Foster and Ramlogan (2006) and a simulation-based one elaborated by Saviotti and Pyka (2013)[21]. The former focuses on process innovation whereas the latter on product innovation (mainly the creation of new sectors).

Both models abandon Nelson and Winter's ambition to elaborate a macroeconomic analysis by extrapolating from the competition process within a single industry. Instead they seek to develop evolutionary macroeconomics by working at the meso level, that is to say the relations between the different sectors of the economy. In this new version of population thinking, macroeconomic relations are considered statistical epiphenomena or emergent consequences stemming from the workings at the meso level. In a nutshell, the economy is seen as a population of sectors. Finally, regarding content, both models share the same objective which is to integrate the demand side into evolutionary economics. Their focus on the sectoral level allows them to incorporate the interplay between supply and demand already known from authors like Allyn Young and Nicholas Kaldor. This constitutes a major contribution to evolutionary economics and to economic thought in general.

[21] Regarding scholarship in evolutionary macroeconomic modelling during the intermediate period of 1980s and 1990s see Silverberg and Verspagen (2005).

Nevertheless, despite the considerable contribution previously mentioned, the final outcome doesn't really address the concerns of Keynesian macroeconomics. Thus, in Metcalfe et al. (2006) the upshot is that the growth rates of macroeconomic variables (output, employment, and productivity) depends on the *variety* of growth rates among the different sectors of the economy. This application of Fisher's principle in economics is contingent on the hypothesis that "investment is funded via the capital market, and, for this market to clear, the saving ratio must equal the aggregate investment ratio for the economy" (26). In other terms, in order to reduce the macro to the micro, and consequently for Fisher's principle to apply, we must postulate the existence of Say's law[22]. In this specific case we can indeed stipulate that "market capitalism … has ... the characteristic of inducing anarchy and translating it into order" and that growth will "depend upon the open, unbiased operation of market institutions" (29)[23]. We find a similar postulate about Say's law, although more implicit in nature, in the last and most comprehensive model elaborated by Saviotti and Pyka (2013). Their study of the co-evolution between innovation, demand and growth seeks to explain "how the emergence of innovations can give rise to the disposable income required to purchase them" (470). The answer is that disposable income "is created due to the combination of the growing productive efficiency of pre-existing sectors and of the increased output and employment following the

[22] The dismissal of the Keynesian critique of Say's law does not characterize the totality of the evolutionary camp. For an extremely interesting integration of Schumpeterian and Keynesian perspectives, see Dosi et al. (2008, 2010). However, the authors interpret their agent-based models (ABMs) as providing the evolutionary microfoundations for macroeconomics. I think that such a claim dismisses the fact that in ABMs, agents interact according to rules prescribed by the researcher. For example, if the rules of the game presuppose the existence of Keynesian product, labour, and capital markets, then the outcomes of simulations will globally advocate the Keynesian point of view. The domination of the rules of the game over agents' actions means that ABMs imply instead *macrofoundations of evolutionary microeconomics*. Certainly, the economy needs ABMs (Farmer and Foley 2009), but the latter are mainly useful for exploring and testing different scenarios *within given macroeconomic theories*. One could hope that they would also enable us to screen different approaches to determine if they accord with stylized facts. Still, the history of modern economics teaches that the empirical screening between alternative theories is a messy and inconclusive undertaking.

[23] In Dopfer, Foster and Potts (2004), faith in market coordination is replaced by the workings of technological and organizational meso-rules. However, the reduction of macro properties to the meso-level still applies.

creation of a new sector based on an important innovation" (ibid.). Thus, once again we have a non-monetary theory of production and growth that regards the financial institutions of capitalism as epiphenomena of the spontaneous order processes occurring in the "real" economy.

Finally, neither model makes much of a case for Schumpeter's notion of structural or paradigmatic change. In fact, their biology-inspired models turn Schumpeter's structural change into gradual evolution. Even in Saviotti and Pyka (2013), where growth mainly results from the creation of new sectors, the latter, instead of being part of a larger techno-economic paradigm (Freeman and Perez 1988), emerge rather randomly. Therefore, if the determinant role of different kinds of macrostructures (models of production and consumption, techno-economic paradigms, institutional set-ups) is *a priori* dismissed, then we can apply population thinking and deduce (the remaining) macro-structures from relationships between individual sectors.

In sum, the bottom-up strategy of evolutionary macro models meets with serious obstacles. In the same way the Darwinian framework cannot account for the structures of the living world explored by Evo-Devo, micro and meso evolutionary approaches in economics lose sight of an important part of macroeconomic reality. This aspect can be studied from the top-down approach that is situated at the opposite end of the Darwinian legacy and that is similar to Evo-Devo. The most well-known macroeconomic school that corresponds to Evo-Devo is post-Keynesian economics (e.g. Kregel 1987, Dutt 2003, Keen 2013, Setterfield and Suresh 2014). Post-Keynesians reject the dominant view that macroeconomic analysis needs micro-foundations. For them the "deep parameters" of the macroeconomic system are not individuals or sectors but in fact the institutional structure of the capitalist economy. As in the case of the Gene Regulatory Networks (GRNs) in the work of Davidson and Erwin (2006), the institutional structure includes different levels. At the highest level there is the kernel of the system. Then follow the intermediate and lower levels that are subject to change.

This can be seen in the example of money, one of the more crucial institutions for the functioning of a capitalist economy. Obviously, money belongs to the kernel of the system. Keynes by pointing to the very fact that a capitalist economy is a monetary one emphasized the importance of uncertainty and expectations and therefore of the inherent instability of

capitalism. One might remark that all this corresponds more or less to H.A. Simon's "bounded rationality". This is true, but with one major difference: Keynes' analysis, instead of starting from the limits to individual rationality to build up the macro-economy, provides the macrofoundations for the limited rationality of individual units. From this point of view, it is interesting to note that the evolutionary microfoundations of macroeconomic relations have in common with the mainstream microfoundations project the notion of money as a veil. Apparently, the notion of bounded rationality has not been enough to dissuade evolutionary approaches from analysing capitalism as a barter economy[24].

At a lower level we find Minsky's "financial instability hypothesis", which signals the Keynesian focus on money in the case of a financially developed capitalist economy, that is, "full-blown capitalism": "The alternative polar view, which I call unreconstructed Keynesian, is that capitalism is inherently flawed, being prone to booms, crises, and depressions. This instability, in my view is due to characteristics the financial system must possess if it is to be consistent with full-blown capitalism" (Minsky 1982, p. 279). Once again, instability is inherent to the system. The cognitive limits and/or the diversity of individual units are incapable of producing the logic of the system or the rules of the game.

Finally, the analysis of modern finance-led capitalism belongs to an even less elevated level. Finance-led capitalism is not only a monetary economy (Keynes) with a full-fledged financial system (Minsky), but possesses its own specific features. The most important of these have already been sketched above while presenting the Lazonick and O'Sullivan analysis about the maximization of shareholder value[25]. One could add or favour other organizational and

[24] As Kregel (1987, p. 528) put it: "Thus it is not macroeconomics that has to be brought into closer touch with microeconomics, but rather one must try to formulate a macrofoundation for uncertain individual decisions". Kregel's remark also applies to behavioural economics, which conceives the structural contradictions of the system as problems of the individual rationality.

[25] It is clear that historicised and structural analyses of the capitalist firm like the one of Lazonick and O' Sullivan are not at all qualified to be published in the "four stars" Journals of economics and management. The question that remains however is what we learn for the world we live in from the ahistorical "theories of the firm" proliferating in the "top Journals". Similar concerns are also raised about the relevance of Darwinian theories of organization. Even those that try to keep track with the historical record they end up by suggesting that the tribal instincts of equality and altruism could be

institutional features, but the critical issue here is that finance-led capitalism makes a system, whose institutional structure is imposed on all the agents and sectors of the world economy. It is this institutional structure that provides the foundations for the macroeconomic analysis of finance-led capitalism.

Clearly, such a systemic or macro-structural analysis is lacking in today's evolutionary economics. Still, the need for structural evolutionary macroeconomics has become even more critical since the 2008-9 crisis of modern finance-led capitalism. Not surprisingly, evolutionary scholars have had a lot to say about the blindness of mainstream assumptions adopted by policy-makers, but too little about the crisis itself and the structures that were "responsible" for it. This seems to be a symptom of their overinvestment at the micro-meso level and thus in population thinking explanations and their underinvestment at the macro-level and in social structures. Perhaps a creative come-back to Schumpeter's macroscopic and developmental point of view, and its affinities with the post-Keynesian thinking (e.g. the endogenous creation of money and the systemic instability of capitalism), could help to bridge the above gap in modern evolutionary economics[26].

**4. Concluding remarks**

Over the last decades evolutionary scholars sparked a scientific revolution in economics by introducing concepts and methods from Darwinian biology. Even now, when evolutionary economists refer to evolutionary theory or biology they mean Darwinism, and usually Modern (neo-Darwinian) Synthesis. The irony of this history is that at the same time that economists were discovering the potential of the Darwinian corpus for economics, the neo-Darwinian consensus was being challenged by the rise of Evo-Devo approaches. What was beyond debate during the golden era of Modern Synthesis - population thinking, the creative role of natural selection and micro-evolution – tends to be considered of secondary importance now. In fact, the bulk of Evo-Devo theory is based on the opposite pillars, that is, on the principal taboos in

again dominant in our knowledge-based society. Unfortunately, this is too far from the reality of the modern capitalist firm.

[26] For a stimulating rereading of Schumpeter's thought through a Minskyan lens see Ülgen (2014).

Darwinian orthodoxy: typological thinking, change from within (development), and macro-evolution.

It has been argued that the case of Evo-Devo sheds light on the limits of population thinking, selectionist explanations and micro-evolutionary mechanisms in the economic realm. As demonstrated by the structural analyses of the capitalist firm in different periods (Smith, Chandler, Lazonick and O'Sullivan …), typological thinking is far from being unimportant. Furthermore, like in Evo-Devo, the development of complex social structures is beyond the range of populational or selectionist mechanisms. The latter presuppose the existence of structural or developmental "constraints" but they cannot plausibly account for the emergence of those constraints presupposing radical innovations or novelties in the social fabric. Change in "big structures" is mainly "change from within". It stems from the formation of important complementarities between different institutions rather than from the competition between quasi-similar institutional variants. Finally, the difficulties faced by evolutionary economists over the last four decades in their effort to advance genuine evolutionary macroeconomics are inherent to the micro-reductionism characterising the Darwinian paradigm. After the last big crisis and the subsequent failure of modern mainstream and evolutionary economics to provide a relevant analysis of the world we live in, the Evo-Devo lesson – i.e. that macro-properties cannot be extrapolated from micro(meso)-evolutionary processes - currently has greater pertinence than ever before.

As already pointed in the Introduction, the bottom line of the present article is not just that taking seriously Evo-Devo could lead to new directions in evolutionary economics. The main argument is rather that the breakthrough made by Evo-Devo in biology reveals the pertinence of already existing approaches in economics and social sciences. In economics the macroscopic, structural, or even developmental approaches initiated by heterodox authors like Marx, Schumpeter, Keynes, Galbraith, and Minsky have been censured or repulsed by the rise of evolutionary economics and more generally by the microfoundations "ideology" (Hoover 2009) or "delusion" (King 2012) that has dominated the economic science over the last decades. This of course does not imply that the macro-structural and developmental legacies in evolutionary economics are without drawbacks. The point is rather that the above traditions

ask different and more relevant questions than the microfoundations ideology governing modern mainstream and evolutionary economics.

A second and more important clarification is needed regarding the position of the present paper vis-a-vis the different versions of Generalized Darwinism. It should be clear that the argument presented here seeks to elaborate an alternative paradigm to Generalized Darwinism and not to provide a complement or a better version of it. Of course, this will not be appreciated by fundamentalists who believe that there is no life beyond Generalized Darwinism, but the author cannot do something for this. The important thing to note here is that what is called "alternative paradigm" has nothing to do with the search for "general principles of evolution" - the Holy Grail of Generalized Darwinism. The priority given in the previous discussion to the productive applications of Darwinism as well as to its analogical or metaphorical uses in social realm is not by happenstance. The rationale behind this choice is that the scholastic debates on the general principles of evolution are based on an ill-founded notion of "naturalism" whose ultimate objective is to impose biological imperialism by creating a complex of inferiority to social scientists. The right naturalist method is not to proceed by "reckless generalisation" (Callebaut 2011a, p. 343) implying that, compared to the unstoppable Darwinian revolution, all the knowledge accumulated by centuries of social thought is either redundant or false. We should be better off if we proceed with biology as Bhaskar (1978) did in his *The Possibility of Naturalism* with physics: ask, *by taking seriously the wealth and diversity of social thought*, what the ontological specificities proper to social realm are and what kind of naturalism (if any) is appropriate to analyze them. Of course, the few paragraphs of the paper seeking to prevent from misinterpreting the Evo-Devo breakthrough as the new General Theory of Evolution they do nothing more than waving the hand to this direction.

Finally, some other important limitations of the argument presented here should be noted. First, the discussion remains at a very abstract level. Each of the three different trade-offs between modern Darwinism and Evo-Devo would require a separate paper to be adequately assessed. And a fourth paper should be devoted to the question of novelty. But in this case the common ground of the three trade-offs would be lost.

Secondly, as already mentioned, the radical opposition between the two paradigms of evolution refers mainly to the macro level. At the micro level they could complete each other nicely. There is much to do in this direction, but this undertaking is beyond the scope of the present article. Let me however draw the attention to Callebaut's (2011b) "shopping list" in favour of an extended evolutionary theory, including *inter alia* Evo-Devo, self-organization, and niche construction theories. Callebaut's list provides the best example of a possible synthesis at the micro level[27]. Unfortunately, most evolutional scholars working on organization theory still prefer the foundational concepts of evolutionary psychology which Callebaut (2011b, p. 361-2) considered obsolete by modern Darwinian research.

Thirdly, it might be remarked that all that modern biology discovers through the ascent of Evo-Devo is more or less *déjà vu* for the social sciences. The developmental biologists Depew and Weber (1995, p. 495) have already made a similar argument: "Perhaps it is not too much to say that what we need is an evolutionary theory worthy of the best social theory, not a social theory trimmed to fit a rapidly receding, overly simplistic evolutionary theory". My guess is that both biology and the social sciences are directed toward pluralistic and multilayered theories of evolution. The traditional opposition between variational and transformational evolution no longer delineates the frontiers between biology and the social sciences. And if this is true, social scientists still have a lot to learn from Evo-Devo scholars, *and vice versa*.

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[27] In the same vein see Stoelhorst's (2005) paper which is informed by Gould's (2002) account of the "formalist" tradition and his pluralist view of evolution considering developmental and/or structural "constraints" as necessary complements to Darwinism. Unfortunately, due perhaps to the ascent of fashionable Generalized Darwinism, the path opened by Stoelhorst (2005) has not then find followers. Consequently, the integration of Evo-Devo at the micro level has remained at the 1980s and 1990s negative perception of developmental processes as "constraints" to the workings of natural selection.

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