Evolutionary Economics via Generalized Darwinism and Multilevel Selection Theory

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Research Area V

Abstract

It is evident that in both business economics (Nelson and Winter, 1982) and organisation studies (Hannan and Freeman, 1989; Aldrich, 1999; Baum and Rowley, 2002) evolutionary scholars seek to conceptualize groups as individuals and units of selection, and equally apparent that while the idea of selection at more than one level is frequently invoked its operation and articulation have yet to be determined.

A number of pertinent developments in key areas of evolutionary theory are poised, in concert, to forge the meaningful expression of multilevel selection in the socioeconomic domain and they are pulled together here for the first time in an exploratory discussion. It is suggested that theoretical and empirical advances in group and multilevel selection theory (Thompson, 2000; Henrich, 2004; Wilson and Wilson, 2007) are consistent with the main tenets of generalized Darwinism (Aldrich et al, 2007; Hodgson and Knudsen, 2006a). And, furthermore, that through the conceptual apparatus of the replicator and interactor (Hull, 1988) it becomes easier to conceptualize an evolutionary multilevel selection theory and, moreover, to ultimately conceptualize and debate ontological similarity and continuity between biology and evolutionary economics.

> There was a time when individualism reigned supreme both in evolutionary biology and in the human social sciences, creating an image of the individual as the only adaptive unit (or rational actor) in nature and of the group as merely a byproduct of what individuals do to each other. Those days are over…
>
> Group level adaptation is here to stay in evolutionary biology, and the human social sciences must follow suit to remain true to first principles.
>
> David Sloan Wilson (2002)

Introduction

It is evident that in both business economics and organisation studies evolutionary scholars seek to conceptualize groups as individuals and units of selection (Dollimore, 2006a). It is equally apparent that in these evolutionary accounts while the idea of selection at more than one level is frequently invoked (Nelson and Winter, 1982; Hannan and Freeman, 1989) or otherwise explicitly acknowledged (Aldrich, 1999) its operation and articulation have yet to be determined. Indeed, wherever multilevel selection has been assumed or implied in socioeconomic accounts, the theories have tended to suffer problems of intractability.

A number of pertinent developments in key areas of evolutionary theory are poised, in concert, to address this deficit. In essence, resolution of the group selection issue (Henrich, 2004; Sober and Wilson, 1998), the theoretical framework and conceptual apparatus of generalized Darwinism (Hull 1988; Hodgson and Knudsen 2006a; Aldrich et al, 2007) and theoretical and empirical evidence of group and multilevel selection (Keller 1999; Reeve and Keller, 1999; Wilson and Wilson, 2006; Okasha, 2006) are collectively paving the way for the meaningful expression of multilevel selection in the socioeconomic domain. However, these developments have not previously been pulled together in one place and their significance for evolutionary economics is yet to be fully explored. Accordingly, the main aims here are to essentially map these theoretical and conceptual developments; to explain the links between them and to demonstrate their relevance for evolutionary economics.

The paper begins by briefly outlining the developments in modern evolutionary theory argued to be ushering in a multilevel conceptualization of socioeconomic evolution. This is followed by a discussion of the implications of these advances for the socioeconomic realm, with particular reference to Nelson and Winter's (1982) evolutionary account. The following sections then discuss key concepts and theories, like interactors, genetic group selection and 'social replicators' in turn, having first illustrated their links through an exploratory table of logical possibilities in multilevel selection theory (MST). The work concludes by measuring these logical possibilities against key evolutionary accounts.

Theoretical Developments on the Path to MST

Resolution of the group selection controversy in the 1980s marked the critical turning point for multilevel selection thinking in both biological (Keller 1999; Gould and Lloyd, 1999) and socio-cultural theories of evolution (Boyd and Richerson 1985, 2005; Sober and Wilson 1998), when it became theoretically plausible to explain group adaptation in terms of selection at the level of the group. Linked with this was the resolution in the late 1980s of what became known as the 'units debate' (Brandon, 1982). Here it became apparent that theorists had been conflating the question of the unit of selection with that of the level at which selection occurred. Earlier theoretical work had established selection as a 'two step' process (Mayr 1978), and Hull's (1980, 1988) incisive contribution was to untangle the units and levels confusion by observing a functional distinction between two entities operating at these distinctive stages of the selection process. These he named the replicator and interactor[1] and they correspond with the genotype and phenotype of the biotic realm and have now become generalized terms amongst evolutionary theorists for entities that function in evolutionary processes (Brandon 1990, p. 78).

Complementing and indeed facilitating some of these developments have been significant advances in the articulation of the theoretical perspective of generalized Darwinism (Hodgson and Knudsen 2006a; Aldrich et al 2007), that is of the idea of generalizing the core Darwinian principles to the social or economic domain. Generalized Darwinism holds that the core Darwinian principles of variation, inheritance and selection are general principles that can be applied to all complex open-ended systems

[1] Hull's definitions of these terms appear on p.12 below

comprised of entities with heritable variation in fitness. Significantly, it is the meta-theoretical framework of generalized Darwinism that accommodates and indeed embraces the conceptualization of multilevel selection across the biotic and socioeconomic domains where, inevitably, there are major differences in detail and where mechanisms, such as inheritance, are notably different. This ontological continuity will be illustrated here in an exploratory table of logical possibilities in MST.

Finally recent theoretical and empirical work in group selection continue to support and advance developments towards a generalized MST, demonstrating consistency, for example, with the notion of group adaptation (Leigh, 1991; Wilson and Wilson, 2007) and the existence of replicators at higher levels of the organizational hierarchy (Boehm, 1997; Thompson, 2000), and providing more detailed and authoritative accounts of the mechanisms involved in multilevel selection, as well as explanations of evolutionary transitions from simple to complex organizations (Okasha, 2006)

It is important to be clear here about the degree of consensus in these interlinked areas of modern evolutionary theory as well as noting where there are ambiguities. Whilst the group selection issue has long since been resolved and the *idea* of multilevel selection thinking is quite well established in both the biotic (Gould and Lloyd, 1999; Keller, 1999; Eldredge, 1985) and the social spheres (Baum, 2002), *theory* in the latter remains conceptually undeveloped. Although multilevel selection models are plentiful and generally consistent scholars outside biology and anthropology remain largely unaware of them (Wilson and Wilson, 2007), and evolutionary theorists are yet to fully understand the mechanisms involved when selection is working simultaneously at different hierarchical levels. Hence, the emphasis here on the replicator and interactor dynamic and the enabling meta-theoretical framework of generalized Darwinism.

Whilst the replicator and interactor are relatively new concepts (Hull, 1988) whose acceptance is far from unanimous and definitions continue to be refined (Hodgson and Knudsen, 2006a; 2006b), it is significant that they have been keenly embraced by many evolutionary scholars (Gould and Lloyd 1999; Brandon 1999; Keller 1999; Baum and Singh 1994; Ziman, 2002) and, as will be shown here, are proving indispensable to ongoing theoretical developments. Certainly the idea of generalized Darwinism has a much longer and stronger history. Indeed Darwin (1859; 1871) himself recognized the

general nature of his theory, suggesting that it would ultimately explain the evolution of language and morals. And ever since Darwin a wide range of scholars have supported its broader application to social phenomena (Bagehot, 1872; Veblen, 1898; 1899; Campbell, 1965; Dawkins, 1976; Dennett, 1995). However, as a result of a general guardedness amongst social scientists about using ideas from biology (Degler, 1991), misplaced fears about biological reductionism and the use of biological analogies and metaphor, objections shown to be easily dismissed (Hodgson, 2002; Hodgson and Knudsen, 2006a; Aldrich et al, 2007), the theory continues to be met with resistance by scholars including some evolutionary economists (Foster, 1997; Witt, 1997; 2004; Cordes, 2006). This is despite the explicit and implicit adoption of Darwinism's core principles by scores of evolutionary scholars in the socioeconomic domain (Baum, 2002; Ziman, 2000; Dollimore, 2006a).

Needs and Possibilities for MST in the Socioeconomic Realm

The importance of this continuing theoretical and conceptual work for the socio-economic domain cannot be overstated, for in both the evolutionary economics and organization studies literature it is very apparent that group selection is assumed and that there is a fervent need to theorize about multiple levels of selection. Indeed the notion of group selection is of particular importance for theories of socio-cultural evolution where there is a patent desire to explain change in collective entities like organizations, firms and social groups.

It will be seen here that central to the articulation and modelling of such phenomena are recent theoretical clarifications about the conditions under which genetic group selection (or adaptation) can occur, in other words, when between-group selection dominates over within group selection (Henrich, 2004). Theorists have long been speculating about the mechanisms involved in sustaining intergroup variation, and conclude that there must be some kind of structural constraints that militate against intragroup variation and which thus enable group variation to prevail (Henrich, 2004; Boehm, 1997; Boyd and Richerson, 1985). Significantly, from this emerges the idea of higher level adaptations and thus the idea of a higher level social replicator or 'heritable unit'. It then becomes apparent that group selection provides the important bridge to the

conceptualization of MST, and furthermore, that the replicator-interactor distinction is key to this development, with the group, for example, being conceptualized as an interactor and higher level unit of selection. Clearly Hull's aforementioned generalized terms facilitate the articulation of these theoretical propositions.

Evidently G. C. William's (1966) forceful condemnation of group selection in the 1960s instigated the long standing perception amongst natural scientists that it was unviable or of no consequence to biological evolution (Sober and Wilson, 1998). Theorists took the view that group-related adaptations (altruism/cooperation) could be explained in individualistic terms, and consequently persisted with the damaging idea that adaptations at all levels of the hierarchy evolve *without requiring a corresponding level of selection* (Wilson and Wilson, 2007). Needless to say, this hampered the development of group selection theory in the cultural domain, where evolutionary theorists (Campbell, 1958; Heylighen and Campbell, 1995) were dissuaded from its serious contemplation, and where methodological individualism reigned supreme.

Today, as suggested, the situation is quite different. The last fifteen years has witnessed the successful resurrection of the idea of genetic group selection in evolutionary theory, with Elliot Sober (1984;1985), David Sloan Wilson (1997;1999;2002), Richard Boyd and Peter Richerson (1985;1990) frequently cited as key architects of the group-selection framework, and David Hull (1980;1988) widely praised for the ontological work that enhanced its articulation. And although, as we are frequently reminded (Dennett, 1994; Reeve and Keller, 1999; Wilson and Wilson 2007),[2] group selection continues to be misunderstood, it must be stressed that it is now broadly accepted by evolutionary scholars, including biologists who admit the possibility of group-level selection in biotic life (Brandon, 1996; Field, 2002;2004; Henrich, 2004). Indeed a significant number of natural scientists have been using group-selection as a working assumption for many years (Keller, 1999; Michod, 2000).

Crucially, it was this acknowledgement of group selection that facilitated the reengagement with MST in the social realm, resulting in a theoretically productive period

[2] Wilson and Wilson (2007) offer an excellent survey of the group selection debate clearly demonstrating the important similarities and well as differences between the earlier 'naïve group selection' (Allee et al, 1949; V C Wynne Edwards, 1962) and today's genetic group selection, and observe that each of group selection's fiercest opponents subsequently changed their minds on the issue (Williams 1985, 1992; Hamilton 1996; Dawkins 1982).

in which multilevel thinking became much more catholic (Field, 2002). However, whilst multilevel selection is recognized as the ultimate consequence of group selection and is increasingly being proffered in evolutionary explanations in both the biotic and the socioeconomic domains (Hannan and Freeman, 1989; Aldrich, 1999; Baum, 2002; Field 2002, 2004), in contrast to group selection, it remains underdeveloped as a theory (Hull, 2001).

Consequently evolutionary scholars offer 'competing' analyses with selection focused on different entities at different levels of the organizational hierarchy. Some organization scholars, for example, investigating 'intraorganizational' or 'within group' selection, posit selection at the level of the routine or competence (Weick, 1979; McKelvey, 1982; Burgelman, 1991; 1994; Miner, 1991; 1994), while evolutionary economists investigating 'interorganizational' or 'between group' selection, posit selection at the level of the firm (Nelson and Winter, 1982), and others suggest even higher, at the level of the industry (Hannan and Freeman, 1989; Baum and Singh, 1994b; Aldrich, 1999). Although multilevel selection is explicitly acknowledged in some of these accounts and its explanation acknowledged to be unknown (Aldrich, 1999), significantly, close reading of others reveal that certain ambiguities in the theory arise *because* Darwinian selection processes are implied at additional levels (Nelson and Winter 1982; Hannan and Freeman, 1989). Hence, although there is increasing acknowledgement of the hierarchical nature of these levels and growing recognition that these are somehow causally related (Baum and Singh, 1994b; Baum, 2002), theorists continue to puzzle over how these causal relationships might be explained (Ziman, 2000; 2002; Murmann et al, 2003; Winter 2005), and indeed for some, these uncertainties continue to provoke disagreement over the 'proper' unit of selection and the true level at which selection takes place.

Certainly in evolutionary economics and organization studies, most empirical and theoretical investigations seem to point to multiple levels of selection. Indeed the growing sympathy for multilevel selection is implicit in the widespread adoption of the Campbellian BVRS model (Baum, 2002)[3] with its acknowledgement of a social replicator. Moreover it is also implicit in the ambiguities that arise in some of these

[3] Campbell's (1965) Darwinian 'Blind-Variation Selective Retention' model, the generic model which, 'opened the possibility of a theory of evolution of human systems freed from the constraining assumptions that genes are the only replicators' (Galunic and Weeks, 2002).

theories through the aforementioned suggestion of additional units or levels of selection or implicit assumption of a social replicator (Hannan and Freeman, 1989).

Indeed this underlines the main purpose of the paper. There is evidently a desire to apply Darwinian selection processes to social phenomena as well as a need to provide the conceptual apparatus to articulate group and multilevel selection. A brief illustration of these needs can be demonstrated in Nelson and Winter's evolutionary theory of economic change (1982).

Evolutionary Economics

In a decisive move away from maximization and equilibrium assumptions and with the firm at the centre of the analysis Nelson and Winter famously reignited interest amongst economists in evolutionary explanations of change in an authoritative and influential account of evolutionary change in industry. Drawing liberally from the biology of the time they presented the idea of 'routines as genes' with firms as their corresponding organisms (or phenotype) in an evolutionary framework which saw the market as the selecting force, operating, like natural selection, on the firms.

With the aid of a modern Darwinian lens it now becomes possible to identify and resolve an acknowledged ambiguity which arises in the theory around the notion of 'search'. This is how Nelson and Winter explain the source and perpetuation of variety in the firm; through 'higher level routines' searching for new routines. Indeed this is why they describe the theory as Lamarckian, because of, 'the 'inheritance' of acquired characteristics and the timely appearance of variation under the stimulus of adversity' (1982, p. 11). The problem arises when it becomes apparent that the theory inadvertently ends up proposing two levels of selection. While one selection process is clearly presented by the authors in the form of 'hidden hand' or natural 'Darwinian' selection and the other ('search') is presented as 'intentional' selection, the latter's handling in other parts of the theory nevertheless reads more like natural Darwinian selection, thus causing confusion and problems of intractability for the theory.[4]

[4] A detailed account of this can be found in Dollimore (2006b)

Theoretical Advances and Proposed Solutions

It is proposed here that such issues can be resolved through the replicator and interactor concepts, multilevel selection and generalized Darwinism. According to the Hull schema (1988) Nelson and Winter's two types of selection can be accommodated within a Darwinian multileveled hierarchy of replicators and interactors.[5] As well as the firm being treated as an interactor at one level of selection, their 'higher level' search routines can also be treated as an additional level of interactors, between the lower level routines and the firm. The point is Lamarckian inheritance, the favoured evolutionary approach of most organization scholars (Singh and Lumsden, 1990), which indeed best describes inheritance in the socioeconomic domain, is accommodated within the overarching framework of generalized Darwinism (Hodgson, 2001; Knudsen, 2001). Contrary to a widely held view, Lamarckism and Darwinism are not mutually exclusive; Darwin himself did not discount the possibility of the inheritance of acquired characters or see it as being irreconcilable with his theory of natural selection (Hull, 2001). In fact, in order for Lamarckism to work it requires a selection process and is thus ultimately dependent on the theoretical foundations of Darwinism.

Implications of Theoretical Progress for Evolutionary Economics

It is evident that as well as seeking clarification over units and levels of selection theorists also want to understand how different levels in an evolutionary hierarchy relate to each other they want to explain the transitions from simple units to more complex organisations and they also want to explain the role of emergent properties in evolutionary explanations (Aldrich, 1999).

Whilst it is acknowledged here that MST is still very much at an exploratory stage, the discussion demonstrates that important progress has nevertheless been made and that on-going research continues to support its development (Okasha, 2006; Wilson and Wilson, 2007). The implications of this for evolutionary economics cannot be overstated where recognition of the evolutionary force of group selection is crucial for scholars working on evolutionary theories of economic change, where group as well as individual level phenomenon are vital to the analysis, and where meaningful explanations of the impact of

[5] See table below on p. 14

micro-level phenomena on macro-level outcomes are also sought (Murmann et al, 2003; Ziman, 2000; Winter, 2005).

It has been indicated here how the aforementioned theoretical and conceptual developments in modern evolutionary theory can combine to facilitate MST for socioeconomic evolution. The next section focuses on the interactor concept to signal its pivotal role in the conceptualization of group and MST. A table is then presented which illustrates the logical possibilities for multilevel selection suggested by Hull's schema which are being explored here. It will be seen that position **V** is proposed for Nelson and Winter (1982). This will then lead into the important discussion of genetic group selection and its implications for MST and socio-economic theories of evolution.

The Interactor Concept and MST

In the wake of the 'units debate' and resolution of the group selection controversy, evolutionary scholars acknowledge that it was Hull's (1988) interactor concept and revamped ontology that finally enabled the formal articulation of the group as a higher level unit of selection and facilitated conceptualization of a multilevel selection framework (Brandon, 1990, p. 78; Keller, 1999; Eldredge, 1985, 1986). Gould and Lloyd (1999, p. 11904) describe the import of this contribution below;

> Two major clarifications have greatly abetted the understanding and fruitful expansion of the theory of natural selection in recent years: the acknowledgment that interactors, not replicators, constitute the causal unit of selection; and the recognition that interactors are Darwinian individuals, and that such individuals exist with potency at several levels of organization (genes, organisms, demes, and species in particular)…

This was undoubtedly a critical turning point in the development and articulation of evolutionary theory. As well as clarifying the selection process and the nature of the entity being selected, Hull provided a generalized terminology and an accessible way of thinking about these complex conceptual issues. It is clear, for example, from the above

that group selection does not deny individual selection, but merely expands the roster of interacting entities that qualify as 'individuals' (Gould and Lloyd, 1999).

Hull (1988, p. 408) defines an interactor as an 'entity that directly interacts as a cohesive whole with its environment in such a way that this interaction *causes* replication to be differential'. The replicator is defined as 'an entity that passes on its structure largely intact in successive replications'. Clearly these could be envisaged as applying to a wide range of collective entities (in the social and biotic spheres). Following Sober's (1984)[6] formula, in a multileveled scenario where various species are interacting with their environment, there could, for example, be selection *of* a particular species, selection *of* a sub-group within that species, selection *of* organisms within that sub-group and, consequently, selection *for* the corresponding genes.

Indeed Hull argues that in order to make any sense of multiple levels of selection it is necessary to embrace the replicator-interactor dynamic. Selection itself was defined by Hull as 'a process in which the differential extinction and proliferation of interactors *cause* the differential perpetuation of the relevant replicators' (p. 409) and evidently this process works at multiple levels. As Hull goes on to explain (my emphasis);

> Selection results from the interplay of these two subprocesses. Genes are certainly the primary (possibly sole) units of replication, whereas interaction can occur at a variety of levels from genes and cells through organisms to colonies, demes, and possibly entire species.

Undoubtedly, conceptualizing the 'unit of selection' in terms of interaction with the environment was a crucial stage in the conceptualization of the group as a unit of selection. And, as can be seen in the above passage, together with the replicator concept it clearly enables evolutionists to speculate about the formulation of MST. It is noted here that in Hull's multilevel schema he was careful to point out that selection can occur at any level of the organizational hierarchy whereas replication tends to be concentrated at

[6] Sober (1984) observed that there was 'selection of' an object and 'selection for' a property. In the generalized Darwinian terminology this amounts to 'selection of' an interactor and 'selection for' its replicator.

the primary or genetic level, 'sometimes at the level of the organisms and possibly colonies, but rarely higher' (1980, p. 324). He did not, however, discount the possibility of replication at higher levels, but observed that the relationship was essentially a 'one and many relationship' (Brandon, 1990, p. 98) with one level of replication and several ascending levels of interaction.[7]

This formulation is, in fact, the one that is currently taken as given by evolutionary biologists in their empirical work (Reeve and Keller, 1999), but, as will be demonstrated in later sections it is not the only one currently being explored. Indeed it is suggested here that there are five logical possibilities for multilevel selection and in order to distinguish between them, they are presented in table (1) below. In order to make the table more meaningful names of evolutionary scholars appear against the position considered here to best describe their theory or perspective.

The five possible positions of 'multiplicity' are identified as, **I**, the traditional single level of replicators and single level of interactors position; **II**, a single level of replicators with multiple levels of interactors position, as discussed above in relation to biotic evolution, this is where the social group is conceived as an additional level of interactor above the organism; **III** is exactly the same as position **II** except that it is perceived as applying 'separately' to the social domain;[8] **IV** suggests a multiple level of replicators and single level of interactor position which is probably not viable; and, finally **V** is a position of multiplicity at both the replicator and interactor levels.

[7] As Brandon (1996, p. 127) counsels however, 'nothing in the definitions [of replicators and interactors] precludes one and the same entity from being both an interactor and a replicator'.

[8] In other words *not* in a continuum from the biotic to the social domain.

	Multilevel Selection Combinations	Description / Assigned positions
I	Single level of replicators / Single level of interactors	Traditional single level theory.
II	Single level of replicators / Multiple levels of interactors ***CONTINUUM BETWEEN BIOTIC AND SOCIAL***	Hull (1981) Keller et al (1999) Henrich? (see p. 22 below)
III	Single level of replicators / Multiple levels of interactors ***SEPARATE SOCIAL ONTOLOGY***	Most evolutionary scholars, eg., Ziman (2000) and co-authors were 'divided' over continuum between biotic and social realms.
IV	Multiple levels of replicators / Single level of interactors	NOT VIABLE: NO ADHERENTS
V	Multiple levels of replicators / Multiple levels of interactors ***CONTINUUM BETWEEN BIOTIC AND SOCIAL***	Darwin; Hull, Henrich, Wilson & Wilson, Brandon, Hodgson Knudsen, Campbell, Boyd, Richerson, Aldrich, **Nelson and Winter (1982).**

Table 1. Logical Possibilities of Multilevel Selection

As illustrated in the table, position **I** is essentially the traditional Darwinian single level evolutionary theory from which all the others are derived. Position **II** is the single level replicator and multilevel interactor position described by Hull above, and is the one assumed by evolutionary biologists, anthropologists and indeed most other Darwinians. Position **IV** is logically not viable and thus has no adherents. And, finally positions **III** and **V** are the most interesting and relevant in terms of the social realm. Essentially whilst position **III** represents the expressed stance of some general Darwinists, position **V** more accurately represents their implicit position, and, moreover, the implicit position of most Darwinian accounts in evolutionary economics and organization studies, and indeed this is where the most promising research is currently taking place.

Basically the difference between **III** and **V** highlights the very important distinction between different interpretations of a generalized Darwinian position. Basically, while some in position **III** see Darwinian multilevel selection, like variation, inheritance and selection, as ontologically grounded, in the sense that there are Darwinian entities and processes at multiple levels of the social hierarchy, they stop short of seeing them in an ascending continuum from the biotic to the social domain. As Ziman (2002, p. 312) and his co-authors explain 'we were divided amongst ourselves on the fundamental issue of whether or not it is proper to see cultural evolution as a human extension of biological evolution, or as an entirely different type of process'. Subsequent works of Nelson (2006) and Winter suggest that they too would 'prefer' position **III**.

In position **V**, on the other hand, which is essentially an 'extension' of position **II**, scholars are clear that there *is* a continuum between the two spheres, and that, as a result of recent theoretical work on group selection (Henrich, 2002; 2004 & others) this is now clearly demonstrable. Indeed this position is most relevant to the discussion here. Position **V** essentially illustrates the view that all evolutionary processes are ontologically similar and basically suggests multiple levels of replication as well as interaction. It is endorsed by Hull (1980, 1981) and Brandon (1996), is *implicit* in much of the evolutionary economics and organization studies literature, and is currently being explored by Hodgson and Knudsen (2004a; 2004b; 2006a; 2006b) in their work on higher levels of replicators in the social domain.

Evidently, the conceptualization of any multilevel account turns on the notion of group selection and its articulation requires the interactor concept. Evolutionary explanations of socioeconomic change appear to be dependent on Lamarckian inheritance, which in turn needs the meta-theoretical framework of generalized Darwinism. Moreover, conceptualization of Darwinian *or* Lamarckian inheritance is impossible without the replicator-interactor distinction (Hodgson and Knudsen, 2006c).[9] Hence the discussion so far has aimed to show how key theoretical and conceptual developments in these areas are linked, and indeed are poised, in concert, to facilitate the meaningful expression of multilevel selection in the socioeconomic domain. The following section will now

[9] Hull (2004) 'In order for any process to be Lamarckian, we need a genotype-phenotype distinction. Of course, in order for a process to count as Darwinian, we also need the genotype-phenotype distinction'.

expand on this proposition by reviewing recent developments in genetic group selection which highlight their relevance for socioeconomic evolutionary explanations and illustrate how it is possible to conceive of the notion of 'social replicators', and thus demonstrate position **V** above with its hierarchy of multiple replicators *and* interactors.

Genetic Group Selection

> 'selfishness beats altruism within groups. Altruistic groups beat selfish groups.'
>
> Wilson and Wilson (2007, p. 44)

The issue at the heart of the group selection controversy was altruism with the contradiction this raised for individual and group level selection. Following Williams (1966)[10] it was long argued that the gene was the primary unit of selection and that selection could not occur above the level of the individual, since individual selection would always militate against any possible group selection force. Thus, dismissive of group selection and faced with the theoretical challenge of explaining the coexistence of competition and cooperation, scholars came up with a variety of explanations for altruistic behaviour. These included the theory of 'inclusive fitness' (Hamilton, 1964) or 'kin selection' (Maynard Smith, 1964), evolutionary game theory (Axelrod, 1980; Hamilton, 1981; Maynard Smith, 1982), and selfish gene theory (Dawkins, 1976; 1982). However, while such models may explain cooperation amongst small groups, none were able to explain altruistic behaviour among large groups of unrelated individuals in one-off encounters (Boyd and Richerson, 1990; Field, 2002, 2004; Henrich, 2004). It has since been recognized that altruistic behaviour can only really be satisfactorily explained by *genetic group selection*.[11] This is where the discussion now focuses on the idea of

[10] While Williams did not deny the theoretical possibility of group selection, he saw it as a cultural phenomenon, with no explanatory validity in biology.

[11] In fact, Wilson and Wilson (2007, p. 21) demonstrate how all the preceding theoretical frameworks assume the existence of multiple groups, and moreover, that they all 'obey the following simple rule, regardless of the value of N, the duration of the groups, or other aspects of population structure: selfishness beats altruism within single groups. Altruistic groups beat selfish groups'.

'social replicators' and 'social interactors,' and addresses the more specific question of multilevel selection in the socioeconomic realm.

Several scholars (Wilson, 1975; Leigh, 1977, 1983, 1991; Dugatkin and Reeve, 1994) have developed models which have consistently shown that there *are* conditions under which genetic group selection can occur, and would explain, for example, the evolution of altruistic or 'pro-social' behaviour. In a recent paper Henrich (2004) offers a very clear statement of these conditions. Using the Price (1970; 1972) equation, which partitions natural selection into individual and group level components, Henrich develops a multi-group model which emphasizes the difference between intergroup and intragroup variation and clearly illustrates how the evolution of 'pro-sociality' can be explained through genetic group selection. He describes his 'culture-gene coevolutionary' approach below (2004, p. 12-15);

> This perspective contrasts *within-group selection*, which acts against altruists who are exploited by free riders from their groups, to *between-group selection* that favors groups with more prosocial individuals because such groups can outcompete groups dominated by free riders …

Genetic group selection occurs when the between-group component of natural selection acting on gene frequencies overcomes the within-group forces to favour an equilibrium different from that which would be favoured by the within-group component acting alone. For evolutionist working in the social realm this has proven an invaluable insight. Indeed it provides an excellent foundation for the study of social behaviour. It is now possible to conceive of group selection as a component vector in a multilevel selection process where the separate components of evolutionary change can be calculated and compared.

Through the logic of multilevel selection and Price's partitioned selection forces, Henrich shows how the variation between groups can become more important than the variation within groups. Through his example of the evolution of pro-sociality, he demonstrates the evolution of group-traits and altruism, and clearly underscores the case for genetic group selection. Otherwise known as 'new group selection', 'intrademic

group selection' or 'trait-group' selection, these models simply partition ordinary individual fitness into within and between group components (Reeve and Keller, 1999).[12] As noted by Wilson and Wilson (2007, p.8), for scholars trying to understand causality in multileveled evolutionary systems they provide incisive tools; 'total evolutionary change in a population can be regarded as a final vector made up of two component vectors, within-and between-group selection, that often point in different directions'.

What is interesting about these models is that attention is paid to the cooperative aspect of evolution not just the competitive. And, notably, according to Henrich, it would seem that compared to other species, the extensive capacity of humans for social learning and cooperative behaviour is what largely explains cultural evolution. Alluding to the mechanisms that bind groups together (encapsulated in 'group traits' or 'social replicators') and increase their adaptive fitness, Henrich below, highlights the significance of this cooperative and imitative behaviour for maintaining intergroup variety whilst at the same time limiting intragroup variety;

> I argue that the nature of our cultural transmission capacities, and of human psychology more generally, creates stable equilibria consisting of combinations of cooperation and punishment that are not available to genetic evolutionary processes in acultural species. The existence of these additional, culturally evolved, behavioural equilibria make the group selection component of cultural evolutionary processes much more powerful relative to the within-group component than can occur in genetic evolution.

These theoretical advances in group selection are very important to the conceptualization and development of a general MST. With the support of the conceptual apparatus of replicators and interactors, a multilevel selection framework now becomes more accessible.

[12] Reeve and Keller (1999, p. 6) and others point out that these models are mathematically equivalent to individual-selection (i.e., inclusive fitness) models and therefore do not point to a fundamentally different kind of evolution (e.g. Dugatkin and Reeve, 1994; Bourke and Franks, 1995).

Current Understanding and Development of MST

What is currently understood about MST and how is it being used? Generally speaking MST tends to be thought of as an advanced articulation of Darwin's original, 'single-level' theory. In other words, it is 'the operation of natural selection - the motor of evolutionary history - at more than one level' (Field, 2004, p. 2). Although it is evidently still at the exploratory stage, and it has not resulted in an appropriately revised theory nor spread to a broader community (Wilson and Wilson, 2007) the multilevel structure nevertheless appears to be widely assumed, and it is evidently being adopted by evolutionists in several disciplines. In evolutionary biology, Nunney (1998) states that 'such theory is already extensively applied in ways that enhance our understanding of gene frequency change; kin selection and gametic selection are examples that have been recognised for many years'.

Indeed, having already assumed a multilevel hierarchy, evolutionists across the natural sciences are now exploring further aspects of the theory which incidentally also have important implications for the social domain. Many scholars, as Okasha (2006) documents, are now exploring 'major evolutionary transitions' (Maynard Smith and Szathmary, 1995; Buss, 1997; Queller, 1997). That is, the mechanisms involved when groups of lower level cooperating units coalesce into larger cohesive individuals at a higher level. For Michod (2005), the interesting question is how these higher level 'Darwinian individuals' acquire the properties of heritable variation in fitness. Organization scientists and evolutionary economists frequently ask the same sort of questions in relation to the emergence of new firms (Aldrich, 1999; Baum 2002), so that it will be interesting to see how research develops here. But for now, the more interesting thing to observe from research on major evolutionary transitions is how it reaffirms group and multilevel selection (Okasha, 2006, p. 222);

> The thematic similarities between the various transitions are emphasized by Michod (1999) and Maynard Smith and Szathmary (1995). Cooperation among lower-level units and suppression of within-group competition are important in all the transitions - without them, no higher-level units can evolve. Mechanisms that promote cooperation include kinship, population structure, synergistic

interactions, and reciprocation; mechanisms that suppress competition include division of labour, randomization (e.g. fair meiosis), policing by fellow group members, and vertical transmission.

Complementing the above findings is a multi-authored work (Keller, ed. 1999) where leading researchers from the fields of biology, genetics, ecology and psychology have been exploring the juxtaposition of competition and cooperation at multiple levels and investigating the impact of this on higher and lower levels. The text is replete with citations of other scholars adopting the same approach. Essentially it is being acknowledged by increasing numbers of scientists that at multiple levels of the biological hierarchy, mechanisms have evolved to prevent potential conflict between the levels. Significantly, for the purposes of this paper, what is common to all these accounts, and those emanating from the social sciences, is the desire to discover the 'policing' *mechanisms* that sustain the intergroup differences; be this at the molecular or the cultural level. It is clear that this is a critical question for the development of MST, and indeed it is essentially the question about social replicators.

It can be seen that the multilevel account is already being pursued by scholars in the social domain. Unsurprisingly, Hull (1988) was one of the early investigators, with a convincing account of science as a selection process. D. S. Wilson (2002) produced a stimulating text on the evolution of religion, treating religious groups, like Hull's scientific concepts, as selectable units. Thompson's (2000) discussion in psychology about the evolution of emergent properties of groups shows remarkable consistency with the propositions here about social replicators, where his emergent properties are presented as group adaptations and equivalent to social replicators. Meanwhile, Landa (2004), with her case studies of businessmen in China, offers empirical evidence of social groups operating as adaptive units, through what she calls 'homogeneous middleman groups'.

It has been demonstrated here that group selection theory provides the vital conceptual apparatus to explore these areas. That is, group selection, via the replicator-interactor distinction and within the meta-Darwinian framework of Darwinism, not only provides the bridge to MST but also the crucial key to its further development. Interestingly, group

selectionists appear uniformly to propose a 'policing mechanism' or some kind of social replicator, and assume that once the social replicator is identified it is possible to identify what is being selected *for* in that particular group. In other words, what is the adaptive trait that favours this particular group over others? What binds it together? The mechanism is evident in Keller and Reeve's (1999, p. 154) observation relating to social insect colonies; 'the multilevel approach is useful because it is well-designed for the analysis of how socially mediated mechanisms that restrain within-group selfishness may evolve and remain stable.' Nunney (1990, p. 240) concurs, 'because cheats, by definition, are not following rules, we expect group-selected systems to evolve policing mechanisms'. Similarly, Boyd and Richerson (1985) proposed 'conformist transmission'[13] to describe the elusive stabilizing mechanism of the social world, while Boehm (1997) proposed 'egalitarianism and Henrich (2004) proposed 'prosociality'.

Evidently, so long as such a mechanism exists then group selection will occur. Thus, establishing the existence of such a mechanism facilitates the assertion of group and multiple levels of selection. The replicator and interactor concepts then guides exploration of functionality at and between each level.

Logical Possibilities in MST

Linking these insights to the logical possibilities of MST discussed above it is now possible to categorize the developing formulations. Position **II** could be used to describe the work of Keller and his colleagues in the natural sciences, where following Hull they acknowledge that 'entities from molecules of DNA, cells, and organisms to colonies, demes, and possibly entire species interact with ever more inclusive environments in ways that bias replication' (Hull, 2001, p. 61). It could also be used to describe the perspective adopted by Henrich whose work on genetic group selection clearly demonstrates the continuity between the biological substrate and groups at the cultural level. Henrich talks about the evolution of 'prosociality', perceiving cultural group selection as being instructive in bringing this into existence, and this position admits a

[13] a popular term which continues to be used in the literature (Heylighen and Cambell, 1995; Henrich and Boyd, 1998, 2000).

single level of replicators, which in his case would be the biological gene, and a multiple level of interactors, which would include the individual organism and the cultural group. Notably, perception of the group in this account is as an interactor.[14]

Interestingly, however, Henrich's perspective, as well as that of most other theorists commenting on socio-cultural evolution, is probably best described as position **V**. Henrich explored the conditions under which between-group selection prevailed over within-group selection, the classic tension between individual selection and group selection. And, with regard to social groups he considered immigrating and emigrating 'free riders' and wondered why more variety was not occurring within the groups as a result. He supposed that there must be something that militated against free riders in social groups concluding that there had to be some kind of cultural structure that maintained the group within its boundaries. Essentially, once it is established that such a structure exists *and* that it is somehow being maintained, the notion of a cultural group replicator emerges. And this begs the question, are there replicators as well as interactors in the social realm?

It is suggested here that this is indeed the case and moreover that this is what is implied in many socio-cultural evolutionary accounts. In *Science as a Process* (1988), Hull observes that the replicators in scientific change are *not* genes and he posits instead things like, 'beliefs about the goals of science, proper ways to go about realizing these goals, problems and their possible solutions, modes of representation and accumulated data' (p. 434). He goes on to suggest that 'scientists in their conversations, publications, and classroom lectures broach all these topics' and that 'these are the entities that get passed on in replication sequences'. Indeed the idea of a social replicator has been endorsed by several others (Brandon, 1996; Landa, 2004; Wilson, 2002), it was proposed in the 'meme' concept (Dawkins, 1976; Blackmore, 1999) and, as noted earlier, its conceptual viability is currently being explored by Hodgson and Knudsen in their work on 'habits' and 'routines'.

Certainly it would appear that position **V** is the most logical and promising multileveled framework given current research and development of theory. Indeed the

[14] Significantly, this is the position that was originally denied by Williams but then later accepted.

exploratory work of Hodgson and Knudsen is demonstrative of its potential. Building on Hull's definitions and drawing on the important work of Henrich, they first suggest the firm as an interactor and clearly illustrate how we might conceive of a social group as a interactor and unit of selection (2004a, p. 298);

> Group selection occurs under specific conditions only. The group itself has to be sufficiently cohesive and influential to overcome the adverse effects of immigration and emigration, thus minimizing the possibility of altruistic and other group-oriented behaviours being diluted and undermined by free-riders. There must be differential success of groups, that is due in part to the properties of groups, not merely to their components. In general, a significant degree of group structure and cohesion are required to make group selection meaningful (Henrich, forthcoming). In short, group selection operates when the individuals in the group are bound together in a sufficiently cohesive manner to share a mostly common fate.

In a follow-up paper on the replication of habits Hodgson and Knudsen (2004b) then effectively propose extending the roster of entities that count as replicators, by positing individual habits and organizational routines as social replicators. The justification for this follows from the above logic. Where there is some kind of structure which persists and acts as a restraint on variation within the group, then the structural constraints or factors become the factors that are being selected *for*. The structures are effectively being selected because these are the things that cause the groups to vary between themselves rather than within themselves.

Significantly, with regard to evolutionary economics and the socioeconomic realm, in addition to these explicit endorsements of position **V** and its notion of multiple replicators and interactors, there is the implicit acknowledgement of such a position in many of the evolutionary theories in evolutionary economics and organization studies. It is apparent, for example, in the theories of Nelson and Winter (1982) and Aldrich (1999). Both approaches assume group selection, they invoke the replicator-interactor distinction and they involve a multileveled selection account which mirrors the 'one and many' replicator-interactor dynamic that ascends from a social replicator (organizational

routine). Furthermore, there are increasing numbers of scholars in these disciplines who are recognizing the replicator interactor distinction and are promoting the idea of multilevel selection (Baum and Singh, 1994b; Ziman, 2000; 2002; Baum, 2002).

As suggested earlier, however, whilst it is the view here that such accounts implicitly map on to position **V**, their authors, for the most part, would probably identify more with position **III**. That is, with a separate 'one and many' replicator-interactor hierarchy which does not run in a continuum from the biotic to the social sphere. In other words, even for Darwinians who acknowledge Darwinian entities and processes in the social world will still see ontological separation between the two spheres.

In summary, although still very much at an exploratory stage, MST has important implications for social theories of evolution, where group selection is assumed and multilevel selection is increasingly invoked. Indeed, as well as presenting the possibility of a more advanced and coherent evolutionary account of the socioeconomic realm, position **V** is consistent with a raft of work already accomplished in the social sciences.

Implications of MST for Evolutionary Theories of Socioeconomic Change

A more inclusive multileveled evolutionary theory would certainly have much to offer social scientists. Indeed evidence suggests a pressing need for the clearer conceptualization and articulation of multilevel selection. It could help, for example, to unravel conceptual confusions around the unit of selection in Nelson and Winter's theory, where the role of the firm becomes unclear in an evolutionary account promoting an additional level of Darwinian selection, in the shape of 'organizational routines.' As suggested above, following position **III**, MST would enable the accommodation of selection at the level of organizational routine *as well as* the firm. Alternatively, following position **V**, the 'routines as genes' analogy could become more ontologically-grounded by asserting a higher level replicator at the organizational routine level.

Similarly for Darwinian organization theorists like Aldrich (1999), the multilevel approach and replicator-interactor dynamic has much to offer. While Aldrich assumes multilevel selection, and a replicator-interactor distinction is implicit in his account, he admits he has yet to explicitly address the mechanics of these in his theory. Undoubtedly, the above insights would assist here.

For organizational ecologists (Hannan and Freeman, 1989) where there was decisive movement away from firm-level 'adaptationist' explanations of change towards the population-thinking perspective, which instead promotes a 'selectionist' explanation of 'adapting industries', a multilevel account would similarly enhance theory. The problem with this perspective is that it is destined to tell only one part of the evolutionary story. MST, however, would allow organizational ecologists to reinstate the firm to a central position, and speak not only of adaptation of the industry but also of adaptation of the firm. Moreover, for the more traditional 'organization-level adaptationists', MST permits a richer explanation of phenomena because scholars can retain Lamarckian explanations of change within a generalized Darwinian multilayered selection framework. Significantly, this approach dismisses the need for theorists to *choose* between adaptationist and selectionist approaches, enabling them seemingly to have both.

Concluding Remarks

Multilevel selection theory remains conceptually underdeveloped and still very much at the exploratory stage. Nevertheless it is clear from the above discussion that theoretical, conceptual and empirical advances in several key areas suggest the possibility of progress for a Darwinian ontologically grounded multilevel selection theory. While the aim here was to pull these all together for consideration, the challenge, of course remains - to link these up into a coherent tractable theory.

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Pavel Pelikan, 2011. "Evolutionary developmental economics: how to generalize Darwinism fruitfully to help comprehend economic change," Journal of Evolutionary Economics, Springer, vol. 21(2), pages 341-366, May. Handle: RePEc:spr:joevec:v:21:y:2011:i:2:p:341-366 DOI: 10.1007/s00191-010-0178-0. as. Keywords: Evolution, Economics, Novelty, Innovation, Darwinism, Variation, Selection, Replication, Game Theory. Contents.Â natural selection and evolution should not be viewed as concepts developed for the specific purposes of biology and possibly appropriable for the specific purposes of economics, but rather as elements of the framework of a new conceptual structure that biology, economics and other social sciences can comfortably share.Â [A full modern statement of generalized Darwinian theory, showing its application to socio-economic evolution.] Nelson, Richard R. and Winter, Sidney G. (1982) An Evolutionary Theory of Economic Change (Cambridge, MA: Harvard University Press). [The classic text on modern evolutionary economics.] II Organization-theoretic foundations of economic evolutionary theory. III Textbook economics revisited. IV Growth theory.Â 9 An Evolutionary Model of Economic Growth 10 Economic Growth as a Pure Selection Process 11 Further Analysis of Search and Selection. 3 23. 51 72 96.