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ABSTRACT

This paper builds on previous work within the conceptual framework of a generalized Darwinism that clarifies such concepts as selection and replication. One of its aims is to refine the concept of the interactor. An overview of the conditions under which group selection may occur helps us identify factors such as structural coherence that are useful in defining the interactor. This in turn leads to the question of selection on multiple levels. An additional level of replication emerges when we consider routines within organizations and the social positions related to them. The analysis here establishes that social organizations including business firms are often interactors. Such organizations are more than simply groups because of the existence of routines and social positions. Accordingly, to understand firms and other organizations, we need more that a “dual inheritance” theory; we have to consider the replication of social positions and routines as well.

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1. Introduction

This paper is part of a larger project to extract and clarify general Darwinian principles and show that they are also applicable to evolving entities in the social, economic and cultural domains (Hull, 1988; Hodgson and Knudsen, 2006a).[1] Criticisms of the basic idea behind this project have been answered elsewhere (Aldrich et al., unpublished; Hodgson, 2007b; Vanberg, 2006). It is important to bear in mind that the project does not assume that the details and mechanisms of evolution in the biological and social domains are similar: they are certainly not. Accordingly, against the critics, it is not about the use of biological *analogies* in the social sphere. Instead, the claim is that there are some shared *ontological communalities* at a highly abstract level. If there is a general theory of the kind of evolutionary processes that can produce novelty and sustain variety, then it is essentially Darwinian in nature.[2]

In earlier work we have shown how the abstract formulation of the selection concept can span both biological and social phenomena (Knudsen, 2002b; Hodgson and Knudsen, 2006c). We have also previously established the analytical importance of the replicator-interactor distinction, with social as well as biological evolution (Hodgson and Knudsen, 2004, 2006b, 2008).

Turning now to the interactor, one aim of this paper is to provide a workable definition of this concept.[3] However, this task is tied up with two other relatively controversial issues, namely the question of group selection and the possibility of multiple levels of selection. Fortunately, an overview of the group selection issue and the conditions under which group selection may occur helps us identify factors such as structural coherence that are useful in defining the interactor. We relate the selection of interactors to the selection for “component” replicators such as individual habits or genes. This in turn leads to the question of selection on multiple levels, as habits and genes are different types of replicator on different levels. When

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[2] This proposition is different from, but does not overturn, the ‘continuity thesis’ (Witt, 2003, 2004), which involves the acceptable claim that biological evolution ‘shapes the ground’ and ‘defines the constraints’ for cultural and social evolution.

[3] We here amend and refine our definition significantly in comparison with our previous attempt (Hodgson and Knudsen, 2004b). Such refinements have been prompted by an extended reflection on possible real-world cases, in both the social and natural world.

group selection occurs the group functions as an interactor, but it may involve the selection for different kinds of replicator on different constituent levels.

A third level of replication emerges when we consider routines within organizations and the social positions related to them. The analysis here establishes that social organizations including business firms are generally interactors. But such organizations are more than simply groups because of the existence of routines and social positions, in addition to individual habits. Accordingly, to understand firms and other organizations, we need more that a “dual inheritance” theory; we have to consider the replication of social positions and routines as well.

Another aim of this article is to demonstrate how the analytical framework of a generalized Darwinism leads us to pose particular questions, such as those concerning the evolution of business organizations. An indispensible part of this framework is the abstract distinction between replicators and interactors in evolving systems.

The question of group selection is reviewed in the next two sections, establishing the importance of group cohesion as a condition for group selection to occur. The next section takes up the issue of cohesion in defining the interactor. This leads to discussions of organizations in general and business firms in particular as interactors, along with their component replicators. The final section ties the threads together.

2. Group selection in biology

The idea that natural selection could operate on groups, as well as individual organisms, was suggested by Charles Darwin and famously promoted much later by the biologist Vero C. Wynne-Edwards (1962). Wynne-Edwards argued that the alarm cry of a bird, telling others in its group of the presence of a predator, would give its group a selection advantage, compared with other groups where there was a lower propensity to give such warning alarms.

Critics such as George C. Williams (1966), Richard Dawkins (1976) and others proposed that the arguments in favor of group selection were false. With the same example of a group of birds, it is possible that a genetic mutation might occur, causing some members of the group to lose or diminish their instinctive disposition to give the alarm in the presence of a predator. Birds with this mute mutation would “free-ride” in the group, benefiting from the warnings given by others who retained the genetic propensity to cry the alarm. Furthermore, birds with no propensity to give the alarm would be at a selection advantage compared with the others, for any crying bird draws attention to itself and places it at greater risk from the predator. The critics explained the survival of specific group behaviors in terms of the natural selection of the genes that determined those behaviors, and not in terms of the fitness or selection of the group as a whole. The hard-hitting critiques of Williams, Dawkins and others made the idea of group selection unpopular, and it fell out of favor for several years.

Defenders of group selection quickly refined their arguments. Prominent in this revival were Niles Eldredge, Richard Lewontin, Elliott Sober, Michael Wade, David Sloan Wilson, William Wimsatt and several others. Some of their main arguments are briefly summarized below. The possibility of group selection in the biotic world, but under restricted conditions, is now quite widely accepted among biologists, and is supported by a substantial scientific literature.[4]

However, the mechanisms and issues involved in biological group selection are very different from those in the social and cultural context. Hence it is useful to distinguish between "genetic group selection" and "cultural group selection" (Henrich, 2004). They both involve the selection of groups; in the former case the focus is on the changing gene pool that results from group selection, in the latter the possibility of changing cultural or social entities is considered. This section concerns genetic group selection. Cultural group selection will be addressed later.

In some of the criticisms of genetic group selection, notably those by Dawkins, the emphasis on genes as the sole biotic replicators was used to undermine the idea of the group as a unit of selection. But, even if true, the proposition that the gene is the sole replicator says nothing about the units of selection. As Sober (1981, p. 113) pointed out, the group selectionists "do not deny that the gene is the mechanism by which biological objects pass on their characteristics ... this shared assumption about the unit of replication simply cuts no ice. That genes are passed along leaves open the question as to what causes their differential transmission". David Hull (2001, p. 61) later observed: "When Dawkins says that genes are the units of selection, he means replication." Dawkins, by false logic, had moved from the proposition that genes are the primary units of replication, to the idea that they must be also the main or exclusive units of selection.

A mistake here, as Sober (1984) elaborated, was to muddle two different aspects of the selection process, involving a confusion between "selection of" and "selection for". The selection *of* individual organisms leads to changes in the population and the gene pool, leading in turn to the selection *for* specific genes that may bestow fitness advantages in particular contexts.

The difference between selection *of* and selection *for* relates to the distinction between replicators and interactors (or vehicles).[5] Dawkins (1982) himself distinguished between "replicators" and their "vehicles", where the genes are the replicators and the organisms their vehicles. Later writers, after Hull (1980), often prefer the term "interactor" to "vehicle", stressing not only the cohesive nature of the replicator-carrying unit, but also the importance of its interaction with its environment. Both critics and proponents of genetic group selection agree that there is always selection *for* the genes in the population. At the biological level, the group selection controversy is not about group replicators: it concerns the identification of group interactors. Both sides agree that individual organisms are interactors (or vehicles). The proponents of genetic group selection argue that groups are additional interactors, giving rise to a hierarchy of interactors and with selection operating at multiple levels, including both individuals and groups. Hence the group selection controversy was about the number of levels of selection, in the sense of selection *of,* rather than selection *for*. When selection occurs at a particular level, the object *of* selection must be an interactor at that particular level (Brandon, 1996).

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[4] See, for example, Boyd and Richerson (1985), Hodgson (1993), Sober and Wilson (1998), Bergstrom (2002, 2003), Henrich (2004) and Wilson and Wilson (2007).

[5] However, as shown below, while replicators are always selected *for*, there can be both selection *of* and selection *for* interactors.

Accordingly, the question whether groups are selected depends partly on whether or not they are successful candidates for interactors. 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”.[6] A necessary condition of genetic group selection is for the group to constitute itself in this way as an interactor. The viability of genetic group selection thus depends on the cohesiveness of the group with regard to its influence over the selection process, and in particular the capacity of the cohesive group to influence the selection outcomes at the genetic level.

While biological organisms pass on their characteristics via their genes, this leaves open the question as to what causes differential genetic transmission. To answer this question we must look to the interactors and how they are structured. Just as individual organisms involve integrated groups of genes that have become functionally organized by natural selection to perpetuate themselves, also groups may sometimes cohere together to the extent that the individuals within them are largely “bound together by a common fate” as Elliott Sober puts it. As Sober (1981, p. 107) elaborates: “Group selection acts on a set of groups if, and only if, there is a force impinging on those groups which makes it the case that for each group, there is some property of the group which determines one component of the fitness of every member of the group.”

The viability of genetic group selection depends in part on the group bestowing fitness advantages on the individual: it depends on the existence of fitness benefits emanating from membership of the group. Hence the group context is vitally important. A serious underlying error in some arguments against genetic group selection is to underestimate that the fitness value of any gene depends on its context. Below we show that context matters in the case of cultural group selection as well. A prominent error in the social sciences – particularly in economics, where various individualistic notions are fashionable – is to downplay the extent to which individual characteristics are molded by their institutional or cultural context.

Some of the arguments against genetic group selection are based on mathematical models of the selection process. Many of these models show that while group selection is possible, it is highly unlikely.[7] Such models suggest that the differential selection *between* groups cannot override the effects of individual selection *within* groups except for a highly restricted set of parameter values. However, within such mathematical models of selection, several simplifying assumptions are made. For example, a number of non-linearities and environmental interdependencies are excluded to obtain a tractable mathematical solution. However, the existence of such interdependencies is a crucial factor in determining whether or not group selection exists.

Michael Wade (1978) noted restrictive assumptions in the basic models of the selection process. It is typically assumed that probability of survival of a population can be significantly dependent on the frequency of a single allele. In several models, all populations contribute migrants to a common pool, normally in a number independent of the population size, from which colonists are drawn at random to fill vacant habitats. Variance between populations is assumed to be created primarily by genetic drift between populations, rather than by differential sampling from the migrant pool. Finally, group and individual selection are assumed to be operating in opposite directions with respect to the allele in question. Wade

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[6] Below we suggest some refinements to this definition.

[7] See, for example, Maynard Smith (1964, 1976) and Williams (1966).

(1978) examined the weaknesses of these assumptions in turn. He showed that relaxing these assumptions has a significant positive effect on the viability of genetic group selection. Wade's work demonstrated that the mathematical selection models in the literature are based on oversimplifying and restrictive assumptions which reduce the apparent likelihood of group selection, and group selection is much more plausible than these models suggest.

In a series of works, Sober and D. S. Wilson also took issue with some of the assumptions in the mathematical selection models (D. S. Wilson, 1980, 1983, 1999; Wilson and Sober, 1994; Sober and Wilson, 1998). For instance, they pointed out that all such models assume a spatial homogeneity in the genetic composition of populations, and that selection is insensitive to the fitness of the population as a whole. Although these assumptions are mathematically convenient, they are neither necessary nor realistic, and they bias the models against the possibility of genetic group selection.

Under specific conditions, selection in nature may occur between groups as well as within groups. A necessary condition of the selection of groups is that membership of the group bestows fitness advantages on individuals. For genetic group selection to occur, these additional fitness advantages must lead to differences among groups. Furthermore, they must be sufficient to ensure that selection between groups, acting indirectly on gene frequencies in the group, overcomes selection forces within each group, and thus leads to an outcome that is different from the selection of individuals alone.

Genetic group selection is undermined when individual migration between groups and other processes diminish the variation between groups. If migration were unbounded and extensive, then the mixed-up outcome would be much less variation of individual characteristics between groups than within groups themselves, and the variation within groups would approach the variation in the population as a whole. In these circumstances the groups would have few differentiating features and group selection would be undermined. By contrast, if migration is constrained, then differences between groups can be maintained. This is a necessary, but not sufficient, condition for group selection to occur.

The Price (1995) equation is useful for clarifying these issues:

$$e\Delta X = Cov(e_i, x_i) + E(e_i \Delta x_i). \tag{1}$$

The term $e\Delta X$ refers to the change of average fitness due to the change through selection in population property X, related to property x of the individual members. The equation shows that this population level outcome can be regarded as the sum of two distinct effects. The first is the selection effect captured by the covariance of the individual properties (x_i) and their individual fitness values (e_i) showing the extent which possession of the property bestows fitness on individuals. The second is a transmission effect $E(e_i \Delta x_i)$ whereby properties change in existing individuals leading to a change in their individual fitness.

Following William Hamilton (1975) and others, Joseph Henrich (2004, p. 14) used an expanded form of the Price equation to examine the conditions under which group selection may occur. This equation is applied to populations of groups, where groups (themselves composed of individuals) substitute for the individuals in the preceding case. Where i above refers to individuals, we use g to refer to groups:

$$e\Delta X = Cov(e_g, x_g) + E(e_g \Delta x_g). \tag{2}$$

Price's formalism is very useful because equation 2 can be obtained from equation 1 by recursive expansion:

$$e\Delta X = Cov(e_g, x_g) + E(e_g\, \Delta x_g)= Cov(e_g, x_g) + E(Cov(e_{gi}, x_{gi})) + E(E(e_{gi}\, \Delta x_{gi})). \qquad (3)$$

This modified Price equation tells us again that the outcome of the selection process can be partitioned into two effects. The first is the covariance of the range of *group* properties (x_g) and their *group* fitness values (e_g) showing the extent which possession of a property bestows fitness on *groups*. This term captures selection among groups. The second effect is a transmission effect $E(e_g\, \Delta x_g)$ where the changing properties of *groups* lead to a change in their *group* fitness. As equation 3 shows, this group transmission effect encompasses both intra-group selection effects $E(Cov(e_{gi}, x_{gi}))$, and intra group transmission effects. Intra-group selection effects capture those changes in the characteristics of individuals that occur because of selection processes that are specific to that group. Intra group transmission occurs through processes that are not caused by selection forces decomposed to the level of individuals within groups. Examples include developmental processes, individual level innovation, or other effects which alter the characteristics of individuals within a group. Notably, some of these effects can be attributed to selection processes at lower levels. Formally, this can be achieved by further recursive expansion of equation 3.

Note that, in the context of a discussion of *genetic* group selection, when we refer to properties and fitness values in the preceding paragraph we refer to genes (alleles) and genetic fitness values. We did not insert these extra words because we wish to reinforce the point that the Price equation is not confined to the selection of genes. This should be apparent in our further use in the following section below.

Note also that this conceptual switch in the Price equation from the individual to the group level neither ignores nor replaces the individuals involved. Individuals and individual properties are still present, through their essential contributions to the properties of groups, including variation within groups. Group selection itself encompasses processes of individual selection. With the selection *of* groups there is still the selection *of* individuals, as well as the selection *for* genes.

Crucially, this group-level Price equation tells us that the process of genetic selection (where groups are involved) can be partitioned into the effects of between-group variation, and the effects of within-group variation caused by individual migration or other factors that tend to increase variation within groups. Consequently, genetic group selection becomes a stronger force when migration is limited, or when other constraints maintain or enhance between-group variation. Knudsen (2002a) provides a detailed analysis of how the effect of migration among competing groups may support or undercut group selection.

In their enthusiasm to ditch the group selection concept, some gene-centered biologists maintain that in nature such conditions are rare. This misses the point that in principle *any* genetic selection process in a population can be formally partitioned into between-group and within-group components, even in the extreme case where groups have no real substance and the partitioning is arbitrary. In such extreme cases, group effects may be negligible, but that does not undermine the formal result that selection can generally be partitioned into the effects of between-group and within-group variation. Furthermore, meaningful groups exist in nature within populations of several species, so we are not confined to extreme cases. Consequently, genetic group selection cannot be ruled out *a priori.* Determining the degree to which it operates in nature is very much an empirical matter, which depends upon the species involved and its environment.

3. Cultural group selection

If cultural transmission is regarded as a process by which individuals of a species can learn from one another, then the phenomenon is not confined to humans (Bonner, 1980). However, learning is much more profound and extensive among humans than other species. Learning in other animals is rarely cumulative from generation to generation. Observational learning or high-fidelity detailed imitation is confined to a few species, including apes and possibly some birds. Consequently we largely confine our attention to cultural phenomena among humans.

To the alarm of some of his individualistic followers, Friedrich Hayek (1979, 1988) promoted the idea of cultural group selection in his later works. The crucial impact of cultural transmission on the issue of group selection was elaborated by anthropologists Robert Boyd and Peter Richerson (1985, pp. 204-40) and developed by Henrich (2004), D. S. Wilson (2002) and others. The key point is that cultural transmission effects can generate high degrees of conformism and cooperation within groups and overcome such factors such as individual migration or genetic mutations that tend to increase variation within groups. For example, cultural factors such as religious allegiance can help to reduce cheating and free-riding, where individuals enjoy the benefits of group solidarity without sharing fully in its costs.

Simon (1990) adds the further important possibility that individuals within groups will on average benefit from receiving and relying on the information received through social channels.[8] Unless society and its organizations generally cumulate bad information, docile people who enjoy a capacity to be instructed by society and to acquire skills on the basis of this socially transmitted information will experience a fitness advantage over those lacking the capacity. Thus, according to Simon, docile individuals experience a fitness advantage over non-docile people because of their use of socially transmitted skills and their conformity to socially sanctioned behaviour.

One of the most important processes involved is conformist transmission, namely a psychological propensity to imitate behaviors that are common in the immediate social group. This is widely established in social psychology, including by the famous experiments of Solomon Asch (1952) who showed that subjects generally conform to the opinions of others even when the majority were secretly instructed to make claims that were manifestly false. It has been argued that people increase their probability of imitating others when uncertainty, difficulty or incentives are greater (Baron *et al.*¸ 1996).

A second process is prestige-based transmission, involving a propensity to copy successful individuals that are sufficiently similar to themselves (Henrich and Gil-White, 2001). Like conformist transmission, this process can create clusters of individuals adopting similar behaviors. However, its evolutionary significance differs from that conformism. It means that actions that promoted the success of prestigious individuals may spread more rapidly than other less effective behaviors, thus shortcutting the haphazard processes of trial-and-error learning for many individuals.

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[8] See Knudsen (2003) for an elaboration and qualification of Simon's (1990) argument.

Although most social cultures teach people to conform to others and to emulate prestigious individuals, there are strong reasons to believe that these conformist and prestige-oriented propensities are also inherited as instincts. Their universality among human cultures supports this view, as well as the observation that other animal social species have similar propensities. In any social species there are strong reasons why these hard-wired propensities would be selected over time, as they generally bestow survival advantages for the group, even if the behavior generated is not necessarily optimal for the individual. Among humans these genetically inherited propensities are massively reinforced by our exceptional learning capacities in groups.

However, even if the instinctive component is large, these mechanisms do not mean that cultural differences between groups will disappear. On the contrary, conformist and prestige-transmission involve positive feedback effects that can lead to clusters of behaviors that are very different from group to group. Among humans, the learning effects and positive feedbacks are so strong that accidental factors and minor differences in the environment can lead to huge, path-dependent differences from group to group, and especially from culture to culture. In different cultures people cooperate in different ways over very different tasks. Customs and religious beliefs vary to an enormous degree.

Consequently, conformist and prestige-based transmission reduce diversity within groups but can lead to greater variation between groups. This enhances the conditions for strong cultural group selection. In contrast to the skepticism that greeted any idea of group selection in the 1970s, the reality of human cultural group selection is now widely established and accepted in the literature.

The debate over group selection establishes that the selection of groups occurs when interaction effects between individuals are sufficiently strong to mean that the fates of individuals are tied up to a significant degree with the survival of groups. The group has to embody internal structural relations that are sufficiently meaningful to facilitate causal interactions between individuals that enhance their survival as a group.

However, there has been relatively little discussion of how this outcome marries with the conceptual framework involving replicators, interactors and units of selection. Clearly, with the selection *of* groups, the group is established as a possible interactor.

An obvious question arises: when there is cultural selection *of* groups (as interactors), what replicators are selected (*for*)? Obviously, with genetic group selection the appropriate replicator is the gene. However, apart from some vague hand waving by some authors in the direction of "memes", the corresponding cultural replicators are much less clearly defined. Despite the enormous recent success of evolutionary cultural anthropologists in highlighting and modeling key evolutionary processes, this issue has been neglected.

It is now possible to make some progress towards understanding the detailed mechanisms and placing these processes in a generalized evolutionary framework. What would amount to an "internal genetics of culture"? In previous work we establish that habits are elemental replicators in human society and we consider the possibility of social replicators at even higher social levels. According to the criteria previously developed, habits are replicators because a habit *causes* the behavioral propensity that is copied, the acquired habit of behavior is *similar* to the first with respect to the behavior it can promote, and some *information* is transferred in the process. Habits also qualify as *generative* replicators because the original habit and its copy embody a *conditional generative mechanism:* the acquired habit is energized conditionally on the receipt of environmental signals and plays a role in the development of the individual with the habit.

Where do habit-replicators fit in the picture? Table 1 compares both interactors and replicators in both genetic and cultural selection, where groups selection occurs. The distinction between "selection of" and "selection for" is relevant here (Sober, 1984). With genetic group selection, the selection *of* groups is associated with selection *for* individuals (as interactors) and the selection *for* genes (as replicators). Simultaneously, as well as between-group selection, there is a degree of within-group selection *of* individuals leading to selection *for* genes. Between groups, cultural group selection involves the selection *of* groups and the selection *for* both individuals and individual habits. Simultaneously, cultural group selection involves a degree of within-group selection *of* individuals.

	Levels	Interactors	Replicators
Genetic Selection	Higher	Groups	—
	Lower	Individuals	Genes
Cultural Selection	Higher	Groups	—
	Lower	Individuals	Habits

Table 1.
Cultural and genetic selection of groups: interactors and replicators on two levels

Note that table 1 defines two levels of interaction and two corresponding levels of replication. The lower lever biological replicators (genes) relate to both individual human organisms and groups as possible interactors. The lower level cultural replicators (habits of individuals) relate to both individuals and groups as interactors. Consequently, both individuals and groups are carriers for (at least) two kinds of replicator, namely genes and habits.

When cultural and genetic group selection is combined, the result is that there are interactors on two levels (individuals and groups) and replicators on two levels (habits and genes). This establishes a picture of selection on multiple levels, as widely acknowledged in the literature on group selection and elsewhere.[9] We add to this insight a more precise identification of the replicators and interactors involved.

Our relatively simple schema shows that replicators (such as genes) may correspond to multiple interactors (namely individuals and groups) at different levels. Obversely, it shows that some interactors (such as groups) may embody multiple types of replicator (namely habits and genes).

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[9] See, for example, Lewontin (1970), Hull (1980, 1981), Brandon and Burian (1984), Boyd and Richerson (1985), Eldredge (1985), Buss (1987), Durham (1991), Goertzel (1992), Depew and Weber (1995), Maynard Smith and Szathmáry (1995, 1999), Brandon (1996), Sober and Wilson (1998), Keller (1999), and Kerr and Godfrey-Smith (2002).

Our argument leads to conclusion that differs from that of some other authors. For example, Laurent Keller and H. K. Reeve (1999) admit multiple levels of interactor, but consider genes as the only replicators. Accordingly, as well as the aforementioned resistance to the idea of the selection of groups, there is also some enduring resistance to the idea of other replicators above the level of the gene. However, the recent development of a more precise definition of a replicator should help to overcome this reluctance.

Despite Dawkins's (1976) introduction of the concept of the meme as a "new replicator," generally he emphasizes genetic replicators because he sees them as an outcome of the law of the "survival of the most stable" (Dawkins, 1989, p. 13). However, stability is relative to the evolutionary timescales involved. In biological evolution, major evolutionary changes take place over millions of years and timescales of less than about 20,000 years are relevant in a minority of cases only. David Hull (1988, pp. 440-68) has pointed out that some evolutionary processes in biology can be very rapid, such as mutations in viruses. But if we were to travel back 10,000 years in time we would be familiar with most of the plants and animal species that we found on Earth, despite major climatic changes. By contrast, human institutions and technology would be rudimentary and primitive compared to today; even the language would be unfamiliar. With social and cultural evolution we are considering timescales of less than 50,000 years and typically of a few hundred years or less. Relative to a lesser timescale, customs and habits have a sufficient degree of stability to be considered as replicators.

Dawkins (1989, pp. 34-5) says genes, "like diamonds, are forever" while "individuals and groups are like clouds in the sky or dust storms in the desert". Again the issue of timescales is relevant. Dawkins not only denies longevity, but also durable structure to individuals and groups at higher levels. We regard these denials as unwarranted, because they ignore the fact that the timescales of biological and social evolution are very different and consequently underestimate the structural durability of individuals and groups relative to their evolutionary context.

Nevertheless, in work on group selection so far, there has been relatively little discussion of the detailed mechanisms and structures that make the group a sustainable and coherent unit, other than the important reference to the evolution of conformist and cooperative traits among individuals. For example, there is relatively little consideration of why people are less inclined to migrate from group to group; instead a migration frequency is typically assumed as an endogenous variable. While group selection depends critically on structured interaction effects, the structures themselves are relatively neglected. The group is treated as an agglomeration of interacting individuals, with relatively little further consideration of its structural and binding features.

Social structure refers to a set of significant social rules, social relationships or social positions involving a multiplicity of individuals, with properties that are not properties of individuals taken alone. The properties of a social structure are additional to the sum of the properties of the individuals involved.

Even when group selection depends upon a propensity to conformism, implicitly it involves such a notion of structure. It involves more than an individual propensity. Myerson *et al.* (1991), Knudsen (2002a), Bergstrom (2002) and others have shown how the evolution of cooperation can be affected by the spatial clustering of "structured" populations. A social structure is implicated because relevant conformist behavior relates to behaviors and conventions that have become prominent in the group. Without such a social structure, conformist pressures would be less significant.

Typically, such structures bear the marks of the group's own unique history. As Henrich (2004) points out, different groups can develop different patterns of behavior. It is to these historically-determined group patterns of behavior that individuals may conform. The past emergence of prominent group patterns is a matter of path dependence. Once it is established then others must subsequently conform. Group selection is maintained by some sort of structured cohesion in the group, and is undermined as the effects of these structures over individuals are lessened.

The issue of structure bears on the question of the nature of culture and cultural transmission. Boyd and Richerson (1985, p. 33) define culture as "information capable of affecting individuals". They approvingly quote Ward Goodenough (1981, p. 54) who writes that: "People learn as individuals. Therefore, if culture is learned, its ultimate locus must be in individuals rather than in groups." The first sentence is valid: people *do* learn as individuals, and there is no supra-individual brain in which knowledge is stored. But the assumed implication in the second sentence is invalid and does not logically follow. Groups are not simply individuals; they consist of individuals plus interactive relations between individuals. In particular, group selection depends on the existence of beneficial interactive relations. Furthermore, and more generally, what individuals learn depends on their environment, this includes the other individuals with which they interact and is affected by the relations between all the individuals involved. Hence there can be no "ultimate locus" of analysis in individuals alone, without *additional* consideration of crucial *relations between individuals*.

For this reason, social and group entities are in general more than mere aggregates of individuals: they also involve relations between individuals (Hodgson, 2007a, 2007c). Just as culture is about relations between individuals as well as individuals themselves, knowledge in groups and organizations also depends on individual interactions. As Sidney Winter (1982, p. 72) puts it:

> What requires emphasis is that ... the learning experience is a shared experience of organization members ... Thus, even if the contents of the organizational memory are stored only in the form of memory traces in the memories of individual members, it is still an organizational knowledge in the sense that the fragment stored by each individual member is not fully meaningful or effective except in the context provided by the fragments stored by other members.

Winter argues that although tacit or other knowledge must reside in the nerve or brain cells of a set of human beings, its enactment depends crucially on the existence of a structured context in which individuals interact with each other. More broadly, much the "information" that is used and transmitted in a culture is embedded in social structures and organizations, in the sense that its existence and transmission depends on them. The information held by single individuals is typically context dependent; knowledge and structure are mutually intertwined (Langlois, 2001).

We elaborate on this significance of structure at various stages. Having established groups as possible interactors, the next step is to refine the definition of an interactor in the light of the issues involved.

4. Defining the interactor

Hull (1980, 1981, 1988) criticized Dawkins's concept of a "vehicle" because it downplayed the important causal role of the organism. Dawkins suggested that "vehicles" were simply convenient repositories for genetic replicators, which were regarded as doing most or all of the evolutionary work. Hull argued successfully that replication is only part of the evolutionary process, and interaction between the organism and its environment also plays a major part in determining the outcome. Hence he substituted the concept of an "interactor", defined 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" (1988, p. 408). This stresses not only the cohesive nature of the replicator-carrying unit but also the evolutionary importance of its interaction with its environment. These interactions cause differential replication of the replicators and the evolution of the population as a whole. To identify interactors we must look at processes of generative selection and mechanisms of differential replication among such populations.

Many cohesive wholes exist in nature, but only a few of them count as interactors in a selection process. According to Hull (1988, 2001), chromosomes, gametes, organisms, and possibly populations and species interact as cohesive wholes with *their* environment in a way that replication is differential.

As established above, for group selection to occur the members of the group must depend to some degree on one another, and on the group as a whole. Structured interactions in the group must promote conformism, limit migration, or both. Similarly, Hull's term "cohesive whole" indicates that its components mostly stick together and remain united. This suggests that the components depend critically on the survival of the whole, and that to some degree the components depend on the survival of each other.

In another essay (Hodgson and Knudsen, 2008) we also refer to the respective interactor of each replicator. We propose the general principle that every generative replicator is hosted by (at least) one interactor. In this paper we propose another (inverse) general principle: *that every interactor hosts at least one replicator*. With these points in mind we can attempt a more formal definition of an interactor.

This definition depends on the identification of an equivalent set of component replicators. This equivalent component set is defined as the set of replicators at the highest ontological level that are hosted by the interactor in question. For example, individuals host both habits and genes as replicators. Why are habits described as being at the higher level? Generally, entities at higher levels are grounded on those below, but involve novel and qualitative emergent properties resulting from particular interactions of lower-level elements. Habits depend on genes, but genes do not necessarily depend on habits. Crucially, habits have additional properties that are not possessed by genes alone. Consequently, habit replication is at a higher level than genetic replication.

We define $p_{i,j}$ as the probability, with respect to a given environment E, that entity i will (more or less immediately) expire as a functioning unit (losing much of its preceding integrity or cohesion) if entity j expires. By E we refer to one environmental state or a set of possible environmental states that are similar in relevant respects. These environmental conditions also include other interactors. For each interactor there is a corresponding non-empty equivalent component set of replicators R. In cases where an interactor hosts replicators at multiple ontological levels, the R refers exclusively to replicators that are at the highest possible ontological level within the interactor.

The component status of R implies that the replicators are relatively durable in comparison with their host interactor. This does not rule out the possibility of an interactor changing several of its component replicators, as firms may change their routines (Nelson and Winter, 1982). It simply means that the relevant replicators are so transient that they are unlikely to endure for the lifetime of their host replicator.[10]

We assume a world of multiple, competing interactors, and of other replicators that are not members of *R*. If an entity *w* is an interactor, then it must at least satisfy all of the following minimal conditions:

(1) **Integrity**: an interactor is a relatively cohesive entity with effective boundaries between itself and its surrounding environment, including other entities. This means that the internal relations among its component parts are generally more substantial and dense than the relations between the entity and elements in its external environment.

(2) **Sustained integrity despite environmental variation**: given shifting environmental states E_j, where *j* is a positive index over possible states of the environment, the interactor has sustained integrity, due to the nature of the components of the interactor and the internal relations between them.

(3) **Shared dependence of component replicators on the interactor**: given *E,* for every member *r* of *R*, $1 - p_{r,w} < \varepsilon$, where ε is small and nonnegative number.

(4) **Inclusion and shared organization of components**: every member *r* of *R* must be a component part of *w,* in the further sense that every *r* is within the boundary and part of the structure of *w*.

(5) **Replication dependent on the properties of the interactor and its environment**: every *w* has a set of properties C_w that, in the interaction of *w* with the given environment *E,* is a major factor in determining the (possibly different) set *R′* of successors of *R*.

The first of these conditions establishes the interactor as an integrated, cohesive and bounded entity, in a similar manner to the way in which the concept of a system is defined in systems theory (Bertalanffy, 1971; Miller, 1978). The second condition establishes the durability of this entity over a number of environmental states. The third condition means that if the cohesive whole perishes, then all the “component” replicators are also likely to perish. This implies some degree of cohesion and (given that some members of this replicator population are not members of *R)* it creates the possibility of differential replication among a whole population of similar types of replicator. The fourth condition elaborates the status of members of *R* as components of *w*. The first four criteria define an interactor as a cohesive whole. The fifth criterion defines an interactor as an entity that causes differential replication within this environment.

Note how the fifth criterion relates to our earlier discussion of group selection, where we identified the crucial issue of the covariance of group properties (x_g) with group fitness values (e_g), showing the extent which possession of such properties bestows fitness on groups. The identification of the group as a possible unit *of* selection and an interactor depends on this issue, and the fourth criterion generalizes this to apply to all possible interactors. Crucially, the existence of group selection depends on properties that simultaneously qualify the group as an interactor. As Robert Brandon (1996, p. 135) puts it: “when selection occurs at a given

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[10] It is also reasonable to suggest that the relative expected longevities of interactors and their component replicators is a crucial factor in determing the nature of the evolutionary process and its capacity to produce complex adaptations. If replicators were short-lived by comparison with their equivalent replicators, then selection processes would be less likely to replicators that reflected the lifetime adaptive experiences of their interactor hosts.

level, the entities at that level must be interactors." Accordingly, if groups are proper objects *of* selection, then that implies that they are interactors as well.[11]

However, our definition of an interactor is not confined to groups. It applies to all forms of interactor, in both nature and society, including organisms and human individuals. In the following sections we establish that business firms and other social organizations are also interactors.

Note that the use of the imprecise terms such as "relatively cohesive", "a major factor" and "much less than" (the symbol <<) imply a degree of fuzziness in this definition of an interactor. Similarly, our earlier definition of replication is dependent on fuzzy features such as "similarity". We also acknowledged different types and degrees of replication, redolent in some ways of the discussion of different types of replicator in the work of Eörs Szathmáry (2000), and Szathmáry and John Maynard Smith (1997). At least at the present stage, there seems little point in trying to get rid of the fuzziness. Indeed it may be an inevitable counterpart of the conceptual tools involved in trying to understand complex evolutionary processes. Rather than trying to establish sharp boundaries, the important thing is to define the essential and general characteristics of the key entities and mechanisms. The fact that there is a degree of fuzziness in these definitions does not mean that they lack meaning or value.[12]

Are human individuals interactors by this definition? The first condition applies as individuals are bounded and relatively cohesive entities. Their "component" replicators are their genes and instincts at the biological level and their habits at the social or cultural level. Clearly the second condition is satisfied, as these particular genes and habits will expire if the individual expires. Note that this does not rule out the possibility that similar or identical genes or habits continue to survive among other members of the population: it is simply the individual's genes or habits that are relevant in this condition. The third condition is also satisfied: genes are part of the molecular structure of the individual, habits are encoded in the individual's neurons, and both sets of replicators interact with the outside world through the individual. The fourth condition applies because the individual interacts with the environment, including other individuals, and creates the possibility of either genetic (sexual) replication or habit replication through imitation. Overall, individuals qualify as interactors, with respect both to component genes and component habits.

Consider how group selection relates to our definition of an interactor. With regard to the first condition, we have argued above that insofar as groups are meaningful entities in group selection and other terms, they must have a degree of cohesion and boundaries of limited permeability. With genetic group selection the replicators are genes, and the process can be formally partitioned into between-group and within-group components. The first component matters here. Between-group selection depends on the covariance of the genetic properties of different groups and their group fitness values, showing the extent which possession of a property bestows fitness on groups. Genetic group selection thus involves a widely shared

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[11] Brandon (1996, p. 137) considers interdemic group selection, where groups are more or less reproductively isolated. In this case, group selection occurs between by processes of differential group extinction and propagation and hence "the replicators are the groups themselves" as well as the gene replicators. However, Brandon's words were originally written in 1988, and before the recent definitional refinement of the concept of replication.

[12] Fuzziness does not necessarily mean imprecision. Fuzzy sets in mathematics, or "fuzzy" definitions expressed in exact probabilities, are fully and clearly defined. Furthermore, the proposition that all language and knowledge are intrinsically vague is well established in philosophy, by Russell (1923) among others.

genetic characteristic of individuals in a group that gives a fitness advantage to the group, which is not found to nearly the same extent in the genes of other groups. Given this group-related distribution of genes, the survival of the particular genes bestowing the fitness advantage depends crucially on the survival of the related group. The second condition for a group to be an interactor thus applies, as long a genetic group selection is significant.

Given this proviso, then the third condition is also satisfied. Genes are part of the physical structure of individuals and individuals are in turn structured into groups. Hence genes are part of the structure of groups. The fourth condition means in this context that the interaction of the group with its environment partly determines the genes within the group that are replicated. Clearly, this is part of the meaning of genetic group selection, as formalized by the Price equation.

Likewise, the four conditions also apply to groups involving cultural group selection, where habits are the replicators. The first condition for a group to be an interactor is clearly valid. Given a group-related distribution of habits, the survival of a particular habit bestowing a fitness advantage on a group depends crucially on the survival of that group. The second condition thus applies. The third condition is also satisfied because habits are encoded in the physical structure of individuals and individuals are in turn structured into groups. The fourth condition means in this context that the interaction of the group with its environment partly determines the habits prevalent the group that are replicated. If cultural group selection is significant, then groups likewise qualify as interactors.

Note that whether groups qualify as interactors depends critically on whether (genetic or cultural) group selection is significant. Ephemeral or arbitrarily demarcated groups do not qualify as interactors. With less cohesive groups, relations between individuals in the same group are of little or no more significance than relations between individuals in different groups. Consequently, in such cases, the replication of genes or habits depends little if anything on the properties of the group.

However, as argued above, for group selection to occur, groups have to be structured in some significant and cohesive manner, so as to prevent group selection being undermined by cheating, free-riding, mutation, or migration. Significant (genetic or cultural) group selection depends on social structures that promote cohesion and limit migration. Only when such conditions are present will group selection be significant; and it is only with such structural features that groups may qualify as interactors.

Consequently, organized groups such as tribes can be interactors. In such circumstances, while habit transmission is always from individual to individual, the behaviors that express these habits depend crucially on structured relations with others in the group.[13] This leads us to consider more closely the conditions under which organizations become interactors, and the nature of their constituent replicators.

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[13] This point was missed when we previously dismissed the possibility of groups *in general* as being interactors (Hodgson and Knudsen, 2004b). Our position is modified here to admit more openly the possibility of group interactors, as long as the groups have structures that create strong conditions for group selection.

5. Organizations as interactors and their component replicators

As noted above, groups vary enormously in terms of their structure and bonding, and only the more cohesively structured groups may qualify as interactors. This leads us to reflect on whether organizations in general and business firms in particular may qualify as interactors.

Before we do this, consider the companion term "institution". There is now quite a wide consensus that this term refers broadly to systems of rules that structure social interactions (Hodgson, 2006a; Knight, 1992; North, 1990). These rules include norms of behavior and social conventions, as well as legal or formal rules. Accordingly, systems of language, money, law, weights and measures, traffic conventions, table manners, and all organizations are institutions. However, not all institutions are organizations.[14]

Examples of organizations are tribes, families, states, business firms, universities, and trade unions. We define an organization as a special type of institution involving (a) criteria to establish its boundaries and to distinguish its members from its non-members, (b) principles of sovereignty concerning who is in charge and (c) a chain of command delineating responsibilities within the organization.[15] These conditions imply the existence of social roles or positions that have properties irreducible to those of their incumbents. Social positions carry significant powers and obligations that do not emanate from the characteristics of the individuals in those positions (Runciman, 2001, 2002).

A social position is a specified social relationship with other individuals or social positions (such as prime minister, production manager, or sales representative), which might in principle be occupied by alternative individuals. When an individual occupies a social position, he or she brings not only his or her own qualities or powers, but acquires additional qualities or powers associated with that position.

The introduction of social positions brings us to a still higher ontological level. Although the maintenance and replication of an organization and its social positions depends critically on habits of thought or behavior that sustain and buttress this social structure, it involves more than these individual habits. The organizational relations between individuals, including the relevant social positions, have to be sustained and possibly replicated as well.

To determine whether organizations are interactors, first we have to identify the equivalent component replicators at this higher level. Following the seminal work of Richard Nelson and Sidney Winter (1982), we identify and describe these as routines. Note that we are not using the term "routine" in the sense of an individual's routine behavior or schedule. Among evolutionary and institutional economists a consensus has emerged that routines relate to

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[14] Contrary to popular interpretation, Douglass North admits that business firms and organizations are institutions. See Hodgson (2006a) where North's own words are quoted on this point.

[15] This is a broader definition than some others. For example, for Aldrich (1999, p. 2) 'organizations are goal-directed, boundary maintaining, and socially constructed systems of human activity'. Aldrich then excludes 'families and friendship circles' from the set of organizations. The problem here is precisely what is meant by 'goal-directed'. Many firms act routinely, without explicit goals. If a family or friendship circle met together and declared a common objective, would they then become organizations? Because of the difficulty of defining goal-directed behavior in crucial boundary cases, it is suggested here that a better criterion is the existence of principles of sovereignty concerning who is in charge. This sovereignty makes possible the declaration of organizational goals, even if they are not made explicit. Organizations as here defined have the capacity for goal-directed behavior, irrespective of whether goals are actually declared. In this sense, an organization has the capacity to be a 'collective actor' (Knight, 1992, p. 3).

groups or organizations, whereas habits relate to individuals (Cohen *et al*., 1996; Dosi *et al.*, 2000). Individuals have habits; groups have routines. Routines are the organizational analog of habits. But routines do not simply refer to habits that are shared by many individuals in an organization or group. If this were the case there would be no need for the additional concept of a routine. Routines are not reducible to habits alone: they are organizational meta-habits, existing on a substrate of habituated individuals in a social structure. Routines are one ontological layer above habits themselves.

This does not mean that routines exist independently of individuals or that individuals take a subsidiary place in the analysis. Without individuals there would be neither organizations nor routines. Routines exist because structured interactions of individuals give rise to emergent properties that (by definition) are not properties of individuals taken severally.

Just as habits replicate from individual to individual, routines replicate from organization to organization. There is considerable research on this in the area of business studies. In studies of technological diffusion, organization studies, and the strategic management literature there is some discussion of the diffusion or replication of routines (Aldrich and Martinez, 2003; Becker and Lazaric, 2003; DiMaggio and Powell, 1983; Hannan and Freeman, 1984, 1989; Lazaric and Denis, 2001; Levitt and March, 1988; Rogers, 1995; Stinchcombe, 1990; Szulanski 1996, 2000; Zucker, 1987). Prominent mechanisms for the diffusion of routines involve the movement of employees from organization to organization, or independent experts or consultants that help to transfer knowledge and experience gained in one context to another. The above authors cite case studies involving the transfer of technologies, management procedures, corporate multidivisional structures, accounting conventions and much else. What is central to these transfers is the replication of organizational positions and practices, relationships. What is generally critical is the capacity of the receiving organization to accommodate and utilize these practices and relationships in the context of its own ingrained culture of habits and beliefs.

The replication of routines is both the replication of organizational dispositions to energize cue-triggered patterns of behavior within organizations, and the replication of social positions that define legitimate roles associated with the relevant individual interactions and the performance of the routine.

Now consider whether organizations are interactors, with respect to a set *R* of routines as their equivalent component replicators. Note that the habits or genes of individual members of the firm are not members of *R*, because they are at lower ontological level than routines, which are the highest-level replicators hosted by the organization. The protocol established above requires us to consider only those component replicators at the highest level.

The features of membership and internal power relations help to make organizations bounded and cohesive entities, thus potentially satisfying the first condition of an interactor. Crucially, routines that are members of *R* are likely to expire if the organization ceases to exist. If so, the second condition in the above definition of an interactor is satisfied. Routines are also components of the organization in the sense of the third condition. The fourth condition requires that the properties of the organization determine the expected number of its particular routines within a given environment. Depending on the organization’s ability to interact with its environment, its routines may become either more rare or more common. Consider modern business organizations: firms sometimes copy the routines of their more profitable competitors, and more profitable firms may expand by internally replicating their own routines. Many organizations thus qualify as interactors, at least by these minimal and preliminary conditions.

Consequently, organizations such as national states, tribes, families, business firms, universities, charities and churches may qualify as interactors. However, in many cases the definitional issues of boundaries, cohesion and expiration are problematic. Some of these difficulties are explored in the next section, with particular reference to business firms and other related structures.

Levels	Interactors	Replicators
Organizational	Organizations	Routines
Group	Groups	—
Individual	Individuals	Habits
Genetic	Individuals	Genes

Table 2.
The selection of organizations: interactors and replicators on four levels

Nevertheless, we are now in a position to expand the previous picture by considering the multiple levels of selection illustrated in table 2. The higher level – involving social positions and routines – is referred to as the organizational level. The next level is the group level, which is only meaningful for groups that do not qualify as organizations but are sufficiently cohesive for group selection to occur. The third level refers to individual-to-individual learning or cultural transmission, which can occur with minimal social organization: this is described as the individual level.[16] The fourth level is the genetic. Note that "individuals" appear as interactors on two levels. This is because individuals play dual roles in both genetic and cultural transmission.

When we consider the selection *of* organizations or individuals as interactors, the selection process also involves the selection *for* all the replicators at the equivalent and lower levels, plus the selection *of* any interactors of different type below. Hence the selection of organizations involves the selection for individuals, habits and genes. The cultural selection of groups or individuals involves selection for habits and genes. The genetic selection of individuals involves the selection for genes.

6. Business firms and other possible interactors

The firm typically has the structure and cohesion to qualify potentially as an interactor. The firm also has a corporate culture and structured environment, consisting of behavioral norms and routinized practices, which can augment individual skills and output per person (Argyris and Schön, 1996; Hodgson, 1998). In this way the firm can sometimes be a more efficient

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[16] Runciman (2001, 2002, 2005) refers to these as the "social" and "cultural" levels respectively. This terminology is slightly misleading, as all cultures and individual encounters could be regarded as "social".

means of organizing production than the market. The importance of structured relationships within the firm, the effects of corporate norms and culture, and the consequential firm-specific capabilities and learning effects, mean that the firm often has the necessary cohesion to qualify as an interactor (Hodgson and Knudsen, 2007).

Furthermore, the routines within the firm largely and normally share the common fate of the firm itself. If the survival of the firm is jeopardized, then skilled individuals and much physical capital can be moved elsewhere. But the firm is not simply an aggregate of individuals, physical capital and codifiable knowledge. It also consists of idiosyncratic structures, relationships and routines that typically are not readily tradable and are specific to the firm itself (Winter, 1988; Langlois and Robertson, 1995). These routines are important repositories of knowledge that is not readily codified or sold. This means that most or all of the firm's routines share the fate of the firm in which they reside.

The competitive selection of cohesive groups such as firms is due to their differential properties in a common environment. In turn, these differential properties of firms partly emanate from the organized structure of the firms as a whole, and are not merely due to the aggregate properties of the individuals in the firm, taken severally. Structured and cohesive interactions between individuals within the firm give rise to, and are properly regarded as, properties of the firm. These are a cause of differential profitability and thus differential replication of the firm's routines, i.e. competitive selection. This applies in the cases of both external selection (via inter-firm competition) and internal (vicarious) selection (by firm managers) of routines.

In economics and the social sciences more generally, the definition of the firm has been a matter of some neglect, and a consensus is lacking (Hodgson, 2002a). If the firm is identified as a legal corporation, then clear there are some firms in law that are more accurately described as constituents of other firms. Hence not all legal corporations, or "firms" in this sense, are interactors. Nevertheless, what is important about the firm is its integrity, cohesion and relative durability in the face of changing market conditions. The qualities that constitute a firm are illustrative of the more general qualities of an interactor.

The special focus on the business firm is useful because it illustrates some of the problems involved in defining and identifying interactors in the social and economic domain. For example, what about parts of the business firm, such as teams? Do these qualify as interactors?

The key criteria that come into play here are the first (concerning cohesion, durability and boundaries) and the fourth (concerning property-dependent replication) elements in the above definition of an interactor. With regard to the first condition, only in exceptional cases would the internal relations between individuals within the team remain for long periods as more dense and strong than their relations with the firm as such. When these conditions occur the firm is vulnerable to fragmentation, which is a relatively common outcome.[17] Generally, the individuals in the team remain members of the firm and are under the control of its management.

With regard to the fourth condition, we must consider interactions between the team and its environment that might cause the replication of the routines involved to be differential. Such

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[17] Such important cases include firm spin-offs, where a team of employees break away from a parent firm and create a new and separate firm of their own (Bünstorf, 2007). This is an important type of replication process that creates a new interactor.

replication could occur if the management of the firm decides to build another plant and build up a second and similar production team. Another possible mode of replication is the copying of the team type and its routines by another firm. What is notable in these examples is that the firm, as well as the team itself, plays a crucial causal role in team replication. This does not disqualify routines within teams from being replicators, but it does not make the team an interactor. Compared with the definition of a replicator, the definition of an interactor entails the additional criterion that the entity must interact with its environment as a cohesive unit, so causing differential replication. In the case of the team, the firm generally plays a more important role in this regard. Just as genes require very strong connections with organisms in order to bring about differential replication, so too do routines and teams require strong connections with the firm for differential replication to occur. For these reasons we do not generally consider teams within firms to be interactors.

Consider cases when one firm merges with, or is taken over by, another firm. This absorption of one entity into another may keep much of the features of the original entity intact. Component teams can survive the merger or acquisition of their host firm. In the natural world, the consumption of one organism by another means the dissolution of one of these organisms.[18] In the social or economic world, much of the cohesion of an original firm can sometimes be retained when it is merged with or acquired by another firm; absorption does not necessarily mean dissolution.

Does a merger or takeover amount to an expiration of the original firm? If the absorbed firm does not expire, then does it remain an interactor? The constitution, boundaries or title of the firm can change radically with a merger or acquisition. But on the other hand, many of its components, rules, property, routines and structures may remain intact. Some employees and customer goodwill may survive the metamorphosis. Clearly, merger or acquisition is not the same as bankruptcy or dissolution.

We have a case that is atypical of organisms in the natural world. When a cat eats a mouse, then the consumed interactor expires. But when the whale consumed the Biblical Jonah, he remained an interactor and lived atypically to tell the tale. With the takeover of one firm by another, the legal identity of one firm may expire, but some of its teams and their routines may live on, like Jonah, in the belly of the predator. In these Jonah-like cases, we need to develop further criteria to decide whether the original firm has expired or not. Expiration means the loss of preceding coherence, integrity and structure. Although mergers and acquisitions often lead to major structural changes, this is not always the case, and sometimes the acquired firm can function much as before. In other significant cases its preceding integrity and coherence is lost.[19]

Although they are far from the entire story, legal factors are important in defining the boundaries of the firm (Blair, 1999, 2003; Soderquist, 2000; Hodgson, 2002a; Hansmann *et al.*, 2006; Gindis, 2007). The firm is a legal entity, and its legal status is an important element,

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[18] However, there are some cases of symbiotic and close structural integration of separate organisms, as with lichen and the Portuguese Man O'War quasi-jellyfish.

[19] While we fully acknowledge real world cases of acquisitions or mergers resulting in little change, the literature on mergers and acquisitions suggests that the survival of acquired teams or routines within the acquiring or merged firm is relatively rare. With mergers, managers have often found it very difficult to fully integrate the component parts of merged firms. Acquisitions tend to work out better when the unit acquired is relatively small and the acquiring firm breaks up and replaces the prevailing culture of the acquired firm (Kusewitt, 1985; Datta, 1991; Walter, 1991).

alongside others, in its capacity to protect its assets and remain a cohesive whole. The legal status of the firm is crucial in cohering its interactions with a market environment, and its competition or cooperation with other firms. In legal and meaningful sense it is firms, not teams or divisions, that contract with customers or suppliers. Even if the firm has multiple plants or divisions, the firm has a degree of cohesion resulting from its unitary legal status as a single "legal person". Generally, the criterion of legal personhood is helpful in identifying the relevant boundaries between the firm and its environment and thereby identifying the relevant interactor. However, important exceptions do exist, especially where multiple legal entities in practice function as unitary integrated wholes, particularly as a result of concentrated ownership by a group of shareholders, or a single shareholder.

If a firm is broken into parts, or becomes bankrupt, or dissolves, then generally it ceases to exist, both as legal entity and as a specific interactor. Of course, there are examples of firms that appear to have more lives than a cat; often for dubious reasons they go bust to be re-opened the next day with unaltered structures and personnel, but new legal identities. At first glance this may lead us to disregard legal issues and treat the cat-like firm as a single, enduring entity. On closer inspection the legal issues are vital to understand what is going on. Such firms use the legal devices of dissolution or bankruptcy to escape from their former debts and obligations to customers. Such cases are akin to cloning: a new interactor emerges but using the "DNA" (that is component replicators such as routines and habit-based skills) and structures of their predecessors.

It has to be recognized that there are other relevant structures, such as conglomerates, business units, joint ventures, and so on, which involve multiple firms in close and relatively durable relations with one another. Many of these qualify as interactors according the criteria laid down here. Just as both groups and individuals are interactors, it is possible to have a nested hierarchy of different types of organization, where the members of one organization are themselves organizations. As noted above, similar nested hierarchies of objects of selection have been considered in biology. Consequently, there may be multiple levels of social interactors.

However, the existence of evolutionary selection on multiple levels does not necessarily involve replicators at different levels. At least one set of replicators must correspond to each level of interactor in a hierarchy of interactors, but there need not be a one-to-one correspondence between a hierarchy of replicators and a hierarchy of interactors (Brandon, 1998). Rigorous accounts of multiple level selection establish a hierarchy of interactors, without necessarily establishing a corresponding hierarchy of replicators as well. Consider, for example, the "Genetic Group Selection" column in Table 1. This shows two levels of interactor (individuals and groups) but replicators (genes) at one level only.

There is a hierarchy of interactors, including firms at one level and individuals at another. There is also a hierarchy of replicators, namely routines, habits and genes. How do these two hierarchies relate? Just as the selection *of* individual organisms in genetic evolution results in selection *for* the corresponding genes, selection *of* firms in a competitive environment results in the selection *for* some of the replicators associated with the firms, such as their constituent routines. That is, the current properties of the firm determine whether its routines, and the habits of its individual members, will be more common or more rare in the next time period.

Further descending the hierarchy, the selection *of* firms can also have a slight effect in the selection *for* human genes, given that employment opportunities in the firm can have an effect of the survival opportunities for human individuals. The selection *of* firms has effects that cascade down to the selection *of* individuals, and in turn to selection *for* genes. But selection *for* these lower-level, biological replicators can be ignored for purposes of analyzing economic evolution. It is too slight to be of significance, given the much slower evolutionary processes involved.

7. Conclusion

This article has demonstrated the connection between the analysis of group selection and the definition of an interactor. The possibility of group selection depends on the existence of structures and mechanisms in the group that limit migration or promote conformism. When group selection occurs the group functions as an interactor. Our analysis establishes that social organizations including business firms are generally interactors. Our proposal that the firm can be considered as an interactor is consistent with the general line of argument in Nelson and Winter's (1982) work. They considered firms as units of selection in a competitive process and "routines as genes" or replicators. We have endorsed and refined their perspective here, using insights from modern evolutionary theory and the philosophy of biology.

Many of these insights have been gained from the development of a framework of generalized Darwinism, where Darwinian ideas are applied to non-biological, as well as biological, evolving systems. The application of Darwinism to social or economic evolution depends simply on the existence of meaningful variation, replication and selection in that sphere. Understanding this, in turn, depends on adequately precise definitions of those Darwinian concepts. Within evolutionary economics, over a quarter of a century after the appearance of Nelson and Winter's (1982) classic work, these issues are only beginning to be explored.

As noted above, detailed exploration of the processes of replication and selection in any context requires the identification of the interactors and the levels of interaction. The contribution of this paper is, first, to establish in general and formal terms some of the essential characteristics of an interactor, applying to any evolutionary context. Second, on this basis, we have established the status of a firm as an interactor in social or economic evolution.

The motivation has in part been to explore the possible generalization of Darwinism to this sphere. The applicability or otherwise of a generalized Darwinism cannot be determined without such a conceptual, theoretical and empirically grounded exploration. The generalization of Darwinian principles is not a matter of analogy or metaphor, at any level or detail, but the possibility of a degree of general ontological communality at higher levels of abstraction. Such ontological similarity at general levels occurs alongside huge differences in the detailed mechanisms and processes of variation, replication and selection.

However, the exploration of the possibility of a generalization of a generalized Darwinism to within evolutionary economics is not merely a matter of idle curiosity. It is our conviction that the further development of work in this genre requires the development of a conceptual framework alongside detailed empirical work. Indeed, the organization and success of the latter depends to a large degree on success in the former, as all empirical enquiry is prompted and framed by questions of theory. As yet, Darwinism provides the only general evolutionary framework within which a complete causal explanation of evolutionary processes appears possible.

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