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Darwin's invisible hand: Market competition, evolution and the firm

Dominic D.P. Johnson [a,*], Michael E. Price [b], Mark Van Vugt [c]

[a] Department of Politics and International Relations, University of Oxford, Manor Road, Oxford OX1 3UQ, United Kingdom
[b] Department of Psychology, Brunel University, Uxbridge UB8 3PH, United Kingdom
[c] Department of Social and Organizational Psychology, VU University Amsterdam, 1081 BT Amsterdam, Netherlands

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ABSTRACT

Competition among firms has been suggested to reflect the ruthless logic of Darwinian selection: a free market is a struggle for survival, in which successful firms survive and unsuccessful ones die. This view appears to bolster three pillars of neoclassical economics: (1) that economic actors are self-interested; (2) that self-interest leads to public goods (Adam Smith's "invisible hand"); and (3) that together these lead to market optimization. However, this chain of reasoning leads to a paradox. We show that the application of Darwinian selection to competition among firms (as opposed to among individuals) invokes *group* selection, which leads to exactly the opposite predictions: notably altruism and the *suppression* of individual self-interest. We apply an alternative evolutionary model of economic competition, multi-level selection (MLS) theory, which integrates the effects of selection at both individual *and* group levels. This approach reveals that, while individuals may generally pursue their own self-interest (as in the standard evolutionary account), humans also have evolved traits that—as if led by an invisible hand—steer our self-interest to align with the good of the firm or wider society as well. But it is the hand of Darwin, not Smith.

1. Introduction

> Left to itself, natural selection should work fast to eliminate the weakest institutions in the market, which typically are gobbled up by the successful.
> —Niall Ferguson (2007)

> Greed is a vice in personal relations, but the whole point of markets is to turn this vice into an instrument of the public good.
> —Michael Sandel (2009)

> If greed is good, is altruism bad?
> —Hugh Hendry (2009)

Evolutionary theory is increasingly used to explain the behavior of individuals and organizations in a range of disciplines spanning psychology, politics, law and beyond (Barkow, 2006; Fowler and Schreiber, 2008; Gintis, 2007). Economics is no exception and in fact has a long history of drawing on insights from evolutionary theory (Fagerberg, 2003; Nelson and Winter, 1982; Veblen, 1898; Witt, 2003). Economic systems can be considered as Darwinian arenas in which a "survival

* Corresponding author. Tel.: +44 01865 278700.
E-mail addresses: dominic.johnson@politics.ox.ac.uk (D.D.P. Johnson), michael.price@brunel.ac.uk (M.E. Price), m.van.vugt@vu.nl (M. Van Vugt).

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Table 1
Competition among firms has been argued to represent a process of Darwinian selection (theory #1), with implications that match neoclassical economics (#2). In fact, competition among firms invokes group selection (#3). Group selection is also a flawed model, however, because the interests of groups and the interests of individuals within groups often act in opposing directions. Therefore, if we are to apply evolution to market competition, we need to utilize "multi-level selection" (MLS) theory (#4), which accounts for selection and adaptation at *both* individual and group levels. This approach leads to very different implications and novel predictions for the behavior of firms and workers, how they interact, and how they vary with context.

Theory	Level of selection	Implications		
		Economic actors are self-interested[a]	Self-interest contributes to the public good (the "invisible hand")	Market optimization
1. Schumpeter/Friedman/Ferguson	Individual	Yes	Yes	Yes
2. Neoclassical economics	N/A	Yes	Yes	Yes
3. Simple group selection	Group	No	No	No
4. Multi-level selection (MLS) theory	Both	Sometimes	Sometimes	Sometimes

[a] Note that "economic actors" could refer to either individuals *or* firms. Because the observation of interest is competition among firms, but theoretical debates center on assumptions about individual human behavior and human nature, we need to look at both individuals and firms, which is precisely why MLS theory is so important.

of the fittest" environment means successful firms survive while unsuccessful ones die. The idea is commonly invoked by casual observers—especially in the wake of the 2008 financial crisis—but it has been seriously championed by economists and economic historians such as Schumpeter (1961, 2008[1942]), Friedman (1954, 1970), and Ferguson (2007, 2008). However, the Darwinian selection of firms generates a significant paradox.

By invoking the idea that market competition is subject to ruthless Darwinian selection, people tend to conclude that: (1) economic actors are self-interested; (2) self-interest contributes to the public good (Adam Smith's "invisible hand"); and (3) the combination of these two assumptions will lead to market optimization. In short, Darwinian selection among firms appears to perfectly bolster neoclassical economics.

Ironically, however, this vision of events is in fact a *group selection* argument. Firms are by definition *groups* of individuals. Competition among firms therefore implies selection pressure acting on groups, not individuals, and resulting in adaptations that serve the interest of groups, not individuals (van den Bergh and Gowdy, 2009). This has significant consequences. Group selection, as opposed to conventional Darwinian selection at the individual level, leads to the emergence of traits that, in direct opposition to the predictions given above, act *against* self-interest: (1) other-regarding preferences; (2) altruism; and (3) a concern for group welfare which does not necessarily optimize material outputs for individuals or even for the firm or society as a whole. In short, applying evolutionary logic to economics seems to undermine the very behaviors its proponents seek to explain.

A 21st century understanding of evolutionary biology offers a way out of this paradox. We apply multi-level selection (MLS) theory (Okasha, 2006; Wilson, 2006; Wilson and Gowdy, this issue; Wilson et al., 2008; Wilson and Wilson, 2007) to examine two simultaneous and often opposing forces: (1) the interest of the group/firm as a whole; and (2) the interest of individuals *within* the group/firm (Table 1 outlines key differences between these alternative perspectives, along with our own proposal).[1] As in nature, these two forces are in constant interaction, generating complex outcomes, but outcomes that are predictable given knowledge of evolutionary processes and resulting adaptations.[2] In particular, knowledge of evolved human behavioral tendencies (e.g. cooperation, status, leadership, fairness, sex differences, and inter-group competition) allows us to specify conditions under which more individual, or more groupish, behaviors will be expressed. These predictions—unique to an evolutionary approach—may be useful for firms, managers, and society if we are to understand and improve economic efficiency, output or ethics.

Note, however, that there is a sinister implication. Group selection leads to pro-social outcomes such as altruism—*but only within the group*. Between groups, group selection can lead to competition that is even more intense and savage than competition among individuals. In-group members share more common interests than they do with out-group members. Individuals may therefore be selected to jostle with each other, but selected to actually damage or destroy rival groups (Choi and Bowles, 2007; Van Vugt et al., 2007). In the context of modern economic competition, such behavior might be manifested as intellectual theft, hostile take-overs, personnel poaching, costly price wars, fraudulent behavior, misinforming customers and share holders, and sabotage. Schumpeter, Friedman and Ferguson may thus have been right to place the ruthless logic of market competition at the door of natural selection, but for the wrong reasons. Contrary to the reassuring logic of Smith's invisible hand, left to themselves evolved human preferences can lead to disaster in the modern world (Frank, 2011).

[1] Let us define exactly what we mean by "self-interest" because alternative meanings lead to different implications in economics and biology. Self-interest can be defined (among other definitions) in terms of seeking: (1) *absolute* fitness (or utility); or (2) *relative* fitness (or utility) compared to other actors. Throughout this paper, we use definition #2 because, from the standpoint of genetic or cultural evolution, all that matters is which traits do well compared with other traits. Evolution selects traits that perform *better* than others, not the best traits possible. This distinction may be especially important because economic self-interest often follows definition #1, in which entities attempt to maximize their own absolute utility, irrespective of others.

[2] We note the literature on "intrinsic" versus "extrinsic" motivations that affect people's behavior in different ways (e.g. Bénabou and Tirole, 2003; Frey, 1994). Here we take a different approach in deriving evolutionary predictions for when individuals' interests should diverge or converge with the interests of the groups to which they belong.

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2. The market as a Darwinian arena

It is common to view (or criticize) the commercial world as a ruthless one in which individuals, managers, and firms are at each others' throats, vying for market share and profit at the expense of all else. The almost automatic analogy people tend to make is to a Darwinian "struggle for survival", in which the most self-interested, ruthless actors survive while altruistic, hesitant actors fail. Although recognized as an unfortunate state of affairs, there is often a sense of wisdom attributed to this "hard-nosed" or "realistic" outlook, and those who want to succeed—at least in Western capitalist free markets—must deal with it rather than lament it. Indeed, the Darwinian view is often evoked as a recommendation as well as an observation: "Be tough and give no quarter to your rivals or you will be exploited to extinction."

In principle, there is no reason why the logic of evolution should not apply to economic entities. Darwinian selection occurs whenever there are three simple features in place: (1) variation in characteristics; (2) selection of some characteristics over others; and (3) replication of surviving characteristics. One of the reasons Darwin's theory is so powerful is that the process of adaptation by natural selection can apply to *any* interacting agents, biological or not, as long as these three features occur. Such features are present (in some form and to some extent) in a wide variety of domains, including competition among states, firms, machines and ideas as well as among individuals. Where this is the case, the principles of Darwinian selection can be utilized to understand the dynamics of change and how to improve adaptation (Benyus, 2002; Johnson, 2009; Sagarin, 2012). Darwinian "genetic algorithms" are used by engineers to design ship hulls, for example, because testing many thousands of variations in an evolutionary process of trial and error can lead to better designs than a human designer could achieve.

As a simple *analogy*, Darwinian selection appears to be a good fit to many cases of economic competition. Yet some influential authors have argued that it is more than an analogy—that economic competition *is* a Darwinian process. Milton Friedman, for example, did not always explicitly refer to Darwin or evolution, but made a "survival of the fittest" argument for the way firms do—and should—work (Friedman, 1954, 1970). As Gowdy et al. (2013) describe his position, "Given the assumptions of perfect competition and profit maximization, inefficient firms will be driven out of business and regulation will only keep alive those that should be dead." Friedman not only thought this was a good description of how firms behave, but also that this behavior was best for society: "there is one and only one social responsibility of business—to use its resources and engage in activities designed to increase its profits" (Friedman, 1970).

Niall Ferguson *did* explicitly invoke Darwin: "Financial organisms are in competition with one another for finite resources. At certain times and in certain places, certain species may become dominant. But innovations by competitor species, or the emergence of altogether new species, prevent any permanent hierarchy or monoculture from emerging. Broadly speaking, the law of the 'survival of the fittest' applies. Institutions with a 'selfish gene' that is good at self-replication (and self-perpetuation) will tend to endure and proliferate" (Ferguson, 2007, 2008, pp. 350–351). Ferguson also sees that this can be a useful process, culling the weak and growing the strong. Foreshadows of such logic can be traced further back, for example to social conservatives in Britain after Darwin's theory was published, who saw natural selection as a "justification for the 'natural harmony' of unrestrained capitalism" (Gowdy et al., 2013). And as Ferguson notes, there is a more formal precedent in the invocation of Darwinian selection in the economic theories of Joseph Schumpeter and his notion of "creative destruction" (Fagerberg, 2003; Nelson, 2012; Schumpeter, 1961, 2008[1942]).[3]

We are sympathetic to the idea that Darwinian selection offers a useful, if imperfect, model of economic competition. Commercial firms are born, grow, survive and die. The constant innovation, intense competition and high rates of failure among competing firms (Camerer and Lovallo, 1999; Ferguson, 2008)[4] suggest, as per the three conditions for Darwinian selection, that: (1) there is considerable variation among firms; (2) that a process of selection favors some firms over others; and (3) that successful firms (or successful practices within them) proliferate and unsuccessful ones fail. We also agree that this may be a constructive process, because selection is likely to lead to more efficient firms and better products, if not a nicer world.

3. The problem: market competition invokes group selection

Despite its attractions, the evolutionary model of economic competition creates a major paradox. Ferguson goes so far as to say that evolution "offers a better model for understanding financial change than any other we have" (Ferguson, 2008, p. 352).[5] But as currently formulated, the causes and consequences are inconsistent. If selection acts at the level of firms, then we are invoking *group selection* (van den Bergh and Gowdy, 2009; Wilson and Sober, 1994).[6] This means that, contrary to

[3] Schumpeter, Friedman and Ferguson had different approaches and interests. For example Schumpeter focused on innovation, Friedman focused on efficiency, and Ferguson focused on banks and financial institutions. The common theme, however, is their vision of an evolutionary process of selection among competing economic units and if and how this leads to efficient markets.

[4] Ferguson cites evidence of an "extinction rate" of around 10% of American firms every year, and much higher in some specific sectors (Ferguson, 2008, p. 349).

[5] Ferguson does note several important differences between biological and financial evolution, such as the speed of change and the role of human "intelligent" designers behind the latter.

[6] In this article, we use "firms" and "groups" somewhat interchangeably. "Group selection" and "group" are the terms used in the evolutionary biology literature, but the groups of interest to us here are commercial firms, which of course comprise of collections of individual humans.

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Table 2
Differences in the role of selection at the level of workers and firms.

	Level of selection	Unit of selection	Era	Adaptations primarily help
Workers	Individual	Gene	Past	Self
Firms	Group	Ideas/practices	Today/recent	Group

Schumpeter, Friedman and Ferguson, we should expect the *suppression* of self-interest among individuals, not its flourishing. Firms with less self-interested workers will compete more effectively and spread, at the expense of firms with more self-interested workers, which will compete less effectively and decline. In other words, the model predicts nasty firms but nice people. Firms vie for market share and profits, group selection would predict, while individuals within those firms sacrifice their own interests for the good of the group. They will work long hours, accept low status and low salaries, cooperate with each other, share resources, accept hierarchy, obey their bosses, volunteer for extra duties, and never help or move to rival firms.[7]

Schumpeter, Friedman and Ferguson would no doubt immediately claim that they expect no such thing. But it is, in fact, a direct implication of the Darwinian argument they advance. If selection acts at the level of groups (that is, among firms), as they suggest, then individual self-interest will disappear over time.

In reality, firms are made up of individual human beings, with various goals and motives but, most importantly, considerable self-interest. Darwinian selection at the level of groups implies that the interests of individual group-members are weaker or synonymous with the interests of the group as a whole. In the real world, they are not. There is often some overlap, of course: the boss will want his workers to perform well; the workers will want the firm to survive. But we also have strong personal desires for salary, status, rank, reputation, free time, and better jobs. In short, any evolutionary model must account for two opposing processes that operate simultaneously: competition between firms *and* competition between the individuals within them.

4. A new evolutionary framework: multi-level selection (MLS) theory

Multi-level selection (MLS) theory is a new approach in evolutionary biology, which calls for empirical evaluation of the strength of selection acting at all levels (gene, individual, and group), rather than assuming only one or the other. This inclusive and integrative approach offers new insights that previous evolutionary accounts have missed (see Wilson and Gowdy, this issue, for examples). MLS theory is essential to understanding not only so-called "major transitions" in the history of life (groups of organelles forming cells, groups of cells forming multicellular organisms, groups of organisms forming social colonies, and so on), but also the economic behavior of individuals and organizations today (Maynard Smith and Szathmary, 1995; Okasha, 2006; Wilson, 2002; Wilson and Sober, 1994; Wilson et al., 2008; Wilson and Wilson, 2007).

A multi-level selection approach is important not because it supplants Schumpeter, Friedman, and Ferguson's group-level view of market competition, but because it acknowledges and *integrates* those factors at work at the level of the group with other factors at work at the level of the individual. In doing so, it generates novel insights because sometimes these factors align and sometimes they oppose each other, but *when* they do so can be predicted by evolutionary theory. Both levels of analysis are potentially important in the real world (in nature and in economics). What matters is the ability to predict *which* interests—individual or group—dominate in any given case, domain, or time period.

At one extreme, if selection among groups is frequent and severe, we may expect an increased alignment of individual and group interests resulting in successful firms with hard working, groupish, highly committed employees. At the other extreme, if selection among groups is rare and weak, we may expect increased conflicts of interests resulting in inefficient firms and lazy, self-interested workers.

In the following, we focus on commercial firms. Firms comprise several possible levels of analysis: the entire firm, the board of directors, shareholders, employees, work teams, and individuals, among others. However, we focus on the two levels that are most intuitive and important in understanding economic behavior: individuals and entire firms. At each level, selection acts in different ways (Table 2). Individuals have physiological and psychological adaptations that evolved as the result of selection pressures in our evolutionary *past*, which are genetically encoded. Firms, by contrast, have organizational and procedural adaptations that evolved as the result of selection pressures in the *contemporary or recent* environment, and which are not genetically encoded—instead they are passed on by cultural and institutional practices being copied, imitated or transplanted by migrating workers.[8]

[7] It is important to stress that group-level selection favors any mechanism that causes groups to survive and reproduce better than other groups. This can include traits that are overtly altruistic and cooperative, but it can also include forms of within-group competition that are good for the group (such as competition over productivity or "competitive altruism", see Roberts, 1998). Therefore, not all forms of competition among workers are bad for the firm.

[8] Of course, the *interactions* between these levels are also interesting and important: adaptations at the individual level may shape or limit cultural innovation and spread (see Section 6 for more on this).

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4.1. Why the principal-agent literature is not good enough

Much of the above discussion about divergent interests of workers and the firm will already be familiar to economists as an example of the "principal-agent" problem (Laffont and Martimort, 2001). One might therefore think that evolutionists are reinventing the wheel with their own "version" of the principal-agent problem. However, as Wilson and Gowdy (this issue) nicely explain, a MLS theory perspective actually brings a range of original insights. While the principal-agent problem may capture conflicting interests among different actors (such as individuals and groups), it does not inform us as to the underlying *causes* of their differing interests or behavior (rather, it focuses on strategic interaction when their interests are a given). This is where evolutionary theory, and Tinbergen's (1963) four causes of behavior—phylogeny, development, proximate mechanisms and ultimate function—become helpful. Evolution helps to explain *why* people want or do things. We can draw on a wealth of scientific information on human biology, human psychology, and how people interact in groups, to derive specific predictions for when principals and agents should be more or less cooperative and productive (Price and Johnson, 2011).[9]

4.2. Implications of MLS theory for the behavior of individuals

Individual selection and group selection are often presented as mutually exclusive—alternative hypotheses in direct competition with each other, one of which will turn out to be correct and the other wrong. In reality evolutionary change can occur at more than one level; this is the whole point of *multi*-level selection theory, in that it accounts for selection pressures that may be acting at *both* individual and group levels.

The implications of MLS theory for individual adaptations are, in principle, no different from those of current evolutionary psychology. Both approaches are interested in identifying what evolved psychological mechanisms we have and how they work, and both allow for the possibility that the evolution of human behavior was influenced by within-group *and* between-group selection pressures acting on individual fitness in our evolutionary history. However, they are often contrasted because many researchers take a strong stance on *which* level of selection or mode of inheritance has been *more important*. A core contingent of contemporary evolutionary psychologists do not find the *empirical* evidence for group-level selection compelling. This group is sometimes referred to as the "Santa Barbara School" of evolutionary psychology, after the location of pioneers John Tooby, Leda Cosmides, and Donald Symons, but also includes Martin Daly, Margo Wilson, Steven Pinker, David Buss and others. The Santa Barbara School argues that selection pressures have primarily acted at the individual level and evolved adaptations primarily serve individual, not group interests. They object to invoking selection at the group level as fundamentally problematic (theoretically or empirically).

David Sloan Wilson has made efforts to show that that the Santa Barbara School (and inclusive fitness theory more generally) and multi-level selection theory are simply alternative perspectives, not alternative theories (Wilson, 2012). All evolutionary models of social behavior must include individual and group components, whatever they may be called or however they may be represented mathematically. The key point we want to stress is that a MLS approach does not reject the influence of individual selection. It explicitly includes it. The MLS framework, and researchers using it, may often find that in fact selection at the individual level is strong and selection at the group level weak. The mistake, however, is to fail to *examine* the effects of selection at all relevant levels. They must be evaluated, not assumed.

The Santa Barbara school suggests that human neural tissue is organized by virtue of the same fundamental design principle as all other organismal tissue, that is, into domain specific, functionally specialized adaptations (Barkow et al., 1992; Pinker, 2002). These adaptations are "if-then" information-processing mechanisms that produce specific psychological and/or behavioral outputs in response to informational inputs that indicate the presence of some specific adaptive problem (e.g., if you experience hunger, then seek food). These outputs would have been—on average, in ancestral environments—fitness-enhancing solutions to the adaptive problem at hand. Like all adaptations, mental adaptations are "designed" by and for *past* environments; they thus may or may not function adaptively, or produce behavior that seems "rational", in *modern* environments. Therefore, evolutionary psychologists are often careful to emphasize that humans are *adaptation executors*, rather than maximizers of rationality, fitness, or any other currency (Tooby and Cosmides, 1992). For this reason, evolutionary theory makes predictions about human behavior that are not made by standard economic and rational choice theories. Rather, as Wilson and Gowdy (this issue) explain, predicted behavior emerges from a consideration of human evolution along Tinbergen's four dimensions—a traits' evolutionary ancestry, developmental pathways, proximate mechanisms, and ultimate adaptive function. We examine several examples in Section 5.

Although evolutionary psychology is perfectly consistent with MLS theory, these two approaches are often perceived (among scholars, journalists and the informed public) as having divergent expectations: should evolution favor individually fitness-enhancing (self-interested) behavior or individually fitness-damaging (self-sacrificial) behavior? Neither approach inherently rules out adaptation at the other level. They just draw attention to different perspectives on which level has been empirically more important in human evolutionary history.

[9] See Wilson, Ostrom and Cox (this issue) for an examination of how the principal-agent problem can be addressed from an evolutionary perspective. While in economics the solution has been to assign property rights, Ostrom pioneered an alternative approach that fosters group level incentives.

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4.3. Implications of MLS theory for the behavior of firms

Up to now we have introduced group selection without any discussion of what exactly is selected (the "unit" of selection; see Table 2). As should be clear from the context, however, if selection is acting on contemporary firms today, then we are talking about *cultural* group selection of ideas and practices among them. We are not invoking any version of biological group selection in which genes spread as the group expands. A purely *cultural* trait, such as making bows and arrows, can lend advantages to a group in competition with other groups, and such a trait can become more common in the population if the advantaged group tends to supplant rival groups, or tends to be imitated by other groups who wish to emulate its success (Henrich, 2004; Richerson and Boyd, 2004). No genes are involved in such a process of selection (other than those that influence the way in which humans learn or imitate), but the process is a "Darwinian" one nevertheless.[10] As outlined earlier, if there is *variation* among traits, *selection* of those that work and discarding of those that fail, and the *replication* of successful traits, we have Darwinian selection. Because ideas can spread so quickly, not needing to wait for genetic evolution to occur generation-by-generation, *cultural* evolution can be significantly faster and more powerful than biological evolution.

Now to return to the topic of interest: market competition. Competition among firms may be a quintessential example of cultural selection. Indeed, one of the leading scholars of cultural evolution theory, Anthropologist Lee Cronk, uses market competition in his classes to illustrate how cultural selection works (Cronk and Leech, 2013, see pp. 116–117). Although Schumpeter, Friedman and Ferguson highlight the fact that numerous firms emerge, compete aggressively, and many fail, the actual turnover of firms may not really be high enough for Darwinian selection to work in terms of a culling process in which poorly performing firms "die" altogether (the rate of selection may be too slow). Cultural selection, however, has no such constraints. Whatever the rate at which firms appear and disappear, *ideas* and *practices* within them (cultural traits) are under constant and rapid selection as they jump between minds and are copied by other firms. The process of cultural selection has long been recognized (for a review see Cronk, 1999; Richerson and Boyd, 2004), though under different guises and labels, and applied to a wide range of topics including how organizations and institutions adapt (Hannan and Freeman, 1977, 1989; Viola and Snidal, 2006).

4.4. Summarizing the utility of MLS theory

Several implications of MLS theory turn out to be essential to understanding the interaction of firms and workers. First, the concept of individually adaptive psychological mechanisms is fundamental, because these mechanisms enable higher-level outcomes—such as firm formation, and the generation of firm-advantageous cultural adaptations—to occur in the first place. Good managers and entrepreneurs often benefit from the ambition, persistence and search for knowledge that evolution bestowed on them or their employees. Cultural traits cannot arise, change, or spread without evolved human brains to generate and accommodate them. An understanding of these psychological adaptations is also indispensable for predicting many aspects of individual behavior *within* firms, including cooperation, status seeking, leadership, fairness, sex differences, and inter-group competition (discussed below).

Second, if selection also operated at the level of the group in human evolutionary history—that is, if ancestral individuals could often acquire more status and resources via group cooperation than they could via individual action, and mean fitness in some groups was higher than in others—then this process is important for understanding why individuals are motivated to form and join firms in the first place (Bowles, 2006; Wilson and Wilson, 2007).

Third, *cultural* group selection is also important (Cronk and Leech, 2013); most arguments about cultural evolution focus not on *if* it happens but *how* (Bolhuis et al., 2011; Cronk, 1999; Richerson and Boyd, 2004). In the context of economic competition, cultural selection is clearly important for understanding why some firms fail and others succeed, and how it leads to the evolution of corporate cultures that are relatively competitive and functional at the group level.

The point is that both individual and group effects matter. The notion that employees will be motivated to sacrifice themselves for the good of the firm is implied by Schumpeter, Friedman and Ferguson, but it is only one possible outcome of MLS theory. There are of course many examples of firms and other types of groups that exhort their members to work for the good of the group (e.g. a coach telling his players, "there is no I in TEAM!"). But what is interesting about such examples is why such group thinking needs to be exhorted in the first place. People do not seem to need to be cajoled into being selfish, but they do often seem to need to be cajoled into cooperating. A more integrative model we see emerging from MLS—as we describe in more detail below—is one that acknowledges cultural group selection but takes into account the powerful role of individual section as well. Employees strive for the benefits of cooperating in groups, while simultaneously striving to acquire a proportionally fair share of compensation for their efforts, and to avoid being exploited by free riders. The key, therefore, is not to strike some (inefficient) compromise between the interests of individuals and their group, but to work with the grain of human nature to bring individual and group interests into alignment. With subtle management and organizational practices, this might be achieved relatively easily and at low cost.

[10] There may be genetic *consequences*, of course, as per gene-culture co-evolution.

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5. Human nature and the success of the firm: predictions and evidence

Accumulating empirical knowledge of evolved human tendencies offers predictions not only for how individuals are likely to behave in this or that circumstance, but also how they are likely to behave *when in groups*. The thrust of this section is that individual self-interest often serves (or can be aligned to serve) group interests as well.

If humans were blank slates, with decision-making and behavior determined only by experience and learning, it would be extremely difficult to make general predictions about behavior because of factors unique to each individual and situation. Fortunately (at least from this perspective), humans are not blank slates (Barkow et al., 1992; Fuentes, 2008; Pinker, 2002). Instead, our physiology and psychology has been fashioned by evolution into adaptations to solve tasks that were important to survival and reproduction in our evolutionary history. This has resulted in many universal, species-typical behaviors, with known sources of variation, allowing us to make general predictions about human behavior and how it is likely to change across different scenarios. Other factors will be at play too, but predictions derived from evolutionary principles can explain a significant portion of the variation.

One of the triumphs of recent years in experimental psychology and evolutionary anthropology has been simply to document the many regularities of human behavior across individuals and cultures. Here, we draw on research on these regularities to make predictions for how individuals are expected to respond to working in firms, and highlight how these predictions are not generated directly by any other theory, including rational choice theory. Our goal is not to provide a comprehensive review of predictions made by evolutionary theory for human behavior in firms (for some recent reviews, see Price and Johnson, 2011; Saad, 2011; Van Vugt and Kameda, 2012; Wilson et al., 2008). What we want to do is highlight key examples of predictions that have a special salience for MLS theory: (1) cooperation; (2) status seeking; (3) leadership; (4) fairness; (5) sex differences; and (6) inter-group competition (all of which are summarized in Table 3). We devote most space to the first of these—adaptations for cooperation—because this is vital to understanding the balance of individual versus firm interests.

5.1. Cooperation: individually adaptive advantages of group cooperation

Individuals are adapted to cooperate in groups, but do so in individually adaptive ways. That is, we are cooperative, but only so long as our own individual costs and benefits are taken into account. This prediction is supported by a wide range of results from laboratory and field studies, from several different disciplines. For example, equity theory (Adams, 1963)—one of the most successful and well-supported ideas in all of organizational behavior (Miner, 2003; Van Vugt and Van Lange, 2006)—predicts that people will be motivated to contribute to organizational goals when they perceive not only that they are rewarded for doing so, but that their reward-to-contribution ratio is not lower than others. Importantly for us, this means that they cooperate more when they are less individually disadvantaged relative to others (especially relative to free riders) within their group. This makes sense in terms of within-group selection—relative benefits matter. Motivation to cooperate is contingent on the perception that one is being treated "fairly", according to the logic of reciprocity among multiple individuals (Tooby et al., 2006). Similar results have been found in empirical and experimental public good games, in which players lose motivation to contribute to group efforts if their reward-to-contribution ratios are less than those of co-members—that is, if they detect free riding (Kurzban et al., 2001a; Price, 2006). In these games and in real-life collective action problems, if free-riding is perceived, then people attempt to curtail their own exploitation by withholding contributions and/or by sanctioning free riders in proportion to their vulnerability to exploitation (Price, 2005; Price et al., 2002).

More evidence for individually adaptive cooperation in groups includes competitive altruism, reputational effects, and partner choice. In cooperative groups with compensation practices that allocate higher rewards to higher contributors, members compete to be the highest (most "altruistic") contributors (Hardy and Vugt, 2006; Roberts, 1998). However when rewards are not tethered to individual contributions in this way, group members become more likely to free ride, especially if they perceive that they can get away with it (Fehr and Gächter, 2000). When people perceive that they can develop a reputation based on their behavior, they cooperate and punish free riders more (Milinski et al., 2002; Nowak and Sigmund, 1998, 2005) and when cooperators are given a choice of social partners, they choose each other and ostracize free riders (see Johnson et al., 2008, and references therein).

An alternative possible outcome of the interacting levels of selection in MLS theory—that it will generate cooperative behavior that is individually fitness damaging—is much less robustly supported. Some behaviors observed in economic games, such as cooperation in anonymous one-shot games, have been regarded as evidence for self-sacrificial behavior (Fehr and Fischbacher, 2003; Fehr and Gächter, 2002). However, these claims have been widely criticized (Burnham and Johnson, 2005; Hagen and Hammerstein, 2006; Trivers, 2004; West et al., 2011). While these critiques vary in their content, most emphasize that the elicitation of seemingly individually fitness damaging behavior in a research lab hardly constitutes evidence that the behavior would have been individually fitness damaging—or even present—under ecologically valid, ancestral conditions. The observed behavior may thus be an example of "evolutionary mismatch", in which behaviors that evolved to promote individual fitness in the past may not be fitness enhancing anymore in modern social and physical environments, especially contrived ones such as laboratory experiments. Firms are especially intriguing in the light of evolutionary mismatch, because while we have many adaptations for working in groups of other human beings, these adaptations were not designed to operate in groups of strangers working toward abstract tasks via computers and email, for example.

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Table 3
Evolved human traits that affect the performance of groups. For each example, we outline Tinbergen's four causes, the (null) rational choice prediction, predictions from multi-level selection (for individuals and groups), and management recommendations.

Trait	Tinbergen's four questions				Rational choice prediction	MLS prediction		Management recommendations
	Phylogeny	Development	Proximate mechanism	Ultimate function		Individuals	Groups	
Cooperation	Common to many taxa but extreme in humans	Observed early in childhood but many cooperation norms are taught and learned later	Genetics, physiology, hormones, psychological mechanisms	Increase value or stability of resources; obtain resources not possible on own	Maximize own payoffs at the expense of others	Reciprocity; competitive altruism; reputational effects; partner choice	Cooperation relies on equality of effort and reward; or sanctions	Transparency of effort and reward; reputational incentives; choice of work partners
Status seeking	Common to primates and many mammals	Importance of reputation inculcated early on in children	Testosterone, serotonin, psychological mechanisms	Greater access to resources	None (other than salary differences)	Seek status and prestige	Enjoy more motivated workers	Rank and status can be better (and cheaper) incentives than pay
Leadership	Common to primates and many mammals	Expressed early on in (especially male) children	Testosterone, serotonin, psychological mechanisms	Greater control of resources	None (other than salary differences)	Seek positions of power	Hierarchical and this can help or hurt productivity	Participatory decision-making can increase compliance
Fairness	Elements visible in other primates	Expressed in later years of child development	Unknown	Reciprocal cooperation when resources are unpredictable	Richer individuals prefer inequality and competition	Physically stronger individuals prefer inequality, and competition	Have a mixture of workers preferring inequality or egalitarianism	Rewards must be merit based; Windfall resources should be shared equally
Sex differences	Common to all mammals and many other taxa	Behavioral differences emerge very early in child development	Genetics, physiology, hormones, psychological mechanisms	Alternative strategies for maximizing fitness	No difference	Men much more sensitive to status, leadership, and competition	Work better with mixed sex groups (in some settings)	Male/female ratios in teams can be tailored for different tasks; male/female workers can be incentivized differently
Inter-group competition	Common to primates and many other taxa	Emerges early among children	In-group/out-group biases	Prevent exploitation, outcompete other groups	No difference	More motivated, cooperative in presence of rival groups	Are more productive in presence of rival groups	Market competition can increase motivation, efficiency and productivity

5.2. Status seeking and prestige

Unlike a standard rational choice perspective, which focuses on material rewards and punishments as incentives, MLS theory explicitly predicts that individuals will be powerfully motivated to strive for social status and prestige in firms (even at the expense of material rewards or the risk of punishment, Frank, 1985). This prediction is based on the notion that in ancestral environments, high status individuals—that is, individuals who were relatively more capable of bestowing benefits and/or imposing costs on other people—would have had relatively better access to many types of material, sexual, and social resources (Betzig, 1986; Davies and Shackelford 2008; Price et al., 2011; Sell et al., 2009). In short, status was a means to Darwinian fitness benefits and selection favored adaptations to seek and achieve it.

5.3. Leadership and dominance

MLS theory also explains why individuals would want to take on stressful and time consuming leadership and management positions in organizations. While they impose individual costs (partly but not always compensated by higher salaries) they are associated with higher social status rewards (King et al., 2009; O'Gorman et al., 2009). MLS theory also predicts that when competition between firms is fierce (and competition between individuals is comparatively weak), then the interests of managers and workers are relatively aligned and there is more participative decision-making and a fairer distribution of rewards. Yet when competition between firms is weak (and competition between individuals is comparatively strong), then management is more hierarchical and there is a greater tendency among managers to dominate workers and exploit co-workers for individual gain (Van Vugt et al., 2008).

5.4. Fairness and distributive justice

Wealthy people benefit more than poor people from inequality; thus, a common rational choice-inspired view is that individuals with better access to material resources will tend to prefer systems of distributive justice that permit inequality and competition. Although this view has support (Gelman et al., 2010; Piff et al., 2010, 2012), an MLS perspective generates the additional prediction that people who would have been more able to compete for resources in *ancestral* environments—regardless of their ability to do so in *modern* environments—will also tend to prefer less egalitarian distribution systems. This prediction is supported by studies suggesting that males with more physically "formidable" bodies are less egalitarian, and more competitive and disputatious, on a variety of measures (Price et al., 2011, 2012; Sanchez-Pages and Turiegano, 2010; Sell et al., 2009; Zaatari and Trivers, 2007). Further, perceptions about the extent to which a resource ought to be shared can be predicted by information about the resource's availability. For example, people believe that unpredictable "windfall" resources (e.g. an unexpectedly large herd of game animals, or surprisingly high profits) ought to be shared widely. This belief would have made sense as a risk-reduction strategy in hunter gatherer environments, but is not well-explained by rational choice theory (Kameda et al., 2002; Kaplan and Hill, 1985; Kaplan et al., 1990; Van Vugt and Kameda, 2012).

5.5. Sex differences

Unlike rational choice theory, MLS theory predicts fundamental sex differences in behavior. Of course, this is a thorny area because there may be cultural causes of sex differences as well as biological causes, and some people take offense from such proposals irrespective of the cause. But one of the best predictors of behavior among all mammals, including humans, is sex. Evolutionary theory stresses the fundamental differences in parental investment among males and females, which has ramifications for physiological and psychological adaptations (Darwin, 1871; Trivers, 1972). Many of these sex differences are relevant to behavior in firms. For example, evolution has made men relatively specialized for aggressive status competition, and has made women relatively specialized for assuring parental investment (Archer, 2009; Baron-Cohen, 2008; Trivers, 1972); thus in firms, men are on average more inclined than women toward aggressive risk-taking in the pursuit of rank and prestige, whereas women are on average more concerned than men with family friendly policies (Kruger and Nesse, 2007; Scandura and Lankau, 1997).

Sex differences in aggressive risk-taking and status striving may be exacerbated in the financial sector, where the emotional rollercoaster of boom and bust leads to significant fluctuations in testosterone and cortisol among traders (Coates, 2012; Lofton, 2011). These sex differences also help explain why males striving for leadership is still the norm in most societies although the greater social skills of women might make them equally if not better qualified as leaders and managers (Van Vugt et al., 2008; Van Vugt and Spisak, 2008). Many other sex differences—for example, in coalitional behavior, empathy, leadership, and interest in mechanical systems—are also potentially relevant in firms (Baron-Cohen, 2008; Price and Johnson, 2011). Of course, male and female traits have heavily overlapping distributions. But as in politics, in the commercial world women who rise to the top may tend to express male-typical traits—representing the extreme end of female trait distributions—whether as a result of a conscious strategy (to "survive in a man's world"), socialization (if male strategies tend to beget success or promotion), or selection (if women with more male-typical strategies are more likely to seek, gain or keep such jobs).

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5.6. Inter-group competition

A particularly interesting sex difference from the perspective of MLS theory is that whereas groups of males become significantly more cooperative when they are competing against a rival out-group, females do not (Van Vugt et al., 2007). This finding is consistent with the MLS view that success in inter-group competition was important to individual fitness over evolutionary history, especially for males (Johnson and Van Vugt, 2009; Wrangham and Peterson, 1996). Rational choice predicts neither this sex difference, nor the tendency for males to cooperate more in the presence of an out-group.

6. Evolved psychology and cultural success

Even if the term "cultural adaptation" is not widely used, the general idea that a firm's cultural attributes can affect its performance and competitiveness has been widely accepted in organizational behavior since the 1980s, is a common theme of mainstream business books (e.g. Grove, 1999; Kanter, 2004; Lashinsky, 2006), and is a common intuition among casual observers. What is less appreciated, however, is how knowledge about evolved human nature can help illuminate *why* some corporate cultures succeed while others fail.

The main point we wish to emphasize here is that in understanding the success of any corporate culture, it is a mistake to see a cultural explanation as an *alternative* to a biological one. A culture will be successful not because it overrides, subverts, or suppresses evolved human nature, but rather because it privileges and encourages some aspects of human nature over others. Human nature is shaped by myriad adaptations, but in most corporate contexts, only some of these adaptations will produce behaviors that will help an organization to reach its goals (and some traits may be advantageous in some types of firms, or some roles within firms, but detrimental in others). For example: people have adaptations for free riding, as well as for industrious cooperation (Price and Johnson, 2011); for violence and revenge, as well as for constructive methods of dispute resolution (Daly and Wilson, 1988; McCullough, 2008); for individual dominance, as well as for leadership (Van Vugt et al., 2008); for competing in ways that harm the group, as well as in ways that benefit the group ("competitive altruism", Roberts, 1998); and for basing judgments of colleagues on their membership in some perceived in-group or out-group (ethnic, gender, religion, etc.), as well as on job performance and merit (Kurzban et al., 2001b; Tooby et al., 2006). In each of these cases, in most modern circumstances, the more successful corporate culture would be that which encouraged expression of the latter adaptations and discouraged expression of the former ones.

We should also emphasize that just as cultural adaptation will occur if firms succeed or fail based on the content of their cultures, it will not occur if forces of *artificial* selection intervene on behalf of otherwise moribund cultures. This is exactly what has happened in the wake of major bank failures over the past several years. Government rescue missions have artificially prolonged the lives of banks which, due to practices such as encouraging employees to gamble away the bank's future in the pursuit of short-term payoffs, have developed cultures that are dysfunctional and self-destructive in the long-term. These bailouts may have been carried out with the intent of promoting the greater good of the states and societies who subsidized them. They nevertheless interfered directly with the cultural selection of more sustainable and competitive bank cultures. Major maladaptive traits may fall away, but pernicious minor ones may be allowed to remain. As Ferguson suggested, "the possibility of extinction cannot and should not be removed by excessively precautionary rules" (Ferguson, 2008, p. 357).

7. The dark side of group selection: altruism or all-out war?

Above we stressed the fundamental irony that Schumpeter, Friedman and Ferguson, by applying Darwinian selection to competition among firms, invoke *group* selection. Group-selection leads to the suppression of self-interest, high levels of cooperation, and altruism. But this begs an important question: what is this cooperation for? By definition, group selection implies that individuals within the group suppress their self-interest in order to better compete with *other* groups (that is the source of the selection pressure). This is the "dark side" of group-selection. Within-group cooperation promotes (and reflects) between-group competition, raising the specter of inter-group conflict as both a driver and outcome of natural selection. And we must remember that, if group selection is at work, then it must be quite strong to trump individual self-interest acting in the opposite direction. Therefore, in a group selection scenario, competition among groups can be expected to be particularly fierce and unrelenting. While group selection may lead to remarkable cooperation among members within a given group, it can lead to all out hostility against members of *other* groups.

This point has been used to offer a reason why war may have become so important in human evolution (Bowles, 2006; Choi and Bowles, 2007; Johnson and Van Vugt, 2009). Lawrence Keeley noted that "warfare is ultimately not a denial of the human capacity for social cooperation, but merely the most destructive expression of it" (Keeley, 1996, p. 158). Indeed, group-selection implies that if we are selected to cooperate with our in-group, then we must also be selected *not* to cooperate (or at least to cooperate less) with out-group members—a balance of tolerance within, and intolerance beyond, the group must be struck for it to confer any advantage (otherwise there is no distinction between behavior directed toward group members or outsiders, and free-riders will invade). Compared with the self-interested consequences of individual selection, therefore, group-selection may be even worse. As Matt Ridley put it: "Preferring the morality of group selection to the ruthlessness of individual struggle is to prefer genocide to murder" (Ridley, 1996, p. 193).

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Selection among firms may make for cohesive and cooperative workers, but at the same time inflate inter-group competition to extreme levels, possibly to the detriment of the market and society as a whole. If firms expend resources trying to eliminate each other, consumers will not necessarily benefit from these "wasted" resources or the distractions or monopolies that result.

8. Individual adaptation and group selection can co-exist

We have focused on explaining how individual and group interests may diverge or align in certain settings, as predicted by evolutionary theory. There is, however, a bigger picture that we finish on here. Current debates in the literature tend to set individual and group selection in opposition to each other—two alternative views of how evolution works with widely divergent perceptions about human nature. MLS theory is useful because it reminds us that this binary version of events is unnecessary and unlikely. In the real world, human beings are likely to be (or to have been) subject to some degree of selection pressure at both levels, and their relative influence may also vary across space and time.

The point we wish to make here is that *individual* selection, whether operating in the past and/or today, is in fact essential to understanding *cultural* selection. Cultural selection does not act on a blank slate, any more than economic activity does. Rather, individual adaptations that were under strong selection pressure in the environments in which we evolved have generated an "operating system", shared by all human brains, which sets constraints within which cultural selection must act. Cultural evolution, therefore, is both limited by and somewhat predictable given evolved, individual adaptations.

9. Conclusion

Firms compete. Good ones survive and bad ones die. This looks like the logic of Darwinian selection, as has been periodically suggested over the last century by prominent economists including Schumpeter (1961, 2008[1942]), Friedman (1954, 1970), and Ferguson (2007, 2008). If true, it would be important because it offers independent support for three pillars of dominant economic wisdom: (1) that actors are self-interested; (2) that this self-interest leads to public goods (Smith's invisible hand); and (3) that together these lead to market optimization. However, we have shown that, ironically, applying Darwinian logic to competition among firms invokes *group* selection. If firms compete with each other and experience Darwinian selection at this level, then the firms that are most likely to survive (all else equal) are those with altruistic individuals who accept fewer resources to work harder. So either the theory or the predictions are wrong. A Darwinian view of economic markets may accurately reflect competition among firms, but undermines the individual self-interest assumptions of neoclassical economics.

Our goal has been to propose multi-level selection as a more appropriate evolutionary model to understand economic competition and the behavior of firms and workers. MLS theory examines two simultaneous and often opposing forces: (1) the interest of the firm as a whole; and (2) the interest of individuals within the firm. The relative importance of each can be assessed only by appealing to evidence, that is, by determining which level of selection makes more accurate predictions about actual human psychology and behavior. The interaction between levels is critical because knowledge of how humans tend to behave *within groups*—such as cooperation, status seeking, preferences about leadership and dominance, a sense of fairness and justice, sex differences, and inter-group competition—allows us to generate novel predictions for when we should expect to see more individual (self-interested), or more groupish (self-sacrificial), behaviors (as outlined in Section 5 and summarized in Table 3). These predictions are useful because they suggest organizational, structural, and management practices that can reduce Darwinian competition where it is damaging, or promote it where it improves competition and innovation. System-wide regulation of firms themselves can be useful, especially to interests at levels higher than the firm (e.g. nations and societies), but it can also interfere with the selection of successful cultural adaptations. If we are only now beginning to unify evolutionary and economic knowledge, both of which are vital to understanding how individuals and groups behave and interact in the real world, we should be wary of the potential perils of interference.

Modern economics, as Gowdy et al. (this issue) put it, "focuses selectively on [Adam] Smith's plea for unfettered markets as a source of wealth and welfare." We concur with their view that an evolutionary understanding of human behavior is vital if we are to ensure positive outcomes in economics and public policy. People cooperate with each other and create public goods, but only in the "right" circumstances. A popular reason that they do so is buried in human nature assumptions of economics that everyone knows are wrong. Evolution led to *Homo sapiens*, not *Homo economicus*. The real reason people cooperate the way they do is buried in evolutionary time, but has resulted in evolved cognitive mechanisms that serve individual and sometimes also group interests, often at a subconscious level—as if led by an invisible hand. But it is the hand of Darwin, not Smith.

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