



A naturalistic theory of economic organization

J.W. Stoelhorst^{a,*}, Peter J. Richerson^b

^a Amsterdam Business School, University of Amsterdam, Plantage Muidergracht 12, 1018 TV, Amsterdam, The Netherlands

^b Department of Environmental Science and Policy, University of California-Davis, Davis, CA 95616, USA

ARTICLE INFO

Article history:

Accepted 30 November 2012

Available online 20 December 2012

JEL classification:

B52

C71

D02

D03

D23

Keywords:

Evolutionary theory

Multi-level selection

Gene-culture co-evolution

Cooperation

Economic organization

Ethics

ABSTRACT

We develop a theory of economic organization grounded in the naturalistic paradigm currently emerging at the intersection of biology and the behavioral and social sciences. The crux of this approach is the recognition that an understanding of the evolutionary origins of human organizational capabilities can inform theories of contemporary economic organization. Modern firms sustain large scale cooperation by applying cultural ‘work-arounds’ to tribal instincts that evolved from simultaneous within-group and between-group competition on a much smaller scale. We translate this insight into ten principles of economic organization.

© 2012 Elsevier B.V. All rights reserved.

1. Introduction

Why do humans cooperate on a large-scale with non-kin? This paper develops a theory of human economic organization that is grounded in the naturalistic paradigm currently emerging at the intersection of the biological, behavioral, and social sciences (Binmore, 2005; Blute, 2010; Bowles and Gintis, 2011; Cordes et al., 2010; Fowler and Schreiber, 2008; Gintis, 2006; Henrich, 2004; Hodgson and Knudsen, 2010; Mesoudi, 2011; Richerson and Boyd, 2005; Runciman, 2009; Stoelhorst, 2005; Wilson and Wilson, 2007). Human organizational capabilities are unique in the animal kingdom. We are the only species that has evolved to sustain large-scale cooperation among individuals that are not closely related genetically using the mechanism of cultural transmitted norms and institutions. Extant theories of economic organization take this ability for granted. Rather than explaining the nature and the origins of our organizational capabilities, they tend to it take the manifestation of these capabilities in modern organizations as a given and proceed from there. While this is entirely defensible, this paper is motivated by the belief that we can achieve a deeper understanding of contemporary organizations by explicitly building a theory of economic organization on an understanding of the evolutionary origins of human organizational capabilities.

The starting point of a naturalistic approach to studying economic organization is the explicit recognition that humans are an animal species and that the origins of our behaviors require an evolutionary explanation. This does not mean that a naturalistic approach calls for genetic reductionism: genes alone do not explain human behavior. Our capacity for culture

* Corresponding author.

E-mail addresses: j.w.stoelhorst@uva.nl (J.W. Stoelhorst), pjricherson@ucdavis.edu (P.J. Richerson).

Table 1
The ten principles of a naturalistic theory of economic organization.

Why do humans cooperate on a large-scale with non-kin?		Universal principles of human organization	Implications for modern organizations	Moral implications
Proximate explanations	Mechanistic explanation	4. There are universal mechanisms by which cooperation can emerge and be sustained	5. Organizations sustain cooperation on the basis of local and contested norms	9. Human organizations are susceptible to exploitation by their leaders
	Ontogenetic explanation	3. Humans display a universal mix of cooperative dispositions that both enable and constrain our ability to sustain large-scale cooperation.	6. Modern forms of organization use cultural 'work-arounds' to sustain large scale cooperation	
Ultimate explanations	Functional explanation	2. There are advantages to large scale cooperation, although these advantages are easily undermined by within-group competition	7. Successful organizations channel within-group competition in ways that enhance their success in between-group competition	10. Within-group cooperation goes hand in hand with a tendency toward between-group hostility
	Phylogenetic explanation	1. Humans are social animals with cooperative dispositions derived from a long history of living in tribal scale groups in which culturally transmitted norms and institutions favored cooperation.	8. Specific cooperative solutions are historically and culturally contingent	

is vastly more developed than that of other animal species, and this capacity plays a central role in explaining why our organizational capabilities are such an outlier in the animal world (Gowdy et al., 2013). While there are people who think that genes control human cultures and cultural evolution, and others who think that culture has nothing to do with genes or genetic evolution, neither of these views accord with the evidence: genes and culture coevolve (Richerson and Boyd, 2005).¹ The crux of a naturalistic approach, therefore, is not an exclusive focus on genes, but rather an insistence on ultimate as well as proximate explanations of animal, and by extension, human behaviors.

The distinction between proximate and ultimate explanations goes back to Mayr's (1961) classical statement of the nature of causal explanation in biology and is incorporated in Tinbergen's (1963) famous four 'Why's', which capture the naturalistic approach to theory building (Wilson and Gowdy, 2013). Tinbergen made clear that animal behavior could be explained in four complementary ways: in mechanistic terms, in ontogenetic (developmental) terms, in functional terms, and in phylogenetic (evolutionary) terms. So if we ask: 'Why do humans cooperate on a large scale with non-kin?' there are four possible answers, and a complete explanation of human cooperative behaviors requires a combination of all four.

Below, we use Tinbergen's framework to derive ten principles for a naturalistic theory of human economic organization. These principles are summarized in Table 1, where they are numbered in the order in which they will be discussed. In the next section of the paper we first derive four universal principles of human organization. Central among these is the principle that humans are social animals with cooperative dispositions derived from a long history of living in tribal scale groups in which culturally transmitted norms and institutions favored cooperation. We subsequently turn to four principles that capture the implications of the evolutionary origins of our organizational capabilities for modern organizations. We argue that modern organizations can be understood in terms of the interaction between the 'tribal instincts' that underlie human cooperative dispositions and the cultural 'work-arounds' that have evolved to build organizations on a very different scale than that for which our social instincts originally evolved. We subsequently develop the ethical implications of a naturalistic understanding of human organization. A positive implication of our theory is the importance and prevalence of pro-social dispositions that go against the standard assumption in economic theory that humans are self-regarding. A more worrying implication is that two ethical problems are endemic to human social organization: within-group exploitation of members of the organization by their leaders, and between-group hostility toward members of other organizations. In the concluding section of the paper, we reflect on the potential of modern knowledge-driven organizations as vehicles to counteract these two moral problems of human economic organization.

2. Universal principles of human organization

This section develops four universal principles of human organization. Together, principles one and two provide an explanation of the evolutionary origins of our cooperative abilities, while principles three and four highlight the universal character of the behavioral dispositions and psychological mechanisms that explain how humans are able to sustain large-scale cooperation among non-kin.

¹ Genes no doubt influence what cultural variants we adopt. Because our heads are rich in pain sensing neurons we tend to raise door jams high enough not to bump into them. However, the opposite is also true. As human populations became dense after the evolution of agricultural subsistence systems, human populations underwent a burst of genetic evolution as our bodies adjusted to new diets and new diseases. Since cultural evolution is generally faster than genetic evolution, once humans became highly cultural much if not most genetic evolution would have become about adapting to the new environments culture created (Laland et al., 2010; Richerson and Boyd, 2010).

Principle 1. Humans are social animals with cooperative dispositions derived from a long history of living in tribal scale groups in which culturally transmitted norms and institutions favored cooperation.

While cooperative behaviors are widespread in nature, the cooperative behaviors that sustain human economic organization are an anomaly in the animal world. From a naturalistic perspective any form of cooperative behavior presents a puzzle, let alone the nature and scale of the cooperative behaviors of the human species. This is the case because it would seem that natural selection, which rewards behaviors that leave more offspring in the next generation, would lead to selfish individuals. Consistent with this expectation, solitary and non-cooperative species are common and what cooperation exists in nature is usually small in scale. Yet, the relatively few species that cooperate on a large scale, like ants and termites, are often highly successful. By itself, the workhorse of a naturalistic approach, the Darwinian variation-selection-retention algorithm (cf. Campbell, 1965; Stoelhorst, 2008), cannot explain the emergence of cooperative behaviors in nature.

Although this conclusion already bothered Darwin himself (Sober, 2010), satisfactory theories to explain the evolution of cooperation only emerged relatively recently. They include kin selection, or inclusive fitness theory (Hamilton, 1964), reciprocity (Trivers, 1971; Axelrod, 1984), indirect reciprocity (e.g. Alexander, 1987), and group selection, or multi-level selection theory (e.g. Keller, 1999). Each of these theories proposes a mechanism that can, in principle, explain the evolution of cooperation (cf. Nowak, 2006). This means that we can only hope to reach conclusions about the relative importance of these mechanisms in explaining the evolution of cooperation by confronting the theories with empirical facts. In the case of humans, these facts point to a central role for cultural group selection.²

Remember that the specific puzzle of human cooperation is that it takes place on a large scale, and among individuals that are not closely related genetically. This empirical fact rules out explanations in terms of kinship or reciprocity alone. Kin selection cannot explain that human cooperation extends to individuals that are not genetically related. Direct reciprocity cannot explain the large scale of human cooperation, because cooperation based on reciprocity quickly breaks down when group size increases (Boyd and Richerson, 1988). In fact, the puzzle runs even deeper, because indirect reciprocity also fails in the face of the empirical evidence about human cooperative behaviors. Indirect reciprocity can arguably sustain cooperation in larger groups by way of a reputation mechanism. But humans even display cooperative behavior in one-shot interactions with anonymous strangers without reputation effects (Fehr and Fischbacher, 2003).³

Biologists, economists, and other social scientists alike now recognize that solving the puzzle of human cooperative behaviors is a crucial step in the development of a naturalistic approach that can bridge the gap between biology and the social sciences (e.g. Fehr and Fischbacher, 2003; Gintis, 2000; Henrich, 2004; Kurzban and Houser, 2005; Richerson and Boyd, 2005; Wilson and Wilson, 2007). The explanatory logic that has emerged to explain the evolutionary origins of our unique cooperative capabilities is based on a combination of multi-level selection theory (Sober and Wilson, 1998; Wilson and Wilson, 2007) and the theory of gene-culture co-evolution (Boyd and Richerson, 1985; Richerson and Boyd, 2005). In multi-level selection theory, groups as well as individuals are units of selection (cf. Wilson et al., 2013). The theory distinguishes the selection pressures from within-group competition for scarce resources, which favor behavior that is beneficial to the individual, and between-group competition for scarce resources, which favor behavior that is beneficial to the group. Whenever individuals are organized into groups that compete with each other, the net effect of these two selection pressures may favor cooperative behaviors that are beneficial to the group. Although the evolution of cooperation on the basis multi-level selection acting on genetic evolution alone is possible (Sober and Wilson, 1998), the explanatory value of the multi-level selection framework is much increased if, in addition to genetic mechanisms, we allow cultural mechanisms to play a role as well.

Cultural mechanisms are uniquely suited to create and maintain the two conditions that are needed for group selection to take force: the maintenance of variety between groups to allow cooperation to evolve in the first place, and once it has evolved, the stabilization of this cooperation in the face of within-group selection pressures in favor of free-riding. In fact, theoretical models suggest that between-group variation is much more easily maintained in terms of culture than in terms of genes (Richerson and Boyd, 2005). One simple, but important, mechanism to both maintain variety between groups and stabilize cooperation within them, even in the face of immigration, is conformist transmission. When information is noisy and variable it is in theory almost always an advantage to do what the majority does (Henrich and Boyd, 1998; Kameda and

² There is an ongoing controversy about the relative importance of each of these theories in explaining the evolution of cooperation. Much of this controversy has centered on the role of group selection in explaining the evolution of eusociality. There is a long history of opposition to group selection and multi-level selection theory (MLST) by adherents to inclusive fitness theory (IFT) who claim that kin selection offers a better explanation of the evolution of eusociality in non-human species, or even that group selection arguments are simply misguided. Despite this opposition, there now seems to be an emerging consensus among experts that group selection has in fact played a central role in the emergence of eusociality in non-human species such as social insects (Wilson, 2012). In fact, the controversy has recently been rekindled by an attempt to turn the tables on IFT by dismissing it in favor of MLST (Nowak et al., 2010; Wilson, 2012). However, there is a third position that recognizes that IFT and MLST are inter-translatable (see <http://www.thisviewoflife.com/index.php/magazine/articles/clash-of-paradigms>, accessed on November 24, 2012). This means that for the case of non-human species, where the main source of phenotypic variation among groups like ant colonies is underlying genetic variation, the resolution of the controversy between IFT and MLST on purely theoretical grounds may be impossible. On this view, reaching conclusions about the relative importance of the different mechanisms proposed by IFT and MLST becomes a matter of empirical evidence. Note that for the case of humans, the empirical evidence strongly suggests a central role for group selection.

³ As Bowles and Gintis (2011) point out, even if cooperative indirect reciprocity equilibria could be established *in principle* through direct bargaining among self-regarding agents in combination with reputation and sanctioning mechanisms, in the case of humans such equilibria are *in fact* reached by the evolution of institutions among agents who are at least to some extent other regarding. We come back to this when discussing principle three.

Nakanishi, 2002). Moreover, in humans, symbolic markers of group membership like dress or dialect limit social contacts between groups and help preserve cultural differences. As a result, the cultural variation between groups seems to be at least an order of magnitude greater than the genetic variation between them (Bell et al., 2009).

The combination of multi-level selection theory and gene–culture co-evolution theory explains the origins of human socio-economic organization as follows (cf. Bowles and Gintis, 2003; Henrich, 2004; Richerson and Boyd, 2005). At some point in our evolutionary history, the evolutionary process gave rise to the human ability to develop culture. The emergence of this ability needs to be understood in terms of genetic mechanisms, or in other words, in terms of natural selection pressures on genetically heritable traits. However, once the ability to develop culture had emerged, it introduced an additional mechanism to pass on adaptive behaviors that allowed group selection to be an important force. In the between-group competition for scarce resources among our tribal ancestors it was not only the genes of the individuals in the group that were selected for, but also their culturally transmitted ideas and behaviors.

On this logic, groups that evolved cultures that supported cooperation would, *ceteris paribus*, be able to out-compete other groups, and cultures that favored cooperation would thus have spread. Moreover, these cultures, in turn, would have changed within-group selection pressures to favor genes that predispose humans to cooperative behaviors. For example, suppose that culturally transmitted institutions stigmatize those who do not follow rules and grant prestige to those who do, and that high prestige individuals are desirable marriage partners. If so, the marriage market will exert selection pressures in favor of those with genes that predispose them to prosocial behaviors and against those who are predisposed to anti-social behaviors. There is ample evidence that social selection favoring prosocial behavior occurs in the simple foraging societies that are our best living model of the Pleistocene societies in which our innate social psychology evolved (Boehm, 2012).

The solution to the puzzle of our unique cooperative behaviors is that in the human species, group selection can take place on large groups of non-kin because cultural, as opposed to genetic, variety is the primary source of phenotypic variation among groups. In addition to genetic mechanisms, our capacity to imitate, reinforced by symbolic language, has resulted in a second mechanism to transmit information about adaptive behaviors. As a result, humans are a highly group-selected species (Gowdy et al., 2013). Culture may change the balance of the selection pressures that result from within-group competition and between-group competition in important ways and create more, or for that matter, less favorable conditions for groups to sustain cooperation and to successfully compete with other groups. Over evolutionary history, groups with culturally transmitted norms and institutions that favored cooperation have been reproductively more successful than other groups. The result of this evolutionary dynamic has been that humans became social animals with moral instincts that allow us to sustain large scale cooperation among non-kin.

Principle 2. There are advantages to large scale cooperation, although these advantages are easily undermined by within-group competition.

The fundamental driver behind the evolution of our cooperative dispositions is the fitness advantages conferred by the division of labor and economies of scale inherent in large-scale cooperation. However, as multi-level selection theory illustrates, the fundamental problem of any type of socio-economic organization, biological or cultural, is that for social groups to function as adaptive units, their members must be able to sustain cooperation. This is a problem because behaviors that are advantageous for the group are seldom in the self-interest of the individual members. At the heart of any form of socio-economic organization is a social dilemma (using behavioral and social science terminology) or a public good game (using the economic vernacular): while the social welfare (i.e. the joint interest of the group) is maximized when all members cooperate, each of the members can maximize its individual pay-offs by free riding on the cooperative efforts of the other group members, thus avoiding the costs of investing in cooperation while still incurring its benefits. It follows that any level of human organization (e.g. a group, a business unit, a firm, a network, or an economy) needs to be explained in terms of how it keeps competition among lower level entities (individuals, departments, business units, firms, or social classes) from undermining its viability (cf. Campbell, 1994; Maynard Smith and Szathmari, 1997; Wilson et al., 2013).

As an animal species we can expect our genetically transmitted instincts to bear the marks of a long evolutionary history of natural selection. We should therefore expect dispositions for behaviors that further our self-interest in the competition for scarce resources, be they food, mates, status, or money. However, given both individual-level and group-level selection pressures, our social instincts are the result of the simultaneous need to compete for scarce resources with other individuals within a social group *and* to cooperate with these same individuals in the competition for scarce resources with other groups. We can therefore also expect behaviors that are the result of a need to belong to a group. A long evolutionary history of group selection pressures has made us a species that has evolved dispositions to cooperate in groups, but our cooperation is fragile because our cooperative dispositions need to override individual selection pressures within groups that favor selfish behaviors. The central problem human organizations need to solve is overcoming the tension that results from instincts that favor pursuing our self-interest and instincts that favor maintaining group cohesion (e.g. Frank, 2011; Turchin, 2007).

Principle 3. Humans display a universal mix of cooperative dispositions that both enables and constrains our ability to sustain large-scale cooperation.

We have so far derived principles for a naturalistic theory of economic organization from an ultimate explanation of human cooperative behaviors. We now turn to principles related to proximate explanations. Proximate explanations can be mechanistic or ontogenetic. An example of the first category is that we could, for instance, point to the role of punishing free riders in sustaining cooperation. A mechanistic explanation would pinpoint the psychological mechanisms that cause such

behavior (e.g. by detailing the neurological pathways by which free riding leads to a behavioral response). Such an explanation can be complemented by an ontogenetic explanation of the preferences underlying the behavioral disposition to punish free riders (e.g. inequality aversion). Together, mechanistic and ontogenetic explanations establish how the behaviors that sustain large-scale cooperation among non-kin occur (e.g. free riding triggers inequality aversion, which leads to punishment, which helps sustain cooperation). Let us first consider the nature of human cooperative dispositions, before turning to the psychological mechanisms that may trigger these dispositions in the discussion of our next principle.

The empirical evidence suggests that there is a universal mix of preferences underlying cooperative dispositions in humans. The traditional behavioral assumption in economic theory that all individuals are self-regarding is consistent with what we would expect if our behavioral dispositions were merely the result of individual level selection. However, this assumption does not accord with the empirical evidence. Findings from experimental and behavioral economics show that there is substantial behavioral heterogeneity among humans. The results of a public good experiment by [Kurzban and Houser \(2005\)](#) are illustrative. They found that their subjects could be classified as one of three stable types: altruists (13%), who contribute to generating group benefits at a cost to themselves, self-regarding free riders (20%), who do not incur these costs, and reciprocators (63%), who respond to other's behavior by using a conditional strategy that reciprocates both cooperative and uncooperative behaviors. This study does not stand on its own. Percentages that have been reported in other experimental studies by economists range from 20% to 40% for self-regarding individuals, 40% to 60% for reciprocators, and 10% to 15% for altruists ([Abbink et al., 2000](#); [Berg et al., 1995](#); [Fehr and Falk, 1999](#); [Gächter and Falk, 2002](#)).

A particularly type of altruistic behavior that strongly contributes to maintaining cooperation is the behaviors of so-called 'strong reciprocators'. Strong reciprocators are willing to sacrifice resources to reward those who cooperate (strong positive reciprocity) and to punish those who are uncooperative (strong negative reciprocity). What is essential is that strong reciprocators are inclined to punish whenever a social norm is violated, even when punishing comes at a personal cost. Strong reciprocators are not necessarily self-regarding when rewarding or punishing: they even punish when the probability of future interactions is extremely low, and punishing therefore yields neither present nor future personal benefits. Moreover, they are also willing to incur personal costs to punish those who are uncooperative toward third parties ([Engelmann and Strobel, 2004](#); [Fehr and Fischbacher, 2004a](#); [Fehr et al., 2002](#); [Fehr and Gächter, 2002](#)).

Social psychologists have an even longer tradition in studying human behavior in situations where decisions among alternative behaviors affect both one's own and others' pay-offs, as is the case in public good games, and economic organization more generally. They have done so on the basis of a typology of so-called 'social value orientations' (e.g. [Messick and McClintock, 1968](#); [McClintock, 1972](#); [Liebrand, 1984](#)). This typology offers a precise definition of cooperative dispositions by assessing individual's self-regarding and other regarding preferences. Most people fall into one of the following three categories: self-regarding individuals ('individualists'), who simply maximize their own absolute pay-off without any regard for other's pay-offs; cooperators, who maximize the joint pay-offs of themselves and others; and competitors, who maximize their own relative pay-off (i.e. they maximize the difference between their own pay-offs and those of others, even if this means that they secure a lower absolute pay-off for themselves).⁴ The empirical findings of social psychologists based on this typology bear a close resemblance to those of experimental economists. For instance, in one representative study of the Dutch adult population, of the 92% of 1728 respondents that could be consistently classified, 65% were cooperators, 20% were individualists, and 7% were competitors ([Van Lange, 1999](#)). The percentage of competitors, in turn, is in the same range as the percentage of subjects in economic experiments that display so-called spiteful punishment, which combines free riding with punishing cooperators, thus increasing the payoff difference between one's own pay-offs and those of others ([Fehr et al., 2008](#)).

That reciprocity, other-regarding preferences, social norms, costly punishment, and relative as opposed to absolute pay-offs play an important role in human behavior flies in the face of standard economic assumptions, but is consistent with what we would expect from an evolutionary history of multi-level selection.⁵ That the empirical evidence from economics and social psychology converges on similar types and similar distributions across these types suggests that these data capture something essential about the heterogeneity of human cooperative dispositions. It is too early to say exactly how stable these types are, to what extent the percentages of types are universal across cultures, or if the types are genetic polymorphisms. But there is evidence pointing in these directions, and [Kurzban and Houser \(2005\)](#), for one, conclude that the findings of their study suggest that the human population may be in a stable equilibrium of genetic polymorphisms.⁶

⁴ In all, the SVO typology distinguishes between five types. In addition to individualists, cooperators, and competitors, there are altruists (who maximize other's returns regardless of own returns) and aggressive individuals (who minimize other's returns regardless of own returns). However, very few individuals can be classified as being altruistic or aggressive. Note that there is a difference between the definition of altruists in this typology and in the work of [Kurzban and Houser \(2005\)](#). This difference is the result of the fact that the SVO typology is based on choices in bilateral interactions, while [Kurzban and Houser](#) classify subjects on the basis of their choices in a four person public good game. In the [Kurzban and Houser](#) study, someone is altruistic if he or she contributes more to the public good than the average contribution of the other group members. In the SVO typology, someone is altruistic if he or she makes allocations that favor the other over the self.

⁵ For discussions of the important difference between maximizing absolute or relative pay-offs, see [Frank \(2011\)](#) and [Wilson and Gowdy \(2013\)](#).

⁶ The main reasons for their conclusion are twofold. The first is that they find evidence of stability of the types. The second is that in their public good experiment, the overall pay offs of the different types did not differ, which suggests a game theoretic equilibrium. Other support for the stability of types includes ([Van Lange and Semin-Goossens, 1998](#)). Support for universal distributions of types across cultures includes [Liebrand and Van Run \(1985\)](#) and [Ishii and Kurzban \(2008\)](#). Evidence for a genetic basis of cooperative behaviors includes [Ebstein et al. \(2010\)](#) and [Zhong et al. \(2010\)](#).

The crucial insight for a naturalistic theory of economic organization is that the majority of individuals are cooperative animals, who are inclined to maximize joint returns when interacting with others. At the same time, there is also a substantial minority of individuals who are inclined to only pursue their own self-interest in absolute terms, as traditional economic theory would have it. And there is a small, but non-negligible, percentage of people who are willing to destroy general welfare to increase their own relative payoffs. The fundamental problem of human organization, then, is to evolve organizational arrangements that allow us to sustain large-scale cooperation in the face of this behavioral heterogeneity.

Principle 4. There are universal mechanisms by which cooperation can emerge and be sustained.

The second type of proximate explanation is mechanistic. Here we face the question which psychological mechanisms underpin the behaviors that allow us to sustain cooperation in the face of the behavioral heterogeneity in the human population discussed above. Nowak (2006) summarized the five mechanisms by which cooperation can theoretically evolve. These mechanisms are kinship, reciprocity, reputation, network interaction, and group selection. While these are evolutionary mechanisms that inform ultimate explanations of our cooperative behaviors, we also can expect these mechanisms to have molded the psychological mechanisms and neurological pathways that provide the proximate mechanisms that help us sustain cooperation. We can therefore expect psychological mechanisms related to kinship (e.g. parental love), which help sustain cooperation among family members; to reciprocity (e.g. empathy, gratitude, guilt), which help sustain cooperation in small groups; and to reputation (e.g. pride, contempt, shame), which allow for an increase in the size of groups in which cooperation can be maintained. We also can expect that for larger scale cooperation, psychological mechanisms that evolved in relation to either network interactions or group selection must come into play. Network interactions require cooperatively disposed individuals to assort themselves into neighboring positions in social networks. This is likely to involve psychological mechanisms to recognize conspecifics. Group selection requires between-group competition while maintaining behavioral variety among groups. This is likely to involve psychological mechanisms that make us sensitive to markers of group membership, rewards for conformity to the norms of the group, and punishment for deviations from these norms.

Given the important role of group selection in our evolutionary history, the more detailed mechanisms that sustain conformity to the norms of a group deserve special attention. Simon (1990) explained our cooperative dispositions as being a result of our ability to learn vicariously, i.e. by accepting the beliefs of others rather than relying on personal experience. Simon's argument was that the evolutionary benefit of being able to rely on other's learning has resulted in what he called, for want of a better term, a 'docile' disposition. Humans are predisposed to learn from others because this saves on learning costs. In order to capitalize on the benefits of learning from others, people have to be calm and easy-going so that others tolerate the prolonged close proximity necessary to imitate accurately. This explanation of our cooperative nature ties in with the phenomenon of 'conformist transmission', which is based on the evolutionary benefit of adapting the most common behavior in a group because this increases the probability of acquiring adaptive values and beliefs. The corollary of a docile disposition is that individuals can be taxed more easily to contribute to the benefit of the group at the expense of their individual interest. In behaviorists' terms, humans find social approval and disapproval strongly reinforcing (Baum, 2005).

One of the hallmarks of social organization is status hierarchies (Buss, 2004). Status hierarchies are widespread in nature, ubiquitous among primates, and an important dimension of human social organization. Two type of status hierarchies need to be distinguished: dominance hierarchies and prestige hierarchies (Henrich and Gil-White, 2001). While dominance hierarchies operate on the principle of coercion, prestige hierarchies turn on so-called freely conferred deference. Human social organization is unusual if not unique in making extensive use of the latter type. Henrich and Gil-White explained the evolution of prestige hierarchies in terms of the benefits that learning from the most successful members of a group conveys. Proximity to successful individuals increases the ability to imitate their behaviors, and deference increases the likelihood of proximity. In addition to imitating the most common behavior in a group, imitating the behaviors of the most successful members in the group offers a second mechanism to increase the likelihood of acquiring adaptive values and beliefs. The corollary of a deferential disposition is that successful individuals can more easily impose their norms on the group, something to which we will come back in principle nine.

3. Implications for modern organizations

We now turn to the implications of the four principles derived above for our understanding of modern human organization. While the central theme of the principles above was that the evolutionary origins of our cooperative tendencies suggest a universal set of psychological mechanisms that maintain a universal mix of cooperative dispositions, the central theme of the principles below is that specific organizational and institutional solutions to sustaining cooperation are historically and culturally contingent.

Principle 5. Organizations sustain cooperation on the basis of local and contested norms.

The evolution of the docile and deferential dispositions discussed above helps explain why humans tend to be norm regarding. But the norms that sustain cooperation within groups can take on many forms. Specific organizational cultures and institutional rules can be understood as game theoretic equilibria (Aoki, 2001; Binmore, 2005; Greif, 2006). In essence, organizational cultures are complexes of local norms that govern social interactions. Norms are social 'what-if' rules that help individuals coordinate their actions. These rules are game theoretic equilibria that emerged as the result of past social interactions. Norms stabilize when they lead to social interactions in which all individuals behave in ways that are the

best response to how they can expect other individuals to behave. Norms lead to self-reinforcing games because they are culturally transmitted and affect individuals' expectations about the reward and punishment for different behaviors in a particular local context. As long as these expectations are largely fulfilled, a stable pattern of social interactions will obtain. However, exogenous or endogenous changes may disrupt an organization's equilibrium, which will lead to an evolutionary search for a new set of norms. The relevance of this for the theory of economic organization is that it points to the local and contested nature of social norms. Social norms are local because they depend on specific path dependent local circumstances. Social norms are contested because they are the result of competition for scarce resources among (groups of) individuals with different interests. The corollary of the local and contested nature of social norms is that one of the hallmarks of human organization is that organizational cultures continuously evolve in response to changes in local circumstances.

Principle 6. Modern forms of organization use cultural 'work-arounds' to sustain large-scale cooperation.

The social psychology that underlies our organizational capabilities is the result of instincts that evolved in a tribal context.⁷ In other words, we essentially run our modern organizations with Stone Age minds. An important implication of this insight is that the organizations of complex societies must be understood as cultural 'work-arounds'. Our tribal social instincts are adapted to small-scale, egalitarian societies with little coercion and much autonomy. The large-scale organizations of modern complex societies with their deep hierarchies and social stratification are therefore likely to conflict with our tribal social instincts. We can expect social demands that go against our tribal instincts to generate painful psychological conflicts and resistance and rebellion. This leads to the prediction that organizational arrangements that can reap the benefits of large-scale cooperation in ways that preserve or recreate the sense of operating in a small-scale society will lead to more effective organizations (Richerson and Boyd, 1999).

The prediction that modern organizations that are better adapted to our tribal instincts will be more successful has obvious managerial significance. It would mean that modern organizations should be structured to reflect the size of the social units for which our social psychology originally evolved and managed in ways that minimize coercion and maximize autonomy. For instance, Richerson and Boyd (1999) present evidence that armies are more successful when they are better able to combine these naturalistic principles with the typical command and control structures that characterize the way in which modern organizations exploit the advantages the division of labor and scale.

In essence, complex societies engage in a balancing act. On the one hand, from an internal operations point of view, human organizations can expect to increase their effectiveness if they are able to maximally tap into our tribal instincts. On the other hand, modern organizations are not autonomous tribes. They rather play distinct roles in the large-scale division of labor on which the economic success of complex societies is based. There is a danger that the more the institutions of complex societies allow organizations to become like tribes, the more they will behave like them. Organizations that become too much like tribes will operate only for their own good and find themselves in high risk of conflict with other tribes. Mafias and gangs are obvious examples of tribal-like social organizations that are able to exploit the institutions of modern societies, often with considerable economic success. The evolution of the organizations of complex human societies is best understood as a process that depends on pro-social tribal instincts, that is driven by cultural group selection that favors large-scale organizations, but that is also ever undermined by selection in favor of individual advantages and narrower loyalties.

Principle 7. Successful organizations channel within-group competition in ways that enhance their success in between-group competition.

Given the universal nature of our social instincts, human organizations essentially compete on the basis of cultural rather than genetic differences. But as already suggested by our discussion above, cultures can be economically more or less successful. While there are many possible cultural arrangements that would allow cooperation to be sustained, in the long run, organizations must also be able to sustain cooperation in ways that allow them to secure sufficient scarce resources from their environment in the competition with other organizations. Therefore, the nature, success, and size of organizations depend on their ability to channel intra-organizational competition in ways that are beneficial in inter-organizational competition. Or in other words, successful organizations need to simultaneously solve the problems of the efficient creation and fair distribution of wealth. The relevance of this principle for a theory of economic organization is that it points to the need to always consider organizations as both social and economic systems. While Barnard (1938) already highlighted the importance of acknowledging the dual nature of organizations, economic theories have traditionally downplayed the importance of the social nature of human organization. In contrast, a naturalistic theory insists on seeing human organizations simultaneously as social entities that sustain cooperation among their members and as economic entities that compete with other organizations for scarce resources.

⁷ Note that we are here adopting the current consensus position in evolutionary psychology. However, recent evidence from studies of human genetics suggests that there has been wave of accelerated human evolution in the wake of the Neolithic revolution as a response to changes in diet, population density, and social complexity (Hawks et al., 2007). It is an interesting and important question if the resulting gene-culture co-evolutionary dynamic also may have strongly affected our social psychology. Since, until recently, the vast majority of the human population continued to live in villages and small towns that seem to have replicated the tribal scale of social life from the deeper past, we believe that our innate social psychology probably has not changed substantially in the last 10,000 years.

Principle 8. Specific cooperative solutions are historically and culturally contingent.

While an understanding of the evolutionary origins of our organizational capabilities provides the foundation for a naturalistic theory of human economic organization, this understanding only provides half of the ultimate explanation of modern organizations. The other half of the explanation would require a detailed phylogeny of the path by which tribal-scale human organizations evolved into the large-scale organizations of modern complex societies. While such a phylogeny is far beyond the scope of this paper (cf. McKelvey, 1982), a naturalistic perspective on human organization nevertheless suggests the contours of the path that we may expect. We would, for instance, expect that small family-owned firms preceded larger firms based on family and ethnic ties, which subsequently evolved into firms in which management and ownership became separated.

The historically and culturally contingent nature of modern organizations ties in with a central theme in institutional economics: that economic organization depends on a host of informal norms and formal institutions (e.g. Nelson and Sampat, 2001; North, 1990). Modern organizations, then, are the result of a long process of cumulative development of informal norms and formal institutions that allow us to sustain large-scale cooperation among non-kin on the basis of social instincts that were shaped by a long evolutionary history of living in tribal scale societies. From a naturalistic perspective we would expect that it is difficult to develop the norms and institutions that engender the trust that is necessary to sustain large-scale cooperation on the basis of social instincts that originally evolved to sustain cooperation on a much smaller scale. A particularly difficult transition is from an institutional setting where cooperation largely depends on personal face-to-face interactions to one where cooperation is impersonal in the sense that it no longer depends on an individual's personal network (North, 2005). That large joint stock companies are largely limited to societies that have evolved institutions that engender widespread trust among strangers, and that economic organization in societies where such trust is limited is mainly based on family firms and personal networks (Fukuyama, 1995; North, 2005), is consistent with such expectations.

A number of comparative experimental studies also illustrate the historically and culturally contingent nature of human organizations. Henrich et al. (2004) and Henrich et al. (2006) conducted two waves of cross-cultural studies using the Ultimatum Game and the Dictator Game with third party punishment. The thirty societies that participated in these experiments were mainly a diverse array of relatively simple village scale social systems. In no society so far sampled does behavior match the expectations of selfish rationality, yet the range of behaviors in these studies was large and dependent on the cultural norms that prevailed in the societies in question. These results are strong evidence for the hypothesis that human organization depends on the evolution of specific organizational cultures on the basis of universal tribal instincts. People everywhere seem to have cooperative dispositions, yet the variation in the culturally transmitted norms and institutions that sustain cooperation is large (Ostrom, 2010).

Another comparative study that illustrates the historically and culturally contingent nature of human organization provides evidence that universal psychological mechanisms can lead to very diverse norms that may even be dysfunctional. In a study of punishment in a public goods game in 16 different developing and developed complex societies from Western Europe (plus the US and Australia), Eastern Europe, Southern Europe, the Middle East and the Far East, Herrmann et al. (2008) present evidence that while punishment is universal, punishment behavior varies substantially across cultures. They found a notable difference among different societies in the balance between altruistic punishment (punishing low contributors) and antisocial punishment (punishing high contributors). Weak norms of civic cooperation and the weakness of the rule of law in a country were significant predictors of antisocial punishment. Societies with a lot of antisocial punishment were greatly handicapped in successfully solving the dilemma of cooperation, and the degree of antisocial punishment was negatively correlated with participants' earnings in the game.

4. The moral problems of human organization

Cultural evolutionary dynamics guided by the universal cooperative dispositions and psychological mechanisms that allow us to sustain cooperation do not necessarily lead to desirable outcomes. Cooperation can break down, organizations can fail, and there is nothing inherently 'progressive' about evolutionary processes. Moreover, while sustaining cooperation may seem to be a worthwhile goal in and of itself, this is not always the case. Rule-based punishment can stabilize arbitrary norms and institutions, even ones that are sub-optimal or wholly dysfunctional (Boyd and Richerson, 1992). The corollary of this insight is that even when cooperation is sustained, it need not result in outcomes that are ethically desirable. For example, economists have long warned against cooperation in cartels and other undesirable associations that conspire against the general welfare. Because of the nature of our tribal instincts, two problems in particular are endemic to human organization: intra-group exploitation of group members by their leaders and inter-group hostility.

Principle 9. Human organizations are susceptible to exploitation by their leaders.

In the context of a multi-level selection framework, status hierarchies based on dominance or prestige are double-edged swords. On the one hand, they can increase the stability of a group by reducing within group conflict. By eliminating the costs that would ensue when group members would have to continuously reassess their rank, status hierarchies benefit all group members, including lower ranked individuals. On the other hand, status differences also easily can lead to exploitation of the group by the dominant members.

Consider the situation of an isolated social group where membership is fixed. In such a case, there is no incentive for self-interested dominant individuals *not* to exploit the other group members. If we assume that there is some minimal benefit to membership of a group (say, protection against predators) and that individuals are born into the group with a random endowment of what determines their social rank (say, strength), then dominant individuals can exploit their lower-ranked group members with impunity. In survival terms, they can only do this to the point where a sufficient number of members survive to keep group size at the level where the benefit of living in a group is sustained. In terms of reproduction, they can only do this to the point where sufficient genetic variability is maintained to produce healthy offspring. But within these natural constraints, the logic of natural selection does not put any limits on monopolizing resources.

Given their ubiquity among primates, status hierarchies most likely preceded the evolution of our ability to sustain large-scale cooperation among non-kin, so that this evolution needs to be explained within the context of groups that consisted of individuals of different status. Interestingly, however, the anthropological evidence suggests that the small-scale societies in which our pro-social behavioral dispositions evolved did not tolerate the type of power relationships that could easily lead to exploitation (Boehm, 1993). Tribal societies were egalitarian and involved little coercion and much autonomy. It therefore seems that our human ancestors evolved a way to suppress the central role that power typically plays in primate social organization. However, a central role for power relationships re-emerged as the scale of human organization increased in the wake of the transition to a sedentary agricultural economy some 10,000 years ago.

This U-shaped curve suggests that one of the problems of our tribal instincts may be that they reinforce the problem of intra-group exploitation of individuals by their leaders when the scale of social organization increases. In large scale organizations, a combination of freely conferred deference and docility can easily lead to organizational cultures where individuals are taxed for the benefit of their leaders, rather than the benefit of the group as a whole. Large-scale organizations typically have offices with a large measure of coercive power over subordinate individuals. For example, firms have executive officers charged by shareholders to maximize their returns. In recent years, there have been sufficient examples to remind us that executives can also abuse the power that this organizational arrangement gives them to enrich themselves at the expense of other stakeholders, and even in defiance of the law.

Principle 10. Within-group cooperation goes hand in hand with a tendency toward between-group hostility.

We should also not forget that our morality evolved at least in part as the result of a long history of between-group selection. We should therefore expect that our pro-social behavioral dispositions are primarily triggered in interactions with those to whom we feel culturally or genetically related. We should not be surprised if our cooperative behaviors are much attenuated, or even reversed, when interacting with those who we perceive as out-group individuals. Even other-regarding individuals that are extremely cooperative in within-group interactions may well behave in ways that are strictly in the interest of their group, rather than the more general welfare, in between-group interactions.

This brings us to the second problem that is inherent in human organization, which is hostility to individuals from other groups. We saw that for between-group competition to work well in sustaining cooperation within groups, situations with small groups, limited immigration, and frequent conflicts between groups work best (Sober and Wilson, 1998). In other words, to sustain cooperation we should expect group boundaries to be maintained. We can expect our evolutionary heritage to include psychological mechanisms that reinforce the maintenance of differences between groups by increasing cooperation between in-group members, excluding individuals on the basis of group markers, and reinforcing between-group competition (McElreath et al., 2003). This is consistent with Bowles and Gintis' (2003) notion of 'parochialism': a group trait that refers to a group's selectiveness in accepting members or ideas from outside the group. The evolutionarily most important group markers are genetic relatedness and ethnicity. Both still play an obvious role in contemporary social organization, and especially so when social organization leads to between-group hostility. But the problem is much more widespread. For instance, different divisions in the same firm or different departments in the same university easily evolve a cliquish distinctiveness that may harm the success of the larger organization (e.g. Jackal, 2009).

5. Modern organizations as vehicles for emancipation?

We saw that sustaining cooperation is challenging and that the scale at which humans are able to sustain large-scale cooperation among non-kin is very unusual among animal species. The naturalistic research paradigm that is emerging at the intersection of biology and the behavioral and social sciences suggests principles for a theory of economic organization that offers both ultimate and proximate explanations of our unique organizational capabilities. At the heart of this naturalistic approach is an ultimate explanation of the origins of human cooperative dispositions that combines the well-known Darwinian variation-selection-retention algorithm with multi-level selection logic and gene-culture co-evolution theory. The interaction of individual selection and group selection has led to the co-evolution of genetically transmitted instincts and culturally transmitted norms that favor large-scale cooperation among individuals that are not directly related genetically.

This ultimate explanation also informs theory development aimed at proximate explanations of our ability to sustain cooperation in modern organizations. The fundamental problem that organizations need to solve is that cooperative behaviors are seldom in the direct self-interest of individual organization members. Organizations compete on their ability to solve this problem by channeling intra-organizational competition in ways that increase their success in inter-group competition. Human organizations sustain cooperation on the basis of a universal set of generic psychological mechanisms that interact with a universal mix of heterogeneous cooperative dispositions. At the same time, specific organizational solutions

are historically and culturally contingent. Because genetic evolution proceeds at a much slower pace than cultural evolution, modern organizations are cultural work arounds that build on tribal instincts that originally evolved to sustain cooperation on a much smaller scale. Given the nature of these tribal instincts, cooperative arrangements on a large scale do not necessarily lead to ethically desirable outcomes. Specifically, our evolutionary heritage leads to the prediction that the major ethical problems of human organization are to keep competition peaceful and leaders honest.

The degree to which these ethical problems present themselves depends on how the interaction between within-group competition and between-group competition plays out. Under the right conditions, evolutionary dynamics may counteract the problems. On this view, there is reason to be optimistic about knowledge-based competition among modern firms as an emancipatory force. One of the remarkable things about modern organizations that sets them apart from more traditional socio-economic systems is that they seem to have evolved ways to sustain large-scale cooperation on the basis of group markers that are not fixed at birth. Group boundaries between firms are much more permeable than the boundaries between our ancestral tribes. Instead of being born into a family, clan, tribe or social class, the membership system of modern firms is based on voluntary, temporary, and part-time membership. Individuals can choose the firms they want to work for, can freely move between firms, and can simultaneously be members of other social systems. These characteristics of the membership system have important consequences for human organization in general because they are likely to counteract the two ethical problems inherent in human social organization.

To understand how the particular membership system of modern organizations may attenuate the ethical problems of human organization, we need to consider how between-group competition may affect the likelihood of between-group hostility and within-group exploitation. In general, a group's success in between-group competition depends on the following factors: The *size* of the group; the *health* of the group members; the level of *skill* of the group members; the level of *coordination* achieved among group members; the level of *technology* that the group has mastered; and the *resolve* of the group members to achieve common goals.

Let us abstract from the purely biological characteristics of individual group members, such as health and strength, as well as from possible differences in the size of groups. Let us also, for the moment, abstract from differences in technological endowment. What remains are the characteristics of groups that are related to group composition and identity: the variety in individual skills and the level of cooperation toward the common goal. In the competition between groups, then, there are two ways to out-compete other groups: having individual members with better skills than other groups and achieving more cooperation toward the common goal. Genetic relatedness and reciprocal relationships increase cooperation, and this would favor the maintenance of strict boundaries between the group and the external world. However, limiting immigration also fixes the group's endowment of individual skills. In contrast, allowing immigration can increase the success of the group by attracting members with better skills, but adding strangers to the group exposes it to the incorporation of selfish individuals. This leads to an interesting trade-off between achieving high levels of cooperation and attracting members with superior skills.

This trade-off puts groups that evolve ways to sustain cooperation among strangers at an advantage. In other words, between-group competition puts a premium on norms and institutions that counteract parochialism and between-group hostility. The voluntary, temporary, and part-time membership system of modern organizations is a strong indication that complex societies have evolved in ways that counteract parochialism and support cooperation among strangers. Modern firms, in particular, are good examples of organizations that are successful at attracting members on the basis of the value of their skills. Moreover, there is reason to be optimistic about the likelihood that they will further evolve along this path. The rationale for this prediction is that the advantage of an open culture is reinforced if we also allow technological change, or in other words, the accumulation of knowledge to play a role in the competition between groups (Hwang and Horowitz, 2012; Mokyr, 1990). Technological change is an obvious feature of the competition between firms that puts an additional premium on being able to integrate individuals with the best skills, regardless of their background.

While modern firms thus emerge as socio-economic systems that may help keep between-group competition peaceful, whether or not they also keep their leaders honest is another matter. In light of recent discussions about CEO compensation, many may argue that they do not. However, in the longer run, there may be reason for optimism about modern firms as a vehicle for emancipation on this matter as well. Competition among modern firms is increasingly knowledge driven and, unlike land and capital, knowledge cannot be easily monopolized. Knowledge driven firms ultimately depend on the voluntary contributions of their knowledge workers, and unlike factory workers in the wake of the industrial revolution, knowledge workers are typically in a position to 'vote with their feet'. On this logic we may hypothesize an evolutionary dynamic whereby knowledge-based competition among firms will favor firms that evolve more equitable ways of dividing the value they create among their different stakeholders. In a setting where their knowledge is increasingly becoming the critical resource for the firm, employees should therefore better be able to keep their leaders honest (cf. Hwang and Horowitz, 2012).

The eminent evolutionary biologist Dobzhansky (1973) once remarked that "nothing in biology makes sense except in the light of evolution". His point was that evolutionary theory was the only way to connect the various facts of biology in an intelligible way. When evolution is narrowly interpreted as genetic evolution, it would certainly be an overstatement to make a similar claim for the social sciences. Although it is no doubt true that human behavior already begins to make more sense when understood in the context of genetic evolution, the social sciences also need to incorporate into their theories the equally important role of cultural evolution in shaping human behavior. But on a broader interpretation of evolution as a process in which genetic evolution and cultural evolution interact to shape both individual human behavior and collective

organizational arrangements, the idea that nothing in the social sciences makes sense except in the light of evolution may not be that farfetched.

References

- Abbink, K., Irlenbusch, B., Renner, E., 2000. The moonlight game: an experimental study on reciprocity and retribution. *Journal of Economic Behavior and Organization* 42, 265–277.
- Alexander, R.D., 1987. *The Biology of Moral Systems*. Aldine de Gruyter, Hawthorne, NY.
- Aoki, M., 2001. *Toward a Comparative Institutional Analysis*. MIT Press, Cambridge, MA.
- Axelrod, R., 1984. *The Evolution of Cooperation*. Basic Books, New York.
- Barnard, C.I., 1938. *The Functions of the Executive*. Harvard University Press, Cambridge, MA.
- Baum, W.M., 2005. *Understanding Behaviorism: Behavior, Culture, Evolution*, 2nd ed. Blackwell, Oxford, UK.
- Bell, A.V., Richerson, P., McElreath, R., 2009. Culture rather than genes provides greater scope for the evolution of large-scale human prosociality. *Proceedings of the National Academy of Sciences of the United States of America* 106, 17671–17677.
- Berg, J., Dickhaut, J., McCabe, K., 1995. Trust, reciprocity and social history. *Games and Economic Behavior* 10, 122–142.
- Binmore, K., 2005. *Natural Justice*. Oxford University Press, Oxford, UK.
- Blute, M., 2010. *Darwinian Sociocultural Evolution: Solutions to Dilemmas in Cultural and Social Theory*. Cambridge University Press, Cambridge, UK.
- Boehm, C., 1993. Egalitarian behavior and reverse dominance hierarchy. *Current Anthropology* 34, 227–254.
- Boehm, C., 2012. *Moral Origins: The Evolution of Virtue, Altruism, and Shame*. Basic Books, New York.
- Bowles, S., Gintis, H., 2003. The origins of human cooperation. In: Hammerstein, P. (Ed.), *The Genetic and Cultural Origins of Cooperation*. MIT Press, Cambridge, MA, pp. 429–444.
- Bowles, S., Gintis, H., 2011. *A Cooperative Species: Human Reciprocity and its Evolution*. Princeton University Press, Princeton, NJ.
- Boyd, R., Richerson, P.J., 1985. Culture and the evolutionary process. University of Chicago Press, Chicago, IL.
- Boyd, R., Richerson, P.J., 1988. The evolution of reciprocity in sizable groups. *Journal of Theoretical Biology* 132, 337–356.
- Boyd, R., Richerson, P.J., 1992. Punishment allows the evolution of cooperation (or anything else) in sizable groups. *Ethology and Sociobiology* 13, 171–195.
- Buss, D.M., 2004. *Evolutionary Psychology: The New Science of the Mind*. Pearson Education, Inc., Boston.
- Campbell, D.T., 1965. Variation and selective retention in socio-cultural evolution. In: Barringer, H.R., Blanksten, G.I., Mack, R.W. (Eds.), *Social Change in Developing Areas: A Reinterpretation of Evolutionary Theory*. Shenkman, Cambridge, MA, pp. 29–49.
- Campbell, D.T., 1994. How individual and face-to-face group selection undermine firm selection in organizational evolution. In: Baum, J.A., Singh, J.V. (Eds.), *Evolutionary Dynamics of Organizations*. Oxford University Press, Oxford, pp. 23–38.
- Cordes, C., Richerson, P.J., Schwesinger, G., 2010. How corporate cultures coevolve with the business environment: the case of firm growth crises and industry evolution. *Journal of Economic Behavior and Organization* 76, 465–480.
- Dobzhansky, T., 1973. Nothing in biology makes sense except in the light of evolution. *American Biology Teacher* 35, 125–129.
- Ebstein, R.P., Israel, S., Chew, S.H., Zhong, S., Knafo, A., 2010. Genetics of human social behavior. *Neuron* 65 (25), 831–844.
- Engelmann, D., Strobel, M., 2004. Inequality aversion, efficiency, and maximin preferences in simple distribution experiments. *American Economic Review* 94, 857–869.
- Fehr, E., Falk, A., 1999. Wage rigidity in a competitive incomplete contract market. *Journal of Political Economy* 107, 106–134.
- Fehr, E., Fischbacher, U., 2003. The nature of human altruism. *Nature* 425, 785–791.
- Fehr, E., Fischbacher, U., 2004a. Third party punishment and social norms. *Evolution and Human Behavior* 25, 63–87.
- Fehr, E., Fischbacher, U., Gächter, S., 2002. Strong reciprocity, human cooperation, and the enforcement of social norms. *Human Nature* 13, 1–25.
- Fehr, E., Gächter, S., 2002. Altruistic punishment in humans. *Nature* 415, 137–140.
- Fehr, E., Hoff, K., Kshetramade, M., 2008. Spite and development. *American Economic Review: Papers & Proceedings* 98, 494–499.
- Fowler, J.H., Schreiber, D., 2008. Biology, politics, and the emerging science of human nature. *Science* 322, 912–914.
- Frank, R.H., 2011. *The Darwin Economy: Liberty, Competition and the Common Good*. Princeton University Press, Princeton.
- Fukuyama, F., 1995. *Trust: Social Virtues and the Creation of Prosperity*. Free Press, New York.
- Gächter, S., Falk, A., 2002. Reputation and reciprocity: consequences for the labour relation. *Scandinavian Journal of Economics* 104, 1–26.
- Gintis, H., 2000. Solving the puzzle of prosociality. *Rationality and Society* 15, 155–187.
- Gintis, H., 2006. A framework for the integration of the behavioral sciences. *Behavioral and Brain Sciences* 30, 1–61.
- Gowdy, J.M., Dollimore, D.E., Wilson, D.S., Witt, U., 2013. *Economic cosmology and the evolutionary challenge*. *Journal of Economic Behavior and Organization* 90, s11–20.
- Greif, A., 2006. *Institutions and the Path to the Modern Economy: Lessons from Medieval Trade*. Cambridge University Press, Cambridge, UK.
- Hamilton, W.D., 1964. The genetical evolution of social behavior. *Journal of Theoretical Biology* 37, 1–52.
- Hawks, J., Wang, E.T., Cochran, G.M., Harpending, H.C., Woyzis, R.K., 2007. Recent acceleration of human adaptive evolution. *Proceedings of the National Academy of Sciences of the United States of America* 104, 20753–22075.
- Henrich, J., 2004. Cultural group selection, coevolutionary processes and large-scale cooperation. *Journal of Economic Behavior and Organization* 53, 3–35.
- Henrich, J., Boyd, R., 1998. The evolution of conformist transmission and the emergence of between-group differences. *Evolution and Human Behavior* 19, 215–241.
- Henrich, J., Boyd, R., Bowles, S., Camerer, C., Fehr, E., Gintis, H., 2004. *Foundations of Human Sociality: Economic Experiments and Ethnographic Evidence from Fifteen Small-Scale Societies*. Oxford University Press, Oxford, UK.
- Henrich, J., Gil-White, F.J., 2001. The evolution of prestige—freely conferred deference as a mechanism for enhancing the benefits of cultural transmission. *Evolution and Human Behavior* 22, 165–196.
- Henrich, J., McElreath, R., Barr, A., Ensminger, J., Barrett, C., Bolyanatz, A., Cardenas, J., Gurven, M., Gwako, E., Henrich, N., Lesorogol, C., Marlowe, F., Tracer, D., Ziker, J., 2006. Costly punishment across human societies. *Science* 312, 1767–1770.
- Herrmann, B., Thöni, C., Gächter, S., 2008. Antisocial punishment across societies. *Science* 319, 1362–1367.
- Hodgson, G.M., Knudsen, T., 2010. *Darwin's Conjecture: The Search for General Principles of Social and Economic Evolution*. The University of Chicago Press, Chicago, IL.
- Hwang, V.W., Horowitz, G., 2012. *The Rainforest: The Secret to Building the Next Silicon Valley*. Regenwald, Los Altos Hills, CA.
- Ishii, K., Kurzban, R., 2008. Public goods games in Japan: cultural and individual differences in reciprocity. *Human Nature* 19, 138–156.
- Jackal, R., 2009. *Moral Mazes: The World of Corporate Managers*. Oxford University Press, New York.
- Kameda, T., Nakanishi, D., 2002. Cost-benefit analysis of social/cultural learning in a nonstationary uncertain environment: an evolutionary simulation and an experiment with human subjects. *Evolution and Human Behavior* 23, 373–393.
- Keller, L., 1999. *Levels of Selection in Evolution*. Princeton University Press, Princeton, NJ.
- Kurzban, R., Houser, D., 2005. Experiments investigating cooperative types in humans: a complement to evolutionary theory and simulations. *Proceedings of the National Academy of Sciences of the United States of America* 102 (5), 1803–1807.
- Laland, K.N., Odling-Smee, J., Myles, S., 2010. How culture shaped the human genome: bringing genetics and the human sciences together. *Nature Reviews Genetics* 11, 137–148.
- Liebrand, W.B.G., 1984. The effect of social motives, communication and group size on behaviour in an N-person multi-stage mixed-motives game. *European Journal of Social Psychology* 14, 239–264.

- Liebrand, W.B.G., Van Run, G.J., 1985. The effects of social motives on behavior in social dilemmas in two cultures. *Journal of Experimental Social Psychology* 21, 86–102.
- Mayr, E., 1961. Cause and effect in biology. *Science* 134, 1501–1506.
- Maynard Smith, J., Szathmari, E., 1997. *The Major Transitions in Evolution*. Oxford University Press, Oxford.
- McClintock, C.G., 1972. Social motivation: a set of propositions. *Behavioral Science* 17 (5), 438–454.
- McElreath, R., Boyd, R., Richerson, P., 2003. Shared norms can lead to the evolution of ethnic markers. *Current Anthropology* 44, 123–129.
- McKelvey, B., 1982. *Organizational Systematics: Taxonomy, Evolution, and Classification*. University of California Press, Berkeley.
- Mesoudi, A., 2011. *Cultural Evolution: How Darwinian Theory can Explain Human Culture and Synthesize the Social Sciences*. University of Chicago Press, Chicago.
- Messick, D.M., McClintock, C.G., 1968. Motivational bases of choice in experimental games. *Journal of Experimental Social Psychol* 4, 1–25.
- Mokyr, J., 1990. *The Lever of Riches: Technological Creativity and Economic Progress*. Oxford University Press, New York, NY.
- Nelson, R.R., Sampat, B., 2001. Making sense of institutions as a factor shaping economic performance. *Journal of Economic Behavior and Organization* 44, 31–54.
- North, D.C., 1990. *Institutions, Institutional Change and Economic Performance*. Cambridge University Press, Cambridge, UK.
- North, D.C., 2005. *Understanding the Process of Economic Change*. Princeton University Press, Princeton.
- Nowak, M.A., 2006. Five rules for the evolution of cooperation. *Science* 314, 1560–1563.
- Nowak, M.A., Tarnita, C.E., Wilson, E.O., 2010. The evolution of eusociality. *Nature* 466, 1057–1062.
- Ostrom, E., 2010. Beyond markets and states: polycentric governance of complex economic systems. *American Economic Review* 100, 641–672.
- Richerson, P.J., Boyd, R., 1999. Complex societies: the evolutionary origins of a crude superorganism. *Human Nature* 10, 253–289.
- Richerson, P.J., Boyd, R., 2005. *Not by Genes Alone: How Culture Transformed Human Evolution*. The University of Chicago Press, Chicago.
- Richerson, P.J., Boyd, R., 2010. Gene-culture coevolution in the age of genomics. *Proceedings of the National Academy of Sciences of the United States of America* 107, 8985–9899.
- Runciman, W.G., 2009. *The Theory of Cultural and Social Selection*. Cambridge University Press, Cambridge, UK.
- Simon, H.A., 1990. A mechanism for social selection and successful altruism. *Science* 250, 1665–1668.
- Sober, E., 2010. Darwin and group selection. In: Sober, E. (Ed.), *Did Darwin Write the Origin Backwards: Philosophical Essays on Darwin's Theory*. Prometheus, Amherst, NY, pp. 45–86.
- Sober, E., Wilson, D.S., 1998. *Unto Others: The Evolution and Psychology of Unselfish Behavior*. Harvard University Press, Cambridge, UK.
- Stoelhorst, J.W., 2008. The explanatory logic and ontological commitments of generalized Darwinism. *Journal of Economic Methodology* 14, 343–363.
- Stoelhorst, J.W., 2005. The naturalist perspective on universal Darwinism: an application to the evolutionary theory of the firm. In: Finch, J., Orillard, M. (Eds.), *Complexity and the Economy*. Edward Elgar, Cheltenham, pp. 129–147.
- Tinbergen, N., 1963. On aims and methods in ethology. *Zeitschrift für Tierpsychologie* 20, 410–433.
- Trivers, R.L., 1971. The evolution of reciprocal altruism. *Quarterly Review of Biology* 46, 35–57.
- Turchin, P., 2007. *War and Peace and War: The Life Cycles of Imperial Nations*. Pi Press, New York.
- Van Lange, P.A.M., 1999. The pursuit of joint outcomes and equality in outcomes: an integrative model of social value orientation. *Journal of Personality and Social Psychology* 77, 337–349.
- Van Lange, P.A.M., Semin-Goossens, A., 1998. The boundaries of reciprocal cooperation. *European Journal of Social Psychology* 28, 847–854.
- Wilson, D.S., Gowdy, J., 2013. Evolution as a general theoretical framework for economics and public policy. *Journal of Economic Behavior and Organization* 90, s3–10.
- Wilson, D.S., Ostrom, E., Cox, M.E., 2013. Generalizing the core design principles for the efficacy of groups. *Journal of Economic Behavior and Organization* 90, s21–32.
- Wilson, D.S., Wilson, E.O., 2007. Rethinking the theoretical foundation of sociobiology. *The Quarterly Review of Biology* 82, 327–348.
- Wilson, E.O., 2012. *The Social Conquest of Earth*. Liveright Publishing Corporation, New York, NY.
- Zhong, S., Israel, S., Shalev, I., Xue, H., Ebstein, R.P., Chew, S.H., 2010. Dopamine D4 receptor gene associated with fairness preference in ultimatum game. *PLoS ONE* 5 (11), e13765, <http://dx.doi.org/10.1371/journal.pone.0013765>.