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David Sloan Wilson & John M. Gowdy

Journal of Bioeconomics

ISSN 1387-6996

J Bioecon DOI 10.1007/s10818-014-9192-x





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Human ultrasociality and the invisible hand: foundational developments in evolutionary science alter a foundational concept in economics

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Received: 3 September 2014 / Accepted: 8 December 2014 © Springer Science+Business Media New York 2014

Abstract Advances in the study of social behavior require a revision in the economic concept of the invisible hand, which states that self-interested behavior leads to well-functioning societies without individuals having the welfare of the society in mind. Evolutionary theory shows that self-interest does not robustly benefit the common good because behaviors that are "for the good of the group" seldom maximize relative fitness within the group. The evolution of group-level functional organization requires a process of group-level selection. Species that have become highly adaptive at the group level are called ultrasocial. The idea that an invisible hand leads to social harmony is valid primarily for ultrasocial species, where selection at the group level results in individual-level behaviors that produce group-beneficial outcomes. Individuals do not necessarily have the welfare of the group in mind, but neither do their behaviors or underlying proximate mechanisms resemble the economic concept of self-interest. Evolutionary science therefore provides a valid concept of the invisible hand, but one that is different from the received version, with far-reaching implications for economics, politics, and public policy.

Keywords Economics · Evolution · Invisible hand · Multilevel selection · Regulation · Public policy

D. S. Wilson (🖂)

J. M. Gowdy Department of Science and Technology Studies, Rensselaer Polytechnic Institute, 3208 Sage Hall, Troy, NY 12180, USA e-mail: gowdyj@rpi.edu

Departments of Biology and Anthropology, Binghamton University, Binghamton, NY 13902, USA e-mail: dwilson@binghamton.edu

1 Introduction

Smith (1759, 1776) famously observed that economies appear to function well, even when individuals do not have the welfare of the economy in mind. As Smith put it, individuals neither intend to promote the public good nor know how much they are promoting it. Nevertheless, in pursuing their own goals, they are led, as if by an invisible hand, to promote a positive end that was no part of their intention.

The metaphor of the invisible hand stands for one of the most fundamental questions in economics—the degree to which market economies are capable of regulating themselves without government intervention. The idea is so central to economic theory that it is called the First Fundamental Theorem of Welfare Economics, the formal expression of Adam Smith's invisible hand (Mas-Colell et al. 1995). The metaphor can also be applied to the study of nonhuman species. Its two salient aspects are: (1) a society functions as a well-organized, higher level unit; and (2) the actions of members of the society serve to promote the common good even though the members do not have the common good of the society in mind. These two aspects can be evaluated for any biological unit composed of subunits, such as cells, multi-cellular organisms, single-species social groups, and multi-species ecosystems.

Throughout the first half of the twentieth century, biologists commonly assumed that something similar to the invisible hand operates in nature—that in addition to the obvious functional organization of individuals, higher-level entities such as social groups, ecosystems, and even the whole biosphere evolve to function well as units. This position came under scrutiny in the 1960's and a consensus emerged that functional organization above the level of individual organisms, while possible in principle, seldom evolves in nature (Williams 1966; Sober and Wilson 1998; Wilson and Wilson 2007). Individual organisms do not generally behave in ways supportive of the good of their groups, species, or ecosystems, so the first aspect of the invisible hand metaphor does not apply.

The rare exceptions include insect colonies such as ants, bees, wasps and termites, which are manifestly well organized at the colony level. A high degree of group-level functional organization is called *ultrasocial* (the related term eusocial additionally implies a reproductive division of labor). Ultrasocial insect colonies satisfy the first aspect of the invisible hand metaphor. The second aspect is likely to be satisfied as well, since insects don't even have minds in the human sense of the word, but nevertheless behave in ways that cause the colony to function well as a whole.

In short, the invisible hand metaphor can be substantiated for nonhuman species, but only when the conditions for the evolution of ultrasociality are met. These conditions have become greatly clarified during the half-century following the 1960's consensus and provide a foundation for examining the metaphor of the invisible hand in human society (Wilson 2004, 2015). In this article we will: (1) review the conditions for the evolution of ultrasociality in non-human species; (2) show that the same conditions apply to the evolution of human ulrasociality; (3) review the concept of the invisible hand in economic thought; and (4) show that the concept of the invisible hand in human society needs to be placed on an evolutionary foundation, with far-reaching implications for economics, politics, and public policy.

2 Conditions for the evolution of higher-level functional organization in non-human species

The following account is based upon a theoretical framework called multilevel selection, which partitions natural selection into within- and between-group components. It has a history of controversy but is now widely understood to be one of several intertranslatable methods of accounting for evolutionary change. See Gowdy and Seidl (2004), Wilson (2004, 2012a, 2015), Okasha (2006), and Wilson and Wilson (2007) for more depth.

For a society to function well as a unit, members must coordinate their activities and often must spend time and energy on behalf of others or the group as a whole. These behaviors that are "for the good of the group" typically do not maximize the advantage of individuals, relative to others within the same group. Since natural selection is based on relative fitness (Williams 1966), the evolutionary forces operating among individuals within a social group do not necessarily benefit and frequently undermine the welfare of the group. This is the fundamental reason why adaptations do not automatically evolve at all levels of a multi-tier biological hierarchy.

If a group-level adaptation is not selectively advantageous within groups, how can it evolve? When a population consists of many groups that vary in the frequency of group-advantageous behaviors, then the better-adapted groups differentially contribute to the total gene pool. Natural selection operates between groups in addition to within groups and a group-level adaptation can evolve if between-group selection is sufficiently strong to counter within-group selection. The general rule for a multi-tier biological hierarchy is "adaptations at level X require a process of selection at the same level and tend to be undermined by selection at lower levels." Or, as Wilson and Wilson (2007) summarized multilevel selection theory, "Selfishness beats altruism within groups. Altruistic groups beat selfish groups. Everything else is commentary."

Decision-making provides an example of an adaptation that can evolve at either the individual or the group level in nonhuman species, which is highly relevant to the metaphor of the invisible hand. Decision-making is the identification, comparison, and selection of alternative courses of action. In many species, the individual is the unit that gathers and compares the relevant information, leading to the final decision. When the decision-making process is analyzed in mechanistic detail, the many cells in the nervous system involved in the process each play a specialized role. In this sense, the individual is an ultrasocial group of cooperating cells. The individual functions well as a unit (the first aspect of the invisible hand metaphor), without the individual nerve cells having the welfare of the individual in mind (the second aspect of the invisible hand metaphor). The second aspect goes without saying, because the concept of a collective "mind" refers to an emergent property of a system of nerve cells and does not exist within in any single cell.

In ultrasocial insect colonies, the group functions as the decision-making unit with individual insects playing specialized roles, more like single neurons than complete decision-making units in their own right. The ability of social insect colonies to make intelligent decisions and the underlying mechanisms have been studied in impressive detail. To provide one example, when searching for a new home, honeybee scouts evaluate prospective cavities on the basis of numerous criteria such as volume, height, exposure to the sun, and size of the cavity entrance. Single scouts seldom visit more than one cavity, so the comparison among sites is made by social interactions that take place on the surface of the bee swarm, which is a mass of bees (including the queen) in a resting state, waiting for the decision to be made. The social process that results in the scouts from the best cavity ultimately silencing the scouts from the inferior cavities is mechanistically similar to the interactions among neurons in an individual decision-making process (Seeley 2010; Seeley et al. 2012). Individual bees are more complex than single neurons and function as autonomous decision-making units in other contexts, but as far as house hunting is concerned, they behave for the benefit of their group without having the welfare of their group in mind, as if guided by an invisible hand.

Biologists expect ultrasocial insect colonies to function as group-level decisionmaking units because they function as group-level "superorganisms" in many other respects, such as the physical architecture of their nests and reproductive division of labor. More surprising is the discovery of adaptive group-level decision making in other group-living species such as fish schools, bird flocks, buffalo herds, and tadpole groups, in which genetic relatedness can be low or even absent (Sontag et al. 2006; Couzin 2007; Couzin et al. 2011). It is perfectly possible for individuals in these groups to not only function as autonomous decision-making units, but to make decisions that are designed to maximize their relative fitness within the group. Instead, individuals often interact in ways that result in good collective decisions, such as the entire group moving to a better rather than a worse feeding location. The coordination required to make a good collective decision needn't be costly for individuals, but neither can it be explained as a product of within-group selection. In other words, the traits do not evolve by virtue of individuals bearing the trait surviving and reproducing better than other individuals within their own group, but by smart groups contributing more to the gene pool than dumb groups. Even random genetic variation among groups can drive this process. The fact that all members of smart groups profit equally is not an argument against the scale at which the selective differentials occur (between groups, not within groups).

Decision-making is only one of many documented examples of group-level adaptations that could be provided, once the partitioning of natural selection into within- and between-group components is made explicit (Wilson 2015; see Pruitt and Goodnight 2014 for a recently documented example in social spiders). To summarize, not only can group-level adaptations evolve in principle, but they also evolve in nature, satisfying the first aspect of the invisible hand metaphor. Whenever this happens, group members play a role in group-level functional organization without necessarily having the welfare of the group in mind, satisfying the second aspect of the invisible hand metaphor.

One of the most important developments in evolutionary thought since the 1960's is the discovery that individual organisms are themselves highly integrated social groups that evolved by between-group selection. This realization began with the symbiotic cell theory of Margulis (1970), which established that nucleated (eukaryotic) cells did not evolve by mutational steps from bacterial (prokaryotic) cells, but rather by symbiotic associations of bacteria becoming so functionally integrated that they became higherlevel organisms in their own right. This insight was then generalized to include other

transitions from groups *of* organisms to groups *as* organisms, including the origin of life as groups of cooperating molecular reactions, the first cells, multi-cellular organisms, and ultrasocial insect colonies (Maynard Smith and Szathmary 1995, 1999). Very simply, a major transition occurs when mechanisms evolve that suppress forms of selection within groups that are detrimental to the group, making benign forms of within-group selection and between-group selection the dominating evolutionary forces.

To summarize our argument so far, multilevel selection theory specifies the conditions for the evolution of higher-level functional organization—the first aspect of the invisible hand metaphor. Whenever this happens, the lower-level units comprising the higher-level units act for the common good, as if guided by an invisible hand, without necessarily having the common good in mind. The second aspect of the invisible hand usually goes without saying, because the lower-lever units that comprise higher-level biological units, such as genes, cells, and insects, don't even have minds in the human sense of the word.

In addition to the insights forthcoming from multilevel selection theory, the distinction between ultimate and proximate causation in evolutionary theory (Mayr 1961) adds an interesting new twist to the invisible hand metaphor. Ultimate causation explains why certain traits exist compared to many other traits that could exist, often due to the winnowing action of natural selection. Proximate causation explains the mechanistic basis of the same traits. The invisible hand thesis stated for ultimate causation is "selection among individuals within groups results in adaptations that are for the good of the group". As we have seen, this statement is profoundly misleading, since lower-level selection typically *undermines* higher-level functional organization. The invisible hand thesis stated for proximate causation is "individuals behave in ways that are for the good of their group without having the welfare of the group in mind." As we have seen, this statement can be justified only when the group is a product of higher-level selection. Higher-level selection *is* the invisible hand that winnows the proximate mechanisms resulting in group-level functionality from the much larger set of proximate mechanisms that are dysfunctional at the group level.

3 Human genetic and cultural evolution as major evolutionary transitions

Most primates live in groups and even the species that appear solitary usually have a spatially extended social network (Bearder 1999). Cooperation exists to a degree but members of the same group are also their chief rivals in many respects. Even cooperation often takes place in the context of competition among coalitions for dominance within the group (Strier 2011). Thus, the invisible hand metaphor does not apply to most primate groups, to the extent that between-group selection has failed to prevail against within-group selection.

Humans are an exception to the primate rule. Human hunter-gatherer societies are much more cooperative than any primate group, extending to virtually all spheres of activity such as childcare (Hrdy 2011) hunting and gathering (Kaplan and Hill 1985) and between-group conflict (Bowles 2009). Cooperation also has a mental dimension. Most of the psychological, social, and cultural attributes that set us apart from

other primates are falling into place as part of a major evolutionary transition (Boehm 1999, 2011; Wilson 2002, 2012). This is an important synthesis that enables human ultrasociality to be interpreted within the same framework as ultrasociality in nonhuman species. Three points need to be addressed to relate these developments to the metaphor of the invisible hand: (a) the genetic evolution of small-scale human groups; (b) the cultural evolution of large-scale human groups; and (c) proximate causes of cultural change in human groups, which include psychological mechanisms in addition to ongoing cultural evolution.

3.1 The genetic evolution of small-scale human groups

Like any other major transition, the human transition required the suppression of dysfunctional forms of selection within groups, making benign forms of within-group selection and between-group selection the dominating evolutionary forces. In humans, the psychological dispositions, informal norms, and formal institutions associated with morality have precisely this effect. The moral sentiments, as Smith (1759) called them, include an other-oriented dimension such as sympathy and empathy and a coercive dimension such as norms enforced by punishment and status based on good conduct (reputation) rather than coercive power. The two dimensions go together because without the second, the first would be vulnerable to exploitation.

Humans are distinctive among primates not only in their degree of cooperation enforced by social control, but also in their ability to transmit learned behaviors across generations and their capacity for symbolic thought, including but not restricted to language. Yet, cultural transmission and symbolic thought are cooperative activities in their own right. Even an act of communication as simple as pointing requires a degree of shared awareness and propensity to cooperate that is largely lacking in our closest primate relatives (Tomasello 2009). Nearly everything distinctive about our species, compared to other primate species, can therefore be understood as a form of cooperation (or constructive competition) within small face-to-face groups (Dunbar 1996). Other primate species are intelligent, but their intelligence is predicated upon distrust, which prevents teamwork. Human intelligence is predicated upon trust, which makes myriad forms of teamwork possible.

The capacity for symbolic thought led to a new mechanism of inheritance with a combinatorial diversity that rivals genetic inheritance (Deacon 1998; Jablonka and Lamb 2006). A symbolic system is a network of mental relationships that need not bear a direct relationship with environmental relationships. Insofar as any given symbolic system influences human behavior, there is a symbotype-phenotype relationship similar to a genotype-phenotype relationship. Because networks of mental relationships exist in almost infinite variety, individuals and groups can behave in very different ways by virtue of having different symbotypes, even when they are genetically similar (Wilson et al. 2014). There is mounting evidence that humans have unique "social brains" hard-wired to encode one's particular culture (Wexler 2006).

Cultural evolution made our ancestors so adaptable that they were able to spread over the globe, adapting to all climatic zones and hundreds of ecological niches, while genetically remaining a single species. The cultural adaptive radiation of humans rivals the genetic adaptive radiations of major taxonomic groups such as dinosaurs, birds,

and mammals (Pagel and Mace 2004) and is on a par with the ecological dominance of the eusocial insects (Wilson 2012).

The ability of small human groups to function as corporate units satisfies the first aspect of the invisible hand metaphor. The proximate mechanisms can include, but are by no means restricted to a direct interest in the common good. Concern for one's reputation is an example of a motive that is self-interested in a proximate sense but benefits the common good in an ultimate sense, when reputation is contingent on good conduct (Henrich and Gil-White 2001). This is a good example of a second-order public good problem. The people providing benefits (in the form of status) to public good providers are themselves providing a public good that requires between-group selection to explain (Sober and Wilson 1998). Many of the proximate mechanisms that contribute to the public good operate beneath conscious awareness, such as the assimilation of cultural norms during childhood. Thus, people frequently act to benefit the common good without having the common good in mind, satisfying the second aspect of the invisible hand metaphor. As Alexis de Tocqueville wrote in 1835, "The village or township is the only association that is so perfectly natural that... it seems to constitute itself."

It goes without saying (which is to say that it follows directly from multi-level selection theory) that selection at any given level results in functional organization at that level only and tends to undermine functional organization at higher levels. Thus, internally cooperative groups often engage in destructive between-group competition, and so on. Also, evolution at all levels result in non-adaptive byproducts (spandrels) in addition to adaptations. There is nothing "panglossian" about multilevel selection (Gould and Lewontin 1979).

3.2 The cultural evolution of large-scale human groups

For 95–99% of our existence as a species, the worldwide human population was under 4 million and may have dropped to a few hundred thousand at some points. The advent of agriculture led to a positive feedback process between the production of resources and the scale of human societies, leading to the mega-societies of today. Tocqueville appreciated that large-scale human societies, such as the nations of France and the United States of America, do not spontaneously constitute themselves in the same way as a village. They are products of history, resulting in customs and institutions that differ from each other and can be difficult to change once established. Their differences are consequential for how they function as corporate units. Tocqueville observed that Americans were able to mount cooperative enterprises that could not happen in France. He also observed that within the United States, slaveholding states were less enterprising than states that prohibited slavery.

Once history is regarded as a fossil record of cultural evolution, it can be analyzed from a multilevel perspective in the same way as genetic evolution. New cultural traits can spread by virtue of benefitting individuals or factions, compared to other individuals or factions within a society, or by virtue of benefitting the entire society, compared to other societies. Marriage norms provide an example (Henrich et al. 2012). Most human societies throughout recorded history have been polygamous, based on the powerful tendency of men to want multiple wives and women to prefer men

with the most resources. Yet, polygamous societies tend to work poorly as societies, because they result in a large fraction of men without reproductive prospects. Relatively monogamous societies therefore tend to replace (or be imitated by) relatively polygamous societies in economic and military competition. Societies vary in their degree of polygamy because different norms (formalized as laws) become established and are enforced by punishment. The norms that become established in any particular society are historically contingent. Societies that adopted norms favoring monogamy were sufficiently successful in group-level competition for these norms to become the most common marriage norms in developed societies. In the not-so-distant future, all human societies might be monogamous (as far as their laws are concerned), even though most human societies were polygamous in the past. Selection at large societal scales will be responsible for this outcome, not selection at smaller scales.

Turchin (2003, 2005, 2010) has analyzed the rise and fall of empires from a multilevel cultural evolutionary perspective. Geographical zones of intense between-group conflict act as a crucible for the cultural evolution of cooperative societies, which expand to become empires. Then cultural evolution within the empires cause them to fall apart. Religions also exhibit a cycle of growth based on cooperation followed by decline or schism based on within-group conflict (Wilson 2002). Finally, analyses of modern nations reveals strong correlations between their degree of equality and their ability to function as large-scale corporate units for the well-being of their members (Pickett and Wilkinson 2009; Acemoglu and Robinson 2012).

When this view of human history is related to the metaphor of the invisible hand, two conclusions can be drawn. First, large-scale societies *vary* in the degree to which they function as corporate units. For those that function poorly, the first aspect of the invisible hand does not apply. Second, for large-scale societies that do function well as corporate units, most people are no more aware of the cultural causes than they are of the genetic causes. They simply follow the rules prescribed by their society, as if guided by an invisible hand. It should be noted that Hayek (1988) pioneered this approach within the field of economics, as described in more detail below.

3.3 Proximate causes of cultural change in human groups

When we examine the proximate causes of cultural change in human societies, we encounter a number of psychological processes in addition to the raw process of cultural evolution. Some of these mechanisms are conscious, such as deliberate decision-making. Others often take place beneath conscious awareness, such as operant conditioning and imitation. For example, few people are aware that they copy the speech patterns and mannerisms of high-status individuals (Gregory and Webster 1996).

Authors disagree on whether psychological causes of cultural change count as evolutionary (e.g., Pinker 2012). As an example, consider group A, which is competitively inferior to group B. Realizing this, members of group A deliberately copy the practices of group B. The practices of group B have spread, without the actual replacement of group A by group B. As another example, consider a typical policy discussion, which evaluates and selects options to achieve a particular objective. Cultural change has occurred within the group without reference to any other groups.

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These are not examples of cultural group selection in the sense of groups replacing other groups, but they still need to be understood from an evolutionary perspective in two respects. First, all forms of decision making are variation-and-selection processes capable of adapting individuals and groups to their current environments, based on their selection criteria. Second, the psychological mechanisms involved in cultural change need to be understood as products of multilevel selection operating in the past. To continue the previous two examples, members of group A who work to imitate group **B** are providing a public good for their group. They do not increase their relative standing within their group unless rewarded by other group members. In the absence of such rewards, their "for the good of the group" behavior places them at a disadvantage, compared to members of their groups who care only about increasing their relative standing. In a typical policy discussion, the goal is to achieve a common objective such as better education, national security, and so on. These are public goods and efforts to achieve them cannot be explained on the basis of maximizing one's relative standing within the group, without a system of rewards and punishments designed to align the two. In short, psychological mechanisms that promote the common good are typically products of group-level selection operating in the past, even if they do not count as evolutionary processes in their own right. As with genetic and cultural group selection, psychological mechanisms that promote the common good need not involve having the common good in mind. Someone who promotes the common good can care only about their own stake in the common good, for example. This particular form of psychological self-interest cannot be explained on the basis of selection differentials within groups.

To summarize, the invisible hand metaphor can be justified from an evolutionary perspective, for humans in addition to nonhuman species, when certain conditions are met. These conditions are very different from the economic concept of the invisible hand, as we will now show.

4 The economic concept of the invisible hand

Despite its enormous influence on human affairs, the economic concept of the invisible hand rests upon a remarkably weak theoretical foundation. Adam Smith used the metaphor sparingly and clearly understood the need for strong social institutions and "moral sentiments" to check the abuses of unregulated social interactions, economic or otherwise. Smith recognized, for example, the need to check the avarice of businessmen: "People of the same trade seldom meet together, even for merriment and diversion, but the conversation ends in a conspiracy against the public, or in some contrivance to raise prices." (Smith 1776, Book 1, Chap. 10, p. 145).

Many-perhaps even most—branches of the economics profession do not offer a strong defense of the invisible hand metaphor. In other words, they do not propose that societies work best when individual self-interest is given free reign. An exception is the theoretical and mathematical foundation that Walras (1874) appeared to provide for the invisible hand metaphor with his general equilibrium model, upon which modern neoclassical economics is based. We will concentrate on this tradition because of its disproportionate influence on economics and public policy during the last half-century, especially in the United States and United Kingdom but also worldwide.

Walras's goal was to create a physics of social behavior inspired by Newtonian physics (Mirowski 1989; Beinhocker 2006). This required a number of simplifying assumptions about human preferences and abilities that are often summarized by the term *Homo economicus*, as if they are a description of a biological species (Thaler and Sunstein 2008). One of the most important assumptions is that people have *self-regarding preferences*; the well-being (utility) of one individual cannot be influenced by the utility of another.

The ideological purpose of Walrasian theory is to provide an intellectual foundation (a mathematical proof) of the ability of free markets to promote the public good. As Feldman (1987, p. 889): "The invisible hand of competition automatically transforms the self-interest of many into the common good." This idea is so important that it is called The First Fundamental Theorem of Welfare Economics (Feldman 1987). Markets work best if left alone. Again, a critical assumption of the First Theorem is that preferences are self-regarding. It is true that a utility function can take many forms and incorporate many assumptions about preferences and well-being. But the mathematical proof of the efficiency of competitive markets breaks down if preferences are other-regarding (Henderson and Quandt 1980, p. 297).

It should be pointed out that economists also have a Second Fundamental Theorem of Welfare Economics that recognizes the existence of market failure. For a variety of reasons such as monopoly power, public goods, and externalities, prices may be distorted and therefore even perfectly rational actors make wrong decisions. The Second Theorem allows for distributional changes ("lump sum transfers" in economic jargon) but keeps the Walrasian assumptions of self-regarding presences and perfectly rational actors. The effectiveness of governmental intervention through market incentives like taxes and subsidies may be limited if economic decision makers do not act according to the axioms of rational choice theory. The assumption of self-regarding preferences excludes norms and myriad other influences that actual people have on each other's preferences and abilities, which are central to the evolutionary account. Other assumptions include the ability to calculate the direct and indirect consequences of one's actions far into the future. The general equilibrium model also requires assumptions about the social environment, such as markets that are perfectly responsive and have reached equilibrium. Only with these restrictive assumptions, is it the case that welfare theory demonstrates that individuals who care only about maximizing their personal utilities also maximize the public good.

The general equilibrium model differs from the evolutionary account at a paradigmatic level. In the former case, individuals are envisioned as like atoms with fixed properties—"homogeneous globules of desire" in Thorstein Veblen's words—that interact in such a way that robustly benefits the common good. In the latter case, individuals vary and strongly influence each other's properties. A process of selection is required to winnow a small fraction of properties and interactions that are adapted to a given environment, which are like needles in a haystack of properties and interactions that are maladaptive. Furthermore, the process of selection for group-level adaptations must work against opposing selection for lower-level adaptations that undermine the welfare of the group. It would be hard to imagine a greater distance between the two conceptions of the invisible hand.

The general equilibrium model has been criticized by economists and other social scientists throughout its history (e.g., Veblen 1908, Georgescu-Roegen 1971) but became the dominant paradigm during the 2nd half of the twentieth century, especially in the United States and the United Kingdom (Beinhocker 2006). It achieved its dominance in part due to an argument developed by Friedman (1953) that a theory can be predictive, as if its assumptions are true, even when its assumptions are false. Friedman provided three examples to illustrate his "as if" argument: (1) The leaves of a tree are distributed to maximize exposure to light, but no one supposes that the tree is performing optimization equations; (2) An expert billiard player makes complex shots thanks to countless hours of play, not because he is performing complex calculations in his head; and (3) A corporation maximizes profits, not because its managers know what they are doing, but because it is the survivor of a competitive process in which non-maximizing corporations went out of business. These examples invoke genetic evolution, individual learning, and cultural evolution, respectively, to illustrate how an entity can become functionally organized, as if its parts are consciously striving to maximize something, when in fact they are doing nothing of the sort. In the same way, Friedman asserted that people behave as if the assumptions of the general equilibrium model are correct, even when they are false in a mechanistic sense.

In short, Friedman's "as if" argument relies upon the distinction between proximate and ultimate causation in evolutionary theory (Wilson 2012). Evolutionists frequently employ the "as if" argument to think about the functional basis of traits without worrying about the proximate mechanisms, but applying the argument to the general equilibrium model is highly problematic. There is no plausible evolutionary scenario that would result in people behaving "as if" the assumptions of neoclassical economics are correct. One of the most influential articles in the history of economics can be seen as fatally flawed in retrospect.

Along with Friedman, Friedrich Hayek is viewed as the most influential proponent of the invisible hand metaphor. Hayek was a critic of the general equilibrium model and based his justification of the invisible hand on cultural group selection. He understood that the intelligence of a society is to a large extent a distributed process that resulted from more successful societies replacing less successful societies. Hayek was ahead of his time in his appreciation of distributed self-organizing processes that evolve by group selection. When his views are updated, however, they provide little support for economic policies that rely upon his authority.

Within the field of economics, the most recent critics of the neoclassical paradigm include behavioral economists such as Thaler and Sunstein (2008), who call for economic theory and practice based on *Homo sapiens*, not *Homo economicus*; in other words, informed by actual human preferences and abilities, rather than the assumptions of the mathematical models. The field of behavioral economics has made a large contribution by revealing the cognitive heuristics and biases that guide human behavior; however, these departures from *Homo economicus* do not address the central theoretical problem of how a society can function without individuals having the welfare of the society in mind.

Public economic and political discourse has a life of its own that is only loosely based on formal economic theory. Few politicians are economic scholars and few economic scholars would endorse the slogans of politicians. Nevertheless, it is at the level of public discourse that important decisions such as elections are made. At this level, the invisible hand functions as a powerful narrative that portrays unregulated self-interest as a cure-all for improving society, citing Adam Smith, Milton Friedman, Friedrich Hayek, and novelist Ayn Rand for support. Professional economists who know better have had little success combating this narrative. Evolutionary theory might succeed where they have failed by offering a coherent alternative account of the invisible hand metaphor.

5 Conclusions: Implications for economics, politics, and public policy

Human ultrasociality provides a new theoretical foundation for managing human affairs in a practical sense (Gowdy and van den Bergh 2003; Wilson 2004, 2012; Beinhocker 2006; Hodgson and Thorbjorn 2010; Frank 2011;Gowdy and Krall 2013, 2014). One way to see this is by contrasting the received version of the invisible hand, based on the concept of self-interest, with the new and more valid version based on higher–level self-organization.

According to the received version, society works best when individuals are allowed to pursue their own gain, which is typically interpreted as economic gain. In the neo-liberal view, efforts to regulate individual-level behaviors for the good of society are counter-productive. Against the background of evolutionary theory, the received version of the invisible hand isn't just wrong-it's as wrong as it can possibly be. The starting point of all evolutionary theories of social behavior is that behaving "for the good of the group" usually does not maximize relative fitness within the group. The reason is a basic matter of tradeoffs that apply to all group-living species. The unavoidable conclusion is that groups evolve to function as adaptive units only when certain conditions are met. In all other cases, groups are dysfunctional and the basic concept of the invisible hand doesn't apply. The general rule is that adaptation at any level of a multi-tier hierarchy requires a process of selection at that level and tends to be undermined by selection at lower levels. This rule needs to be taken very seriously for formulating policy on scales ranging from global climate change, to interactions among developed nations such as the European Union, to efforts to develop nations in regions such as Afghanistan and Africa, to empowering neighborhoods in cities.

According to the more valid version of the invisible hand, human groups function as adaptive units because certain individual-level preferences and abilities (proximate causation) have been selected at the group level (ultimate causation). These preferences and abilities are most easily observed in the context of small social groups that approximate the human social environment for many thousands of generations prior to the advent of agriculture, such as hunter-gatherer societies or village-sized groups in post-agricultural and industrial societies.

Members of small human groups that function well as units do not necessarily have the welfare of their group directly in mind, but neither do they exemplify the economic concept of self-interest. Instead, they exhibit a complex mix of self-and other-regarding behaviors, concern for their reputations, and the establishment and enforcement of norms. We don't call these propensities "government", but they perform the same role as governments in large-scale societies. Ironically, the emerging view of evolved human nature accords well with Adam Smith's nuanced view in his *Theory of Moral Sentiments*. The new version of the invisible hand represents the views of Smith better than the old version (Gintis et al. 2005).

Human societies that function well at larger scales do so only by virtue of culturally derived mechanisms that interface with genetically evolved psychological mechanisms (Turchin 2003, 2005, 2010; Richerson and Boyd 2005). Some of the culturally derived mechanisms, such as the constitution of the United States, arose from deliberative processes and resulted in social institutions that we recognize as governments. Other culturally derived mechanisms emerged from the raw process of cultural evolution-many inadvertent social experiments, only a few that succeeded. Tocqueville (1835) was again perceptive when he observed that Mexico copied the American constitution but that Mexico is not at all like America because of differences that are vaguely called "custom", which must be studied to be understood, even though they govern our behaviors every moment of the day. An implication of taking cultural evolution seriously is that economic and political theory informing policy can never be reduced to a single set of psychological attributes. Cultural history will always be important for understanding the mechanisms that govern the dynamics of particular societies (Henrich 2003; Henrich et al. 2004; Boyd et al. 2011).

The new and more valid concept of the invisible hand leads to policy recommendations that cut across current political ideologies (Frank 2011; Liu and Hanauer 2011). The idea that the unregulated pursuit of economic self-interest by lower-level entities such as individuals or corporations automatically promotes the welfare of large-scale society emerges as patently absurd. On the other hand, the regulation need not be topdown. Small human groups are the most natural social units for self-regulation, so the more they can govern their own affairs and participate in governance at a larger scale, the better (Ostrom 1990; Bowles and Gintis 2002; Ostrom 2010). Large-scale human society needs to be *multi-cellular*, with individuals participating in small groups as an important intermediate level. Every human sphere of activity has an optimal scale that must be determined on a case-by-case basis to discover the best regulatory framework (McGinnis 1999; Ostrom 2010). For every regulatory framework that works, there are many that don't work. The challenge is to find the best regulatory framework—not to argue for no regulations at all.

The most successful forms of governance have already converged upon these principles because they work and have survived, compared to other forms of governance that don't work. In addition, some schools of economic and political thought have made these principles explicit without necessarily framing them in terms of evolutionary theory. Evolutionary theory places these successful practices and correct theoretical formulations on the broadest possible scientific foundation, supported by principles that apply to all group-living species in addition to all human societies throughout history. All approaches to economics, politics, and public policy strive for consilience—consistency with other branches of knowledge—but some succeed better than others. A new and more consilient concept of the invisible hand, based upon human ultrasociality, can lead to new practical solutions to life's problems where previous conceptions have failed.

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