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New evolutionary foundations: Theoretical requirements for a science of sustainability☆

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A R T I C L E D A T A

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A B S T R A C T

Ecological economics stands in theoretical and ethical opposition to many aspects of neoclassical economic theory. Despite their sound critiques of that theory, ecological economists have not settled on an alternative theory of human behavior. As a potential alternative, Norgaard's socioecological coevolutionary framework remains underspecified in terms of variation, heredity, and selection. I review concepts and insights on human behavior from evolutionary biology and evolutionary social science in order to supply new theoretical tools for ecological economic problems, and help refine the coevolutionary framework. I argue that a synthetic evolutionary theory of human behavior provides a sufficient alternative to the neoclassical perspective, and that cultural evolutionary theory is a necessary prerequisite of a mature economic science, ecological, coevolutionary or otherwise. Finally, I suggest some potential topics that such a mature theory might begin to tackle.

1. Introduction

Ecological economics (EE) has been dubbed "the science of sustainability" (Costanza, 1992). Aware that the practices and mind-sets of neoclassical economics do not help to solve the problems that they must tackle, ecological economists have maintained a distance from traditional neoclassical economics. Positing that economic rationality is theoretically implausible and empirically false (Lea, 2003), EE challenges traditional economic perspectives on growth, valuation, the fixity of preferences, the behavioral response to uncertainty, and the importance of context in valuation and temporal discounting (Costanza et al., 1997). Instead, EE recognizes that human economic processes modify the biosphere, while ecological and environmental factors influence and constrain the economy. This dual-causation has been accounted for in many different ways. A growing number of ecological economists see promise in the concept of coevolution as a framework for the analysis of the linked development of ecosystems and economies (Norgaard, 1981, 1984a,b; Gowdy, 1994; van den Bergh and Gowdy, 2003). Still, applications of 'coevolution' in practice tend to under-specify the components of the evolving system, namely the sources and details of variation, heredity and selection. Recently scholars have made important strides toward a more systematic coevolutionary theory (Gowdy, 1994; Kallis, 2007; Brooks, 2008-this issue; Kallis, 2008-this issue). In such an endeavor, the model of human behavior is of central importance, as it uniquely determines how human-environment interactions are considered. So, while the distance from traditional economic theory has allowed EE

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theoretical and methodological flexibility, the unfortunate result has been a theoretical vacuum on the motivation of the individual.

Ecological economics therefore faces theoretical challenges on two fronts. First, if societies and ecosystems coevolve, what are the mechanisms of heredity, variation and selection that will explain that evolution? Second, in lieu of neoclassical assumptions, EE needs to specify a theory of human behavior. If preferences aren't fixed, how do they change? If individuals are not rational actors, how do they act? I submit that these two challenges are one and the same. Specifying a synthetic model of human behavior will allow ecological economics to tighten the study of socio-ecological coevolution and better achieve a science of sustainability.

The purpose of this paper is to help build an alternative model of human action in EE by reviewing concepts and theories from the evolutionary behavioral sciences. Starting with an historical overview of the role of theory in EE, and a summary of the problems with conventional economic theory, the article demonstrates the importance of a social theory of human behavior to environmental policy and takes steps toward a synthetic evolutionary theory of human behavior. Finally, it suggests some avenues for the further refinement of a coevolutionary science of sustainability.

2. Theory in ecological economics

2.1. *History and pluralism*

In the first issue of Ecological Economics, Norgaard critiqued traditional economic practice as a means of setting the direction for ecological economics. He criticized both the undue conformity of the discipline and the impervious nature of traditional economics in regards to evidence. He argued that ecological economists would need more flexibility, and cautioned them to embrace a methodological pluralism (Norgaard, 1989). Similarly EE textbooks stress a pluralist approach to theory and practice (Costanza et al., 1997). Along with methodological diversity, practitioners have embraced a broad theoretical pluralism (Boulding, 1966; Norgaard, 1989; Costanza et al., 1997; Daly and Farley, 2003). Methodological pluralism is an effective means of maintaining intellectual honesty (Norgaard, 1989), the lack of which is one of the main criticisms of neoclassical economic's narrow vision. Theoretical pluralism can be supported in the same spirit. However, ecological economics seems to be casting the net too wide:

> "It is difficult to determine where ecological economics ends and other approaches to understanding start." (Costanza et al., 1997, p. 72)

It is not that pluralism per se is damaging, but rather that science depends on having both a subject matter and consistent means of addressing it. Ecological economics has a uniquely defined and motivating subject matter–the "science of sustainability." The field has not suffered from a lack of focus, but from the want of a common framework around which disparate arguments and lines of evidence may coalesce (e.g. see Wilson, 1998).

Ecological economics attends to the mutual feedback between ecological and economic systems that Norgaard described as coevolution (Norgaard, 1989)[1]. Since the scope of ecological economics is necessarily broader than either parent discipline, it uses theory and methods from each, and focuses on the problems to be solved over the details of the theories required to do so.

> "ecological economics goes beyond our normal conceptions of scientific disciplines and tries to integrate and synthesize many different disciplinary perspectives. One way it does this is by focusing more directly on the problems, rather than the particular intellectual tools and models used to solve them, … we should consider the task, evaluate existing tools' abilities to handle the job, and design new ones if the existing tools are ineffective." (Costanza et al., 1991)

Although the optimistic spirit of exploration is palpable, this perspective seems ignorant of the importance of basic theory. Eventually the right tools are needed if the job is to be done.

2.2. *Problems with neoclassical economic theory*

EE is full of explications of why neoclassical economics fails to provide the necessary tools for the job. Gowdy (2005), for instance, demonstrates that central aspects of neoclassical welfare economics fail to supply a solid foundation for modeling sustainable societies. But neoclassical theory is also flawed in its own right. Many have noted that neoclassical economic theory seems more like a model of a physical, rather than a social, system. This is partly because the general equilibrium theory of Walras was founded on equations borrowed from statistical physics:

> "The true fons et origo of Walras' multiequational formulation of general equilibrium was Louis Poinsot's once famous textbook in pure mechanics, Éléments de statistique (1803) … In Poinsot we find virtually the whole formal apparatus that Walras later employed in his Éléments d'économie politique pure." (Jaffé, 1983, p. 132)

Mirowski (1989) examined the historical mimicry of theoretical physics in economic theory in depth, and in so doing exposed deep problems in the current application of mathematical formalisms in neoclassical models. Despite the origins of the equations, the general equilibrium framework proved flexible enough to influence the nature of economics for a century. One of the central assumptions of neoclassical theory is the assumption of optimality on the part of the individual, the central tenet of the rational actor model of human behavior. In defense of neoclassical theory, Friedman (1953) argued that any scientific theory "cannot be tested by comparing its "assumptions" directly with "reality." Indeed, there is no meaningful way in which this can be done" (p. 41).

[1] Since the intentional inclusion of both natural-to-social and social-to-natural feedbacks defines both ecological economics and Norgaard's coevolutionary framework, I consider addressing the theoretical needs of both traditions as a single task.

Table 1 – Problems with neoclassical economic theory.

Topic	Traditional problems
Utility	Uni-dimensional, static, no social component
Preferences	Transitive, fixed or exogenous
Uncertainty	Perfect rational reaction to uncertainty
Valuation	Gains valued the same as losses
Substitutability	Perfect substitution assumed, rarely impossible
Backwards induction	Ignores cognitive constraints
Rational action	Ignores cognitive constraints, social motivations
Institutions & technologies	Fixed or exogenous

But assumptions are critical to the validity of any theory, and must be held to the empirical flames. Still, the neoclassical school of economic thought has traditionally overlooked the assumption of human optimality, and continues to uphold aspects of the rational actor model of behavior, despite contradictory empirical evidence.

In fact, for more than two decades behavioral economists have been rigorously testing the assumptions of traditional economic theory of rationality, and have repeatedly demonstrated that it makes poor predictions of actual human behavior. Simon (1957) famously challenged the rational actor model of the individual and the early empirical work of Kahneman and Tversky (1979) drew the optimality assumptions into question. Since these pioneers, behavioral economists have shown that the standard economic model of human decision-making is seriously flawed on multiple fronts. Van den Bergh and Gowdy (2000) argue that because rational choice theory is still practiced despite its failure to withstand the test of evidence, as a tradition it is effectively nonfalsifiable. And the evidence has only grown. Humans do not maximize short-term payoffs, and deep cognitive limitations and nuances constrain our choices and actions. A few new economic texts take the empirical work into account (Camerer et al., 2004; Bowles, 2006; Ariely, 2008). New data highlight the inaccuracy of the rational actor model (Fehr and Gächter, 2002; Henrich et al., 2004; Fowler et al., 2005) and highlight the importance of human sociality to economic behavior.

The accumulated problems with the neoclassical economic framework are so multitudinous that to elaborate them has taken volumes. Readers of this journal will be familiar with critiques from all angles (e.g. Daly and Cobb, 1999). In addition, see Veblen (1898), Green and Shapiro (1994), Gigerenzer (2000), and Manner and Gowdy, 2008-this issue) for complete and nuanced critiques. My point here is simply to list those components of neoclassical economic theory that fail the needs of a science of sustainability Table 1.

I suggest that with respect to the theoretical interests of ecological economics, there are two critical oversights in neoclassical economic theory. The first is the assumption of individual-level optimality. The second is the almost complete lack of attention to cultural concerns, human sociality and altruism.[2] Failure to account for the influence of social norms is a significant problem in current macroeconomics (Akerlof, 2007). This paper aims to provide a fresh evolutionary theory of human behavior that can explain factors such as altruism, culture, and sub-optimality, and is thereby better suited to the practice and goals of ecological economics.

[2] Social factors such as altruism are not just a theoretical matter, but have a significant impact on environmental and economic policy directly (See Appendix A for a mathematical demonstration).

3. Building an evolutionary alternative

In constructing an alternative set of theory for ecological economics, we must be cautious on two fronts. First, evolutionary theories of human behavior have long been the subject of strong criticism. Some of the critique stems from an assumed association with social darwinism or Francis Galton's eugenics, although neither plays a role in modern theories. More informed critics highlight the necessity of developing a social theory that does not overly borrow from biological systems, but is instead acutely focused on and derived from human patterns. Moreover, not all evolutionary social scientists are entirely careful about the application of evolutionary theory to humans as we will see. Nonetheless, modern theories such as gene-culture coevolution and cultural evolution meet and exceed this mark, but suffer instead from under-exposure. Thus, most evolutionary social theories are met with uninformed skepticism across the social sciences today. Second, an evolutionary theory must not fail the charge of empiricism as neoclassical economics has. Since Norgaard's (1981, 1984a,b) generalized Darwinian approach to coevolution focuses on the reciprocal selection of elements in environmental or social sub-systems and does not specify populations, variation, heritability, or selection forces, it is not capable of rendering empirical predictions. Hodgson and Knudsen (2006) argue that a generalized Darwinism is required to understand social phenomena, but not sufficient to explain their workings without greater specificity. Kallis (2007) and Winder (2005) both argue that any useful coevolutionary analytical framework will need to carefully define the nature of the coevolutionary system, especially with regards to variation, heredity, and selection. In recent years, scholars have begun pulling insights from evolutionary fields that might help congeal an evolutionary theory of human behavior suitable for true coevolutionary analysis ecological economics. Below I summarize insights from and explorations into a variety of evolutionary disciplines.

3.1. *The mother discipline: evolutionary biology*

Evolutionary biology is, naturally, the mother-discipline for all evolutionary sciences. Aside from the study of human evolution, which will be addressed in the following sections, the topic of most relevance to human social systems within biology is the existence of cooperation in nature and the evolution of *altruism*.

On first glance, because natural selection is a competitive process, the evolution of cooperation (broadly, altruism) would seem unlikely. However, cooperation and altruism have been key components in major evolutionary transitions such as those that carried life from the simple cells to eukaryotic cells, from cells to multicellular organisms, and from individual organisms to coordinated complex societies such as those of the social insects and human civilization (Maynard Smith and Szathmáry, 1995). Nowak (2006) summarizes five mechanisms under which the evolution of cooperation is possible; the four most salient are kin selection, reciprocal altruism, indirect reciprocity and group selection. I will briefly review each here.

Hamilton (1963) first suggested that altruism between individuals could be explained if the unit of selection was not the individual, but the gene. The conditions under which altruistic acts will be favored by natural selection are known as Hamilton's rule. In effect, this rule states that altruism or self-sacrifice can be evolutionarily advantageous when directed toward relatives, and is formalized as

$$rb>c, \tag{6}$$

where, b is the benefit to the recipient of the altruistic act, c is the cost to the donor, and r, is a statistical measure of the relatedness between such individuals. Given this relationship, evolution can select for altruistic individuals provided they direct their altruism toward relatives. Hamilton's logic, also known as the law of inclusive fitness, became the measuring stick for the development of altruism by *kin selection*, and explains the ultra-social behavior of the colonial insects such as bees, wasps and ants, and in a less dramatic way, the behavioral patterns of mammals and primates (Queller and Strassmann, 1998; Griffin and West, 2002; Silk, 2002).

With an eye to explaining human altruism, Trivers (1971) argued that natural selection could produce altruism even between unrelated individuals, assuming that they recognize each other, remember past interactions, and selectively direct altruistic acts toward those who've helped them in the past. This concept, first formally described by Axelrod and Hamilton (1981), is known in the biological literature as reciprocal altruism, or simply *reciprocity*. Bootstrapping off the cognitive capacities of the individual, reciprocal altruism forms groups of discriminating individuals who only help those who are altruistic in return.

Taking the theory of altruism another step closer to human behavior, Alexander (1987) argued and Nowak and Sigmund (1998) demonstrated that pairs of individuals need not even interact more than once, but that a system of altruistic behavior could be maintained in which individuals would act generously to members of a group from which they could expect to receive altruistic donation. Such indirect reciprocity can maintain cooperation if individuals have reputations which determine how others treat them. Evidence also shows that humans form large cooperative groups with ease. Groupings of altruists are possible due to multiple mechanisms, including altruistic punishment (Fehr and Fischbacher, 2002), cultural conformity, and ethnic marking (Boyd and Richerson, 1987; McElreath et al., 2003).

Finally, and perhaps of most importance in understanding human sociality, is *group selection*.[3] The biological term denotes the competition between and selection of groups of unrelated individuals, and is typically referenced in explaining the behavioral characteristics that evolve under such conditions. Since Wilson's (1975a,b) first complete model of the process, group selection has been implicated in human genetic and cultural evolution. Richerson and Boyd, (2001) argue that humans display the cognitive legacy of group selection in our "tribal social instincts" and further that group selection on culturally inherited behaviors played a crucial role in human evolution. Some economists have begun to realize the importance of such a mechanism on human behavior (Bergstrom, 2002). For a more complete introduction to group selection, see Sober and Wilson (1999). Although there seems to be little evidence of group selection in genetic systems, a culturally mediated form of group selection seems to have been active in human history (Boyd and Richerson 1985; Wilson, 2002; Richerson, 2005; Wilson and Wilson, 2007).

There is of course much more to be gained from the theoretical riches of evolutionary biology, and the vast literature on cooperation and altruism than I can afford to summarize here. Nonetheless, it is clear that from a social science perspective the issue of how genetic evolution has crafted the human behavior in general, and the capacity for altruism and cooperation in particular, should be of keen interest. Camerer (2003) and Manner and Gowdy (2008-this issue) argue that incorporating true altruism, as opposed to reconstructions of altruistic behavior based on rational choice theory, critically changes economic models.[4]

3.2. *The productive boundary: economics & psychology*

The Nobel Prize winning work of Khaneman and Tversky, which focused on replacing the rational choice model of human behavior with an empirically grounded psychologically realistic model (Kahneman, 2003), has become the foundation for both behavioral economics and economic psychology today. Their work comprises three major components: behavior under uncertainty, behavior in regards to risk, and the effects of contextual framing on behavior. All three aspects demonstrate that humans do not behave as pure rational actors, but nonetheless display clear behavioral patterns. Their work on contextual framing uncovered that different social and contextual cues can alter individual behavior regardless of the underlying economic environment. Their discovery that humans naturally value losses more than gains of equal magnitude is the basis for prospect theory (Kahneman and Tversky, 1979). Likewise, we do not conduct rational optimization when we must make decisions under uncertainty. Behavioral economics has now blossomed into a mainstream wing of economics (Camerer et al., 2004), one of the most important advances of which has been the demonstration that humans display genuine care for the welfare of others, or "social preferences" (Fehr and Fischbacher, 2002). This fact alone warrants a deeper exploration of the field.

Knetsch (2003) suggests that EE has much to benefit from the theoretical advances of behavioral economics, which addresses some of the shortcomings of the neoclassical

[3] The existence of group selection has been controversial for many years, but a recent shift of opinion signals a general understanding of the importance of the mechanism among evolutionary biologists (e.g. see Wilson and Wilson, 2007). The issue of group selection is just a part of the larger set of concepts called multilevel selection (Brandon, 1982).

[4] For a friendly, hands-on introduction to much of the mathematics and evolutionary game theory models invoked in discussions of altruism see McElreath and Boyd, (2007).

tradition. At least some of the lessons of behavioral economics have been taken up in EE. Recent environmental cost-benefit analysis texts such as Hanley and Spash (1993) have incorporated the important insight of prospect theory, which demonstrates that humans actually value losses more highly than equal sized gains. Traditional neoclassical rationality assumes that losses and gains are valued equally, however gains are better measured as the maximum amount someone is willing to pay (WTP) to obtain them, and losses as the minimum amount someone is willing to accept (WTA) to endure them. This evolved cognitive asymmetry is important to environmental valuation, where ecosystem services such as water purification and atmospheric regulation will be undervalued if measured as WTP, while WTA values may be astronomic (Knetsch, 2003).

Economic psychology, also situated in the productive greyzone between economics and psychology, offers a source of useful methods and theory. Economic psychology and EE have theoretical commonalities. Both hold that economic rationality is theoretically implausible and empirically false, and both argue that humans display a complex version of utility including multiple utilities and transitive preferences (Lea, 2003). Moreover, the concept of interpersonal utility in economic psychology is closely related to the ecological economic idea of intergenerational utility and equity. Such open-ended utility models in economic psychology have helped to explain trends like green buying, donations and the distrust of labeling (Lea, 2003).

Economic psychologists, influenced by Simon's (1955, 1957) suggestions that humans display a 'bounded' rationality, argue that humans evolved parsimonious minds that can make intelligent decisions based on the limited data available in real ecological settings. Using an evolutionary lens, they propose a model of the mind based on cognitive heuristics–behavioral strategies "that evolved in tandem with fundamental psychological mechanisms" (Goldstein and Gigerenzer, 2002). They reason that humans learn or inherit simple heuristic procedures for different sorts of tasks. While rational choice models often fail under limited information, heuristics excel. For example, one of the simplest of decision-making heuristics, the 'recognition heuristic' is used in cases where the individual needs to choose a subset of objects from a larger set based on some criterion. Simply choosing the recognizable objects is often very successful, and almost more importantly, the recognition heuristic performs well with very little data, a condition that more accurately describes most human choice environments (Gigerenzer et al., 1999; Goldstein and Gigerenzer, 2002). Economic cognitive psychologists have uncovered a whole suite of heuristics that people use in solving real-world problems. Together these evolved heuristics are referred to as ecological rationality (Bullock and Todd, 1999), a perspective that sheds light on the deepest problem with rational-choice theory – "failing to appreciate the role of environment structure in shaping cognition can lead to mischaracterising adaptive behavior as irrational" (Bullock and Todd, 1999). Ecological rationality provides an empirically grounded model of human economic behavior very well suited to use in ecological economics.

Economic psychology has adopted the perspective that evolution crafted human cognitive skills, but the disciplines most devoted to an evolutionary understanding of human behavior are those that sprang from human sociobiology.

3.3. *The new sociobiology: evolutionary psychology & human behavioral ecology*

In 1975, E.O. Wilson labeled altruism the central theoretical problem of sociobiology (Wilson, 1975b), and it is still considered among the top issues in science today (Pennisi, 2005). The problem of explaining altruism continues to generate research and engage the evolutionary social sciences. The most fruitful area of evolutionary insight into human behavior comes from four disciplines that sprouted from the sociobiology debates of the 1970's (Wilson, 1975a,b; Sahlins, 1976; Gould and Lewontin, 1979; Lumsden and Wilson 1981; Laland and Brown, 2002). The first two of these fields that I examine are human behavioral ecology and evolutionary psychology.

Human behavioral ecology (HBE) is a quantitative anthropological field that focuses on behavioral responses to varying ecological conditions. HBE began in the 1970's by applying optimal foraging models to hunter-gatherer societies. Focusing on adaptive strategies, the field treats humans in the same way behavioral ecology treats other organisms–namely that they are expected to exhibit behaviors adapted to the circumstances in which they evolved. HBE typically examines hunting, foraging, resource use, and reproductive strategies. HBE has since expanded to consider the demographic transition, domestication and agricultural intensification (Winterhalder and Smith, 2000). Also of salience for EE is the HBE research on prospects for conservation behavior in light of human adaptations for resource acquisition (Hames, 1987).

One major purpose of the HBE literature has been to explain the uniquely human traits such as human food sharing to non-kin. This pervasive feature of human societies remains contentious with scholars seeking explanations from kin selection, reciprocal altruism, and costly signaling among other theories (Gurven, 2005). The ongoing debate is useful because it makes abundantly clear the central issue of cooperation and altruism in human interactions. Another useful discussion in HBE is over the nature of the extended non-reproductive lifespan experienced by women post-menopause. The simplest version of the theory is that the reproductive success of the menopausal woman is enhanced by menopause because it removes chances of self-endangerment through dangerous late pregnancy and birth, and provides time and energy that is often devoted to caring for her own descendants, and ensuring their reproductive success (Williams, 1957; Hawkes, 2003). Taken together these experiences from HBE suggest that humans are deeply socially adapted organisms who forgo personal reproductive and energetic advantage for related and unrelated individuals. This is yet another confirmation of the importance of evolved social preferences in human behavior.

HBE is closely related to evolutionary psychology, which can provide at least two unique insights of relevance to ecological economics (Jackson, 2002). First, if evolutionary psychologists are right, then humans are evolved not just to consume to satisfy personal requirements, but also in order to signal personal quality in the race to compete for mates. Further, we may have evolved in resource-poor conditions a tendency to hoard that, when enacted in a resource-rich environment, may have great individual (health) and social (equity) cost. Secondly, evolved dispositions such as expensive displays for social and reproductive gain, or costly signaling, also offer a way to understand the "mismatch" between economic productivity and actual human physical and mental wellbeing. Jackson remains wary, though, about other aspects evolutionary psychology theory for EE, as well he might.

Evolutionary psychology and HBE have been criticized for a heavy-handed sociobiological approach to human behavior (Laland and Brown, 2002). Scholars in HBE typically rely on an assumption called the "phenotypic gambit" which states that extreme phenotypic plasticity in humans explains observed behavioral variation. This assumption allows HBE practitioners to avoid stating whether observed behavior is either genetically or culturally realized. The drawback of this approach is that some HBE practitioners and evolutionary psychologists often end up assuming that the observed behavior is adaptive and transmitted genetically, rather than culturally (Laland and Brown, 2002). In this way, the assumption of behavioral adaptiveness has become as dangerous in evolutionary psychology as the assumption of rational optimization is within neoclassical economics. Both assumptions are crippling, and as we will see, unrealistic when one considers the full import of cultural processes. Understanding sub-optimality and maladaptation is a challenge to all social sciences. It is to culture that we will turn in the final section.

3.4. *The grail of culture: gene-culture coevolution & memetics*

Culture is, naturally, the greatest distinguishing characteristic of humans, the significant social capacities and phenotypic plasticity of other organisms notwithstanding (Bonner, 1980). In the 1970's, the Pandora's box of cultural evolutionary complexity was finally opened (Cavalli-Sforza and Feldman, 1973; Dawkins, 1976). Shortly thereafter scholars took to exploring the interactions between cultural and biological evolution (Cavalli-Sforza and Feldman, 1981; Lumsden and Wilson 1981) and the evolutionary dynamics of culture in its own right (Boyd and Richerson, 1985). Dawkins' meme concept blossomed in the popular imagination. As the major focus of *The Selfish Gene* was to argue that genes, as replicators, are the level of selection worth understanding, Dawkins argued that memes, as the cultural replicators, were by extension the key to understanding culture. Since that time a small group of researchers has held out hope for the arrival of a science of memetics (Blackmore, 1999; Aunger, 2000) and the mathematical, theory-rich Journal of Memetics was created (JOM-EMIT, 2007).

Memetics,[5] taking its cue from Dawkins' biological imagery, stressed the virus-like nature of human behaviors that spread through populations via imitation, often at the expense of the human carrier. Because memes are seen as independent of human genes, imitated behaviors can be fitness negative, yet still spread. Memetic studies often focused on maladaptive behaviors, such as the evolution of suicide (Marsden, 2001) that would not be explicable in adaptationist traditions such as HBE or evolutionary psychology. As a culturally transmitted behavior that spreads via imitation rather than biological reproduction, a suicide meme can survive in a population despite the fact that its practitioners remove themselves from it. This 'viral culture' view afforded memetics a rare power of explication. The rising popularity of 'viral' advertising, in which advertisers use tactics to encourage consumers to voluntarily spread product information through their personal social networks, suggests that such a simple theory is nonetheless powerful, and of clear import to EE.

Two decades before memetics had started, however, biologists and anthropologists had been examining cultural evolutionary dynamics and the interactions between cultural and biological evolution. Some of the first attempts to join the dynamics of both biology and culture were problematic. Lumsden and Wilson (1981) argued that all of human culture was ultimately constrained by genetic evolution. A more balanced view came from Cavalli-Sforza and Feldman (1981), who suggested that both genes and culture share the ultimate causation of human behavior. Genes can determine human traits, which can influence human perception, behavior and culture. In turn, culturally controlled behaviors can change the selection environment in which humans survive, and therefore alter genetic selection. Models and studies of gene-culture coevolution have covered numerous topics such as the coevolution of sign language with deafness, lactose-tolerance with dairy farming, incest taboos with brother-sister mating, sickle-cell anemia with forest clearing practices, and the evolution of handedness (Feldman and Aoki, 1992; Kumm et al., 1994; Laland et al., 1995; Aoki and Feldman, 1997). Gene-culture coevolution (also dual-inheritance) theory demonstrates the deep complexity of the interaction between genetic and cultural evolution – a complexity that both memetics and sociobiology tend to ignore. Most gene-culture research focuses on the interaction of culture with human genes, leaving a huge amount of work yet to be done on the linkages between human culture and genetic evolution in other organisms (e.g. Law and Salick, 2005; Norgaard, 1984a).

As gene-culture coevolutionary scholars have shown, understanding human behavior in full depth requires that one take endogenous cultural dynamics seriously. Contra Lumsden and Wilson (1981), culture requires its own system of evolutionary explanation distinct from its genetic cousin. Thankfully, a significant body of cultural evolutionary theory provides an ample system for analyzing culture's unique evolutionary processes.

Scholars of cultural evolution argue that in addition to our ability to learn individually through logic, prediction, trial and error as many animals do, humans also learn from each other through imitation. Boyd and Richerson (1985) suggest that imitative *social learning* is the fundamental mechanism of cultural transmission and heredity, permitting individuals to skip the costs of trial and error, and inherit fully-formed tactics and behaviors which have been accumulated over generations (Boyd and Richerson, 1985). Imitative social learning supplies humanity with a *genetically independent* and

[5] For a useful overview of Memetics, and the other sociobiologically inspired evolutionary social sciences (evolutionary psychology, gene-culture coevolution, human behavioral ecology) see Laland and Brown (2002).

expanding cultural inheritance that includes our technological skills, artistic traditions and social organization. Culture therefore constitutes a second, independent system of evolved inheritance which, in conjunction with our biological inheritance, co-controls human behavior.

As an evolutionary system, culture is wildly different from biological evolution on many fronts. While genetic information is passed 'vertically' down from parents to offspring over generations, culture is not so constrained, and is transmitted 'horizontally' between peers, 'obliquely' between different generations, within complex social networks and even 'upwards' from child to parent. Because cultural items are passed through networks rather than down lines reconstructing cultural phylogenies is not always possible (Borgerhoff Mulder, 2001; Borgerhoff Mulder et al., 2006). Cultural transmission also is much faster than genetic transmission. Cultural items such as words, songs, and ideas can be transmitted rapidly between individuals. Thus the rate of cultural evolution is vastly faster than that of biological evolution. While genetic systems replicate, creating nearly perfect copies, most cultural items (such as actions, concepts, beliefs or values) are not purely discrete and do not strictly 'replicate' as often implied in memetics,[6] Further, while genetic systems only acquire new features during reproduction and mutation, many have observed that cultural change is Lamarckian, meaning that individuals can at any point acquire behavioral characteristics that can be transmitted to others. Unlike genetic evolution, in which the recipients of evolved traits are passive (offspring) in cultural evolution the recipients of evolved traits actively and continuously determine what information to accept and what to reject. Thus, in cultural evolution selection and inheritance are merged into a single process via social learning. Due to such fundamental differences, the mechanisms of cultural evolution are largely not possible in the genetic realm.

Cultural transmission mechanisms are evolutionary in two senses because they support the evolution of cultural traits within societies and are themselves evolved social learning adaptations. Humans have evolved to enhance the effectiveness of social learning by selectively choosing whom to imitate. People frequently use specialized social learning strategies such as imitating the prestigious or successful, imitating others based on traits such as age or sex, and choosing who to imitate based on the content of the behavior itself (Boyd and Richerson, 1985). Another unique mechanism of cultural evolution that has no biological analog is that of conformity. Conformity occurs when each individual follows a "majority rule" imitation strategy, adopting the given behavior only if a majority of others practice it, and eschewing it otherwise.

Like genetic mutation, culture also experiences new changes, but unlike genetics, cultural novelties are often the result of intentional human design. Boyd and Richerson (1985) call the Lamarckian pattern of intentional cultural change *guided variation*. Individuals tend not to mimic observed behavior blindly, but to constantly improve on imitated strategies, guiding the variation of behaviors in the population. Furthermore, social learning mechanisms combine to create powerful behavioral optimization within cultures. For instance, prestige-biased social learning together with guided variation can speed the approach of human populations to ecological adaptive optima (Henrich and Gil-White, 2001).

A final evolutionary process unique to culture is that of the dynamics of *ethnic markers* (Boyd and Richerson, 1987). Ethnic markers are symbolic traits, such as dress, or speech that, unlike substantive behavior, do not directly impact ecological outcomes. Because humans tend to copy behavior in packages from those they imitate (Henrich and Gil-White, 2001), conformist imitation will cause these markers to become associated with the substantive behavior, even if they have no functional relationship. This process leads to ethnic differentiation, in which individuals adopt not just the substantive norms of their group, but also the superfluous styles and symbols that distinguish them (McElreath et al., 2003). Naturally, ethnic marking psychology is of utility for ecological economics and beyond. Nonetheless, if humans automatically exploit symbolic differences in choosing those to interact with and trust, then great care must be given to creating commonality in cases where groups that might naturally differentiate and compete for resources would do better to share and conserve, forgoing selfish over-exploitation to achieve sustainability.

4. A synthetic evolutionary theory of human behavior

As we've seen, many of the components of a synthetic evolutionary theory of human behavior already exist distributed across the evolutionary social sciences, all that is left for us is to pull the insights relevant to EE together into a useable whole. Because evolutionary theory is more complex and less determinate than neoclassical economic models, it will also be less prescriptive yet more demanding (see van den Bergh and Gowdy, 2000). Such a synthetic theory consists of four major themes: (1) Humans are idiosyncratic products of a unique evolutionary history, not idealized selfish problem solving machines; (2) Humans are fundamentally social and cultural beings, and as such their behavior runs the gamut from adaptive to maladaptive for both individuals and society; (3) As cultural organisms, humans support the great second layer of evolution, within which behaviors, beliefs and institutions themselves evolve; (4) Behaviors, beliefs and institutions further coevolve with each other, human genes, other species, and the physical environment.

4.1. *Humans evolved*

Humans have inherited the cumulative result of billions of years of evolutionary history. We are not perfectly suited to our environment, or even to any given historical environment, but rather we are sufficiently suited to have survived. Evolution entails not just selection and positive adaptation, but also adaptive losses, environmental limits to adaptation, and genetic constraints such as drift, population bottlenecks, and pleiotropisms. Furthermore, evolution involves design constraints, spandrels (Gould, 1997) exaptive short cuts, and vestigial characteristics. Humanity is therefore an effective but limited collection of biological and cognitive features. We

[6] Henrich and Boyd (2002) proved that replication is not necessary for the accumulation of adaptive variation, and culture often evolves without it.

do not conduct full backward induction, we do not optimize individual utility, we are habit bound, risk-averse, and we fail the tests of behavioral optimality in nearly every way. Although imperfect, we do make efficient use of information embedded in the environment to solve immediate ecological challenges. However, since the world that we inhabit is not the world to which our decision-making capacities were adapted, our behavior causes significant ecological and social inefficiencies due to adaptive mismatch.

Still, humans are nonetheless the idiosyncratic result of a process of evolutionary optimization. We are indeed self-maximizers, but in an evolutionary rather than an economic sense, and like all organisms, we are geared for survival, growth and reproduction. Yet our abilities for growth vastly outstrip those of all other species, as is demonstrated by our domination of the biosphere, and its ongoing ecological ramifications. Given our evolved animal nature, limited cognition and capacity for ecological exploitation, Dawkins is correct that "sustainability doesn't come naturally" (Dawkins, 2001), and it might seem that human ecological expansion will only be checked by external forces.

Research is needed, then, to bolster our understanding of human cognitive and psychological adaptations, and the ways in which they interact with the built, natural, social environments. However we should be careful not to assume that humans are optimal, or perfectly adapted to any environment present or past. Instead, researchers must seek to understand the detailed nature of human maladaptation, because an appreciation of our adaptive legacy will allow us to create more effective institutions.

Although human ecological growth may be partially self-destructive, evolution has crafted human nature to include an antidote to its own ecological poison. Specifically, humans are uniquely cooperative and social creatures, and our social adaptations, related as they are with our individual maladaptations, deserve special attention.

4.2. Humans are social

Humans are uniquely altruistic among all animals. Altruistic acts such as self-restraint and sacrifice are by definition individually maladaptive. But, while humans are systematically maladaptive on the individual level, our extreme success in groups rides on our cooperative and altruistic nature. These group-beneficial but individually detrimental adaptations suggest that human sociality arose through the process of cultural group selection, and that altruism on the scale of human society cannot occur without the unique, non-genetic form of adaptive inheritance called culture (Henrich, 2004). As inherently social creatures, humans have evolved a sort of social rationality with which we formulate decisions, and we display inherent social motivations, or "social preferences." We are imitative, conformist, and we signal our social identities by adopting symbolic ethnic markers.

Thus, human ecological domination is likely due to the adaptive advantage provided by our cumulative cultural inheritance. Our cooperative abilities open up behavioral equilibria and ecological possibilities that are not possible in species that evolve only by genetic means. Our evolved capacity for cooperation undergirds society and allows for the existence of arbitrary institutions, behavioral systems and traditions, such as voluntary self-regulation, schools, wealth redistribution and market exchange.

Current understanding of human social adaptations is limited, however, and more research is needed, especially on the ways in which our social adaptations build, maintain, and erode institutions. Ecological economists already recognize that human sociality also allows for the possibility of resource conservation, inter-generational equity, and sustainable social systems.

Our altruistic, cultural heritage is not simply beneficial to the goals of ecological economics. Because humans evolved through some process of group selection, individual psychology demands that we trust those of our group, and fear those of others. "Group selection favours within group niceness and between group nastiness" (Sober and Wilson, 1999). This pervasive tendency generates conflict over resources, political tension and ethnic warfare. Ethnic psychology is therefore a hindrance to achieving global sustainability.

4.3. Culture evolves

Evolution is the only process known to produce complex novelty. As the complexity and diversity of human culture are second only to those of the biological world, they can likewise only be explained by a process of evolution. Human culture, as a category that subsumes beliefs, behaviors and institutions, constitutes an independent realm of evolution somewhat linked to human genetics. Culture is not ultimately controlled by selection on genes, but instead genes and culture share the ultimate causation of human behavior. Through imitation, humans are susceptible to adopting behaviors of undetermined, and perhaps even negative value. However, as we have seen, it is our cumulative cultural adaptations that have produced such unprecedented ecological dominance. Culture allows human societies to explore behavioral systems beyond those predicted by genetic evolution or rational choice theory alone.

Human behavior must be understood in terms of uniquely cultural evolution. Although the human cultural capacity evolved genetically, culture itself evolves in a wildly different fashion. Cultural evolution is faster, more flexible, and more Lamarckian than biological evolution. Cultural traits are recombined more frequently, as they flow through dense social networks instead of down the lonely branches of biological inheritance. Where genes mutate, culture innovates. Features of the social environment, such as deference and prestige, cue human imitation. New evidence suggests that our imitation mechanisms may also be cued directly by the environment itself (McElreath et al., 2005), a fact that leads to intriguing possibilities for the study of socio-ecological coevolution. Cultural evolutionary theory offers a lexicon of unique and exotic processes not found in biological evolution, including guided variation, biased social learning, conformity and ethnic marking, unheard of by most skeptics of evolutionary approaches to social science.

The realization that human culture is evolving fundamentally changes the way the economy should be understood; it is no longer the static equilibrial result of predictable individual motivations, but a never-ending process of co-adaptation between companies, governments, traditions, individuals, technologies and the environment. Preferences, evolving over time as individuals experience different social pressures, may be more responsive to forces such as anti-conformity and prestige-biased imitation than rational choice. Humans act as if embedded in social groups even when they are not, generating brand loyalties cued on pseudo-ethnic symbolic markings. Without the restrictive neoclassical assumptions of rational choice there is no optimal policy set (van den Bergh and Gowdy, 2000), but instead every policy change must be viewed as a change in the adaptive landscape to which institutions and individuals will react to preserve their social utility.

Thus cultural evolution is not just helpful, but a necessary pre-requisite for a coevolutionary science of sustainability, as it alone supplies the necessary details of the Darwinian system (variation, selection and heredity) required by the enterprise that Norgaard (1984a) articulated and Kallis (2007) refined.

4.4. *Culture co-evolves*

The realization that culture evolves opens up the potential to discover coevolutionary processes everywhere. Culture coevolves with itself, with our genes and those of other species, and evolves in response to feedback in the natural environment. Cultural traits are themselves co-adapted to survive in groups (Blackmore, 1999); institutions have evolved rules that select between different individual behaviors (Bowles, 2006); and institutions interact, compete, cooperate and imitate each other, in institutional coevolution. Ethnic identities also evolve in response to institutions, technology, individual behaviors and each other. On the grandest of scales, one might argue that societies coevolve with their biological support systems (Diamond, 2005; Gowdy, 2006) as well. To specify a coevolutionary model then, one must ultimately incorporate to the cultural evolutionary processes that underlie the evolution of the larger social phenomena of interest, or be content with imprecise vernacular arguments. As Kallis (2007) argues, coevolution should remain attached to a strict definition of evolving systems,[7] and the only theory ready for such a task is cultural evolution.

In coevolutionary terms, ecological economics is the discipline devoted to finding, studying and generating socio-ecological coadaptation. So, since we must take the human adaptations that undergird cultural evolution as our theoretical foundation, what sort of coevolutionary processes would EE seek to study, develop and encourage? Because evolution is an inherently exploratory and innovative process, the old metrics for "sustainability" based on energy and material flows will not entirely apply. Evolutionary sustainability has not been defined. Indeed, there may be no such thing.

[7] Kallis (2007) also makes the case that co-dynamic change, such as the interaction between evolving social policy and non-evolving energy resources, is equally useful for studying sustainability.

5. Conclusions and beginnings

Primarily, the theoretical and mathematical edifice of neoclassical economics needs to be rebuilt from the bottom up, focusing on the evolved cognitive features underlying the human cultural adaptations that make social institutions possible. To some extent recent microeconomic syntheses have begun this important work (Bowles, 2006; Potts, 2001), but much work is still needed. Even basic economic concepts such as demand and utility have not yet been defined within a fully evolutionary framework. In classical economics of all sorts, individual utility was treated as exogenous. In a cultural evolutionary theory of economic systems, however, utility and behavior will be largely endogenous and the result of the interaction of available behavioral variation, learning and imitation mechanisms, and selective pressures. Demand does not therefore meet supply to set the price, but social demand coevolves with price and supply in an arena where humans define their own utility in reference to the status of others. Furthermore, imitative social learning helps to solve the economic problem of the origin of preferences. While some preferences (food, shelter, mates) may be genetically inherited, many or most modern preferences are culturally determined. These socially acquired preferences therefore evolve, and can only be accounted for with evolutionary models. Refiguring of this type is required for all aspects of economic theory. In this last section I attempt to chart some new waters in which our synthetic evolutionary theory might sail.

5.1. *New discount rates*

The evolutionary idea of inclusive fitness states that individuals value benefits conferred on their relatives in proportion to their relatedness, even at personal cost. This concept can be expressed in economic terms as a type of genetic discounting factor, which should take its rightful place, alongside the standard temporal and spatial discounting factors. Further, because the weight of evidence suggests that humans also value social and cultural similarity and benefits that accrue to those who are culturally similar or those of the same social group, I likewise propose a cultural discounting factor. Although these factors represent obvious everyday human motivations, neoclassical economics makes no mention of such systematic patterns.

5.2. *The forces beneath market forces*

Upon examination competitive markets do not ride exclusively, or even primarily on competition. Although competition is undeniably important, the reason that market exchange systems only exist within our species is that only humans cooperate with unrelated individuals in large groups. Such indirect reciprocity is a fundamentally altruistic behavior, yet nonetheless forms the basis for market exchange that some economists would suggest is based on exogenous preferences and rational optimization. However, pure, individual-level, rational optimization, akin to the individual-level genetic evolutionary optimization that governs most animal evolution, cannot possibly allow for the existence of trust, reciprocity or cooperation between unrelated individuals. Thus market forces and competition, the primary drivers in economic models, are based on cooperative exchanges and interactions that would not be possible in a population of purely self-interested individuals. Future models that rebuild market forces from more fundamental human social tendencies should, therefore, be more predictive.

5.3. *The missing feedback*

In traditional economic theory of all kinds, macro-level features such as demand and prices are set by the action of micro-economic individual motivations, and individual motivations are largely taken to be exogenous. Thus the critical feedback from population-level forces to individual behavior is missing. In evolutionary theory, population-level trends are also determined from the mass-action of individuals, but the behaviors of the individual are determined in part by the forces and factors acting at the population level. Adding this social feedback completes the causal loop of the dynamic system, adding needed realism and enabling recursive mathematical models of behavioral evolution. Model such as this allow scholars to examine evolving economic systems and equilibria through time. In this endeavor evolutionary game theory provides a useful set of tools (Gintis, 2000), as does most of the mathematical structure of formal models in evolutionary biology.

5.4. *Policy*

van den Bergh and Gowdy (2000) suggest that a more realistic model of the individual would lead naturally to some interesting new policy options. For instance, van den Bergh argues that governments must swallow the difficult fact that because their actions already influence and select individual behaviors and preferences, doing so intentionally, carefully, and to good ends is more desirable than assuming that preferences and behaviors are exogenous to government influences. Advertising agencies make millions by avoiding such a mistake. Furthermore, updating the economic model of the individual would naturally lead to the use of

> "instruments that operate directly and have a more certain impact (effectiveness), i.e. a preference for standards such as technical requirements and quantity regulation. (van den Bergh and Gowdy, 2000)."

5.5. *Capitalism*

It may be tempting to believe that genetic group selection will eventually select for human cognitive features that enable long-term sustainability. While there is some logic to this proposition, the loss entailed in the genetic group selection process entailed would fill the world with Easter islands many times over. Ecological economists should be on the look out to find other, faster, more efficient ways to avoid the long, painful group-selected road to sustainability. Interestingly, capitalism offers a potential solution. Capitalism, especially the formation, operation and eventual dissolution of firms in competition, can be viewed as a form of non-destructive cultural group selection. Viewed in this way, capitalism is a cultural innovation that exploits our tribal social instincts and enables competitive social evolution without loss of life. If such a system can be appropriately deployed around the issue of ecological efficiency, society might progress towards a sustainable economy more quickly.

From its inception ecological economics has criticized the traditional economic model, but has yet to adopt a sufficient alternative theory. Similarly, coevolutionary analyses lack sufficient technical detail to be truly evolutionary. Summarizing results and theory from a range of evolutionary disciplines, I present the outline of a synthetic evolutionary theory of human behavior, and argue that cultural-evolutionary theory is a necessary precondition to any science of human behavior, coevolutionary or otherwise. Given the possibility of this synthesis, the time is ripe for an evolutionary theoretical foundation in ecological economics.

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Appendix A

Social preferences and environmental policy

A government can be modeled as attempting to maximize the public benefit of its policies across multiple realms of management. In this sense the ideal government invests in different policy instruments according to the quality and efficiency of the instrument.

Every individual behavior will accrue both private benefits, B_o, and public benefits, B_p. If the individual is strictly self-interested, as rational-choice theory assumes, the private individual utility, U_n, can be calculated as:

$$U_n = B_o - C + I \tag{1}$$

where I is the incentive offered by the government to enhance the frequency of this behavior and C is the private cost of the behavior. On the other hand, if the individual has social preferences her utility would be:

$$U_s = B_o + B_p - C + I \tag{2}$$

Because the government is interested in achieving maximum total social benefit, the amount the government chooses to invest in the subsidy is governed by the efficiency of the policy, E, which is determined by the number of adopters, N, the price per adopter, $P=I$, and the social benefit per adopter B_p, where

$$E = N\,B_p/P \tag{3}$$

The greater E, the more social benefits will be realized per incentive dollar spent. If we assume that N is proportional to

U, by some constant, h, then the efficiency of the subsidy instrument, in the case of social preferences is

$$E_s = h(B_o + B_p - C + I)B_p/P \quad (4)$$

and in the case of traditional (non-social) preferences, $E_n = h(B_o - C + I)\, B_p/P$. Thus, the impact of assuming the existence of social preferences on environmental policy is the difference between the E_s and E_n,

$$E_s - E_n = B_o^2/I \quad (5)$$

If the government assumes that individuals are traditional rational actors, then its incentive will under supply the potential user-base willing to adopt the behavior, and thus fail to deliver the maximum amount of public good. Since the above value is positive, the influence of social preferences on the efficiency of this fictive environmental policy is positive. That is, altruism enhances the efficacy of the subsidy, making it a better public investment than would be assumed under conventional analysis. The above model demonstrates that social preferences are critically important to environmental (or any other) policy.

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