Evolution as a General Theoretical Framework for Economics and Public Policy

Introductory Article for Special Issue of JEBO

David Sloan Wilson and John Gowdy

November 2, 2011 draft

Economic and evolutionary thinking have been entwined throughout their histories (Beinhocker 2006; Hodgson 1993, 2007; Hodgson and Thorbjorn 2010). Darwin, the founder of evolutionary theory, was inspired by Smith and Malthus, two founders of economic theory. Thorstein Veblen, one of the most influential economic thinkers of the late 19th century, wrote an article titled "Why is Economics Not an Evolutionary Science?" in 1898. Fast forwarding to the present, virtually all economists assume that their ideas are consistent with evolutionary theory, along with the laws of physics and chemistry. Various branches of economics explicitly draw upon evolutionary theory to varying degrees (Gowdy and Van den Bergh 2003; Hodgson 2007), and one even calls itself "evolutionary economics" (Nelson and Winter 1982; Witt 2003, 2008a,b)

Yet, evolutionary theory does not play the same role in economics that it does in the biological sciences, where it provides a single framework for studying all aspects of life. The generality of evolutionary theory did not emerge gradually but was apparent from the beginning, as the diverse interests of both Darwin and Alfred Russell Wallace attest. It was repeatedly affirmed during the course of the 20th century, enabling the geneticist Theodosius Dobzahansky to state in 1973 that "Nothing in biology makes sense except in the light of evolution". Today, there is exponential growth in biological knowledge, but all of it continues to be organized by a single theoretical framework that can be easily learned and applied to any particular subject.

Knowledge about humans did not become organized in the same way as biological knowledge during the course of the 20th century—but the reasons are primarily historical rather than conceptual. Every branch of human-related knowledge had its own encounter with Darwin's theory (Hodgson and Thorbjorn 2010; Richards 1987). Many of the early formulations proved to be incorrect—even grossly incorrect in retrospect—such as the view that cultural evolution is a linear progression from "savages" to "civilization" (Carniero 2003). Many of the policies informed by evolution also turned out to be ill-considered in retrospect, to put it mildly (Hofstadter 1959/1992; Leonard 2009). As a result, evolution became stigmatized in many human-related disciplines. A common formulation was that evolution could explain the rest of life, our physical bodies, and a few basic urges such as to eat and have sex, but had little to say about our rich behavioral and cultural diversity. Even when evolution was not marginalized, the particular way that it became incorporated varied among disciplines. The history of evolutionary thinking in relation to economics is just a chapter of this larger history.

During the last few decades, there has been a resurgence of interest in using evolution as a general theoretical framework for the study of our species, similar to the way that it functions in the biological sciences. One reason that the current effort is likely to succeed, despite the failures of the past, is due to advances in the study of biocultural coevolution (e.g., Jablonka and Lamb 2006; Richerson and Boyd 2005, Wilson 2011; Wilson et al. 2011). The human capacity for open-ended behavioral and cultural change can no longer be regarded as outside the orbit of evolutionary theory. Instead, it is a sophisticated set of adaptations that evolved by genetic evolution and often constitutes an evolutionary process its own right. Furthermore, human genetic and cultural evolution have been influencing each other throughout our history of a species. Our genes are a product of our cultures, no less than our cultures as a product of our genes. A sophisticated knowledge of biocultural coevolution is required to make sense of our current cultural institutions and to manage cultural change to achieve positive outcomes (Wilson et al. 2011).

This article, which is part of a special issue of the *Journal of Economic Behavior and Organization*, has two objectives: The first is to concisely describe how evolutionary theory functions as a general theoretical framework in the biological sciences, as a model for how it might function for economics and public policy formulation. The second is to consider reasons why evolution might *not* prove useful for the study of human behavior and culture, even if they are products of biocultural coevolution. Based on conversations with literally hundreds of colleagues, we know that many are as open-minded about evolution as they are about physics and chemistry. What they want to know is how evolution can add value to the study of their particular discipline, such as neoclassical, behavioral, or institutional economics. Based on these conversations, we have identified four plausible reasons why evolution might *not* add value:

1) Human-related subjects have been studied by very smart people for a very long time. If science and scholarship result in the accumulation of knowledge, then people who start out employing different assumptions and perspectives will eventually reach the same conclusions. If so, then approaching a longstanding subject from an evolutionary perspective will merely affirm what has already been discovered. The evolutionary perspective won't be wrong, but it will usually reinvent the wheel.

2) The concept of design long predates the concept of evolution. The fact that an object or process is well designed for a purpose can be established without knowing about the designing process. An insect that mimics a leaf is well designed to avoid detection by predators. Who cares if it is a product of evolution or a supernatural agent? Similarly, if a corporation or market process functions efficiently, who cares if they are products of biocultural coevolution?

3) A reasonable research strategy is to study what is, without worrying much about how it got that way. After all, something like the brain is available to be studied in minute detail, whereas how it got that way is more speculative. Why speculate when you can study the real thing?

4) All branches of knowledge should ideally be consistent with each other, but every branch need not be consulted for the study of any particular branch. Evolutionists rarely feel the need to consult quantum physics, and perhaps evolution rarely needs to be consulted for the study of many traits, in humans and nonhumans alike.

These are good arguments, posed by smart and open-minded people, so they deserve respectful consideration. We will show that while each has a measure of legitimacy—even within the biological sciences—they all fail for the study of any sizeable human-related subject. As a result, evolution can indeed function as a general theoretical framework for economics and public policy, in the same way as for the biological sciences.

Another article in the special issue of *JEBO* (Gowdy, Hodgson, and Wilson 2011) reviews the degree to which evolutionary theory has already been incorporated into the major branches of economic theory. This is important to appreciate the progress that has already been made, but also to show that no major branch of economics has yet adopted all of the "tools" in the evolutionary "toolkit". The remaining articles in the special issue will show how the full toolkit can be used to examine a sample of topics that are centrally relevant to economics and public policy.

How Evolutionary Theory Functions as a General Theoretical Framework in the Biological Sciences: The Other Tinbergen and his Four Questions

Many economists know the name of Jan Tinbergen, who shared the first Nobel Prize in Economics with Ragnar Frisch in 1969 for his work on dynamic models of economic processes (Solow 2004). Many evolutionists know the name of Niko Tinbergen, Jan's younger brother, who shared the Nobel Prize in Medicine with Konrad Lorenz and Karl von Frisch in 1973 for his foundational work on ethology, the study of animal behavior.

A 1963 article by Niko Tinbergen titled "On the Aims and Methods of Ethology" has become a classic for summarizing how evolutionary theory provides a framework for studying all biological subjects. Tinbergen stressed that four questions need to be addressed for all products of evolution.

1) What is the **function** of the trait, or why does it otherwise exist compared to the many traits that could exist in the lineage? The process of natural selection winnows a small subset of traits that adapt organisms to their environments from a much larger set of traits. Evolutionists call this *ultimate causation*. It provides a powerful (but not infallible) way of inferring the properties of organisms, knowing only a little about the environmental context. For example, we can confidently predict that desert creatures are likely to be sandy colored to avoid being detected by their predators and prey. We can

make this prediction for all desert-dwelling creatures, without knowing anything about their genes or physical makeup.

Although this example is simple, adaptationist thinking is full of complexities and pitfalls (Sober 1984; Wilson 2007). Not all traits are adaptive; they can be a product of drift, a byproduct of other traits, or adaptive in the past but not the present. When they are adaptive, they might benefit genes, individuals, or groups. They might be a product of sexual rather than natural selection. Cultural traits can evolve to be parasitic, without benefiting human individuals or groups. What counts as adaptive in the evolutionary sense of the word can be perversely maladaptive in the everyday sense of the word. Species can even evolve themselves to extinction. Thus, although the answer to Tinbergen's first question *can* be self-evident in some cases, in other cases it will require a sophisticated understanding of evolutionary theory. Thinking in terms of ultimate causation is one of the most important tools in the evolutionary toolkit, which will be used frequently in the case studies featured in the *JEBO* special issue.

Many well-designed aspects of human behavior and culture are a product of individual learning and cultural evolution, rather than genetic evolution. The underlying mechanisms can include intentional planning, processes of imitation that take place largely beneath conscious awareness, operant conditioning little different from the way that pigeons and rats learn, and the raw process of natural selection, which can winnow alternative cultural traits in the same way that it winnows genes (Wilson 2002). Thinking in terms of ultimate causation is as important for studying this complex array of mechanisms as it is for species that are largely products of genetic evolution (Wilson et al., 2011).

2) What is the **phylogeny**, or evolutionary history of the trait? Answering this question provides information that was not required to answer the first question. As one example, consider the difference between a marsupial's pouch and a placental mammal's womb. They have the same function (to develop offspring), but they are very different from each other, based on the fact that marsupials and mammals evolved on different continents. Evolution is a historical process and seldom takes the same path twice. A trait will not be fully understood until its particular evolutionary trajectory is known.

As a second example, the cultural evolution of animal husbandry practices created a new resource for adult humans—milk—that never before existed in the mammalian lineage. This cultural innovation altered the course of genetic evolution, selecting for genotypes capable of digesting milk as adults, which has become one of the best documented examples of recent genetic evolution in humans (Holden and Mace 2009; Swallow 2003). The cultural evolution of animal husbandry practices occurred independently in at least two geographical locations, however, and detailed genetic studies reveal that different genes evolved to produce lactose tolerance in adults in each case. Knowing this has important policy implications, such as how to screen for lactose intolerance (Ingram et al. 2007).

The need to understand phylogeny is just as important for human cultural evolution as for genetic evolution. All current human social organizations, such as the European nations, are products of centuries of cultural evolution, resulting in specific mechanism of governance and different capacities for change. Some of the mechanisms were consciously designed, but others evolved in ways that are no more accessible to our conscious minds than the mechanisms of gene action. They must be studied scientifically to be understood and are highly consequential for modern policy issues such as nation building in various parts of the world (Turchin 2003, 2006).

3) What is the **mechanism** of the trait? Regardless its function or history, every trait has a physical basis that must be understood in mechanistic terms. Evolutionists call this *proximate causation*. As one example, the functional answer to why apple tree flowers bloom in spring is because that's the best time for the survival and reproduction of apple trees. Flowers that bloomed earlier were nipped by frost and those that bloomed later failed to develop their fruits. Global warming will probably result in the genetic evolution of apple trees that bloom earlier in spring than before. These are all questions that can be addressed on the basis of ultimate causation. The mechanistic answer to why apple tree flowers bloom in spring is completely different, such as a biochemical process that is sensitive to day length. The proximate explanation need not resemble the ultimate explanation in any why whatsoever. The only constraint is that the proximate mechanism must reliably cause the expression of the trait that is adaptive in functional terms.

The need to distinguish between proximate and ultimate causation, and to study both in conjunction with each other, is one of the most important insights of employing an evolutionary perspective. It is especially important to understand that a single trait in functional terms can be produced by many different proximate mechanisms, as we have already seen for the biological examples of placental mammals vs. marsupials and different mechanisms of lactose tolerance in humans. The particular mechanism that evolves in any particular case can be largely a matter of chance or historical contingency.

To appreciate the relevance of the proximate-ultimate distinction for economics and public policy, consider the work of Elinor Ostrom and her associates on human groups that attempt to manage common pool resources (CPR) such as irrigation systems, ground water, fisheries, and forests. Based on a worldwide empirical database and theories derived from political science, game theory, and increasingly evolutionary theory, Ostrom derived a number of design principles that are required for CPR groups to effectively manage their resources. She also showed that the design features were implemented in a diversity of ways that were largely a matter of chance or local contingency. In fact, it was important for each group to make the best use of local contingencies to effectively implement the design features. The design features could be prescribed, but the specific implementations could not. Some of the implementations bore little resemblance to their ultimate purpose. A group of fishermen might regulate their fish stocks by implementing an efficient turn-taking mechanism, for example, without directly monitoring the fish stocks (Ostrom 1990, 1992, 2005; Cox et al. 2010). Another article in the special issue of JEBO will show how these insights can be generalized to include virtually all groups that must become functionally organized to accomplish their particular objectives (Wilson, Cox, and Ostrom, in prep).

4) How did the trait **develop**? A biological trait such as the vertebrate eye can be studied as a physical and functional structure in its developed form without reference to how it developed. The fact that eye development is so reliable might seem to indicate that it is entirely genetically programmed. In fact, eye development reflects an elaborate gene-environment interaction in which an appropriate environmental input is required at numerous junctures along the way. The reason that eye development is so reliable is

because the appropriate environmental input was so reliable during the evolution of the vertebrate eye. If the environmental input is altered in modern environments, such as a much larger proportion of time spent focusing at close range, then even an adaptation as ancient as eye development can malfunction, as the proportion of people in modern life who need to correct their vision attests.

Examples similar to eye development are increasingly being documented for topics such as immune system malfunction (Jackson et al. 2008), diet-related diseases (Gluckman and Hanson 2004; Gluckman et al., 2009), and socio-sexual development (Del Guidice et al. 2011; Ellis et al. 1999). These topics might seem far removed from economics in a narrow sense, but they are centrally related to economics and public policy writ large. As with Tinbergen's other questions, it is just as important to understand the development of culturally evolved traits as genetically evolved traits. In fact, one of the messages of biocultural evolution is that the two are inseparable (Jablonka and Lamb 2006). Any economic policy requires the development and replication of cultural systems that work, compared to an infinitude of systems that don't work. The adaptive systems will be constructed of "parts" that evolved by past genetic and biocultural evolution and need to be understood in mechanistic detail. Some of the mechanistic details will appear far removed from the cultural systems in their developed form—even as far removed as prenatal and early childhood experiences—but they are just as important as early environmental inputs that are required for the development of the vertebrate eye.

Each of Tinbergen's questions can be addressed independently to a degree, but the main point of his classic paper is that all four need to be studied in conjunction with each other for a fully rounded explanation of any particular trait. This is how evolution functions as a general theoretical framework in the biological sciences, which can serve as a model for the study of all academic and applied human-related subjects, including economics and public policy.

The other articles in the special issue of *JEBO* will illustrate how Tinbergen's "four question" approach can be applied to topics that are central to economics and public policy. Before considering reasons why evolution might *not* prove useful for the study of a particular topic, it is important to clarify the basic role of theory in the study of any complex physical, biological or human-oriented topic. Some branches of economics, especially neoclassical economics, place a large emphasis on formal analytical models. Historically, this emphasis can be traced to the goal of Leon Walras and others during the 19th century to create a "physics of social behavior" comparable Newtonian physics (Beinhocker 2006). Ideally, this would result in a system of equations that could predict human economic behavior with the same accuracy that Newton could predict the orbits of the planets. If this goal could be realistically achieved, then theory alone would be capable of predicting human economic behavior, without closely relating theory to empirical research. Unfortunately, this Olympian view of analytical mathematical models has failed for the study of complex physical systems, not to speak of biological or human economic systems. Formal analytical models still play an essential role, of course, along with other theoretical tools such as computer simulation models, but they are always caricatures of the real world and must be closely related to empirical research to avoid becoming detached from reality. Evolutionary theory reflects this more sensible approach to mathematical models, along with branches of economics that have avoided the excesses of neoclassical economics.

Why the evolutionary perspective might *not* add value

Our next objective is to consider four reasons why evolution might *not* add value to the study of a given subject, based on discussions with colleagues who are open-minded but still want to know how the explicit consideration of evolution can contribute to their professions.

Reason #1: Human-related subjects have been studied by very smart people for a very long time. If science and scholarship result in the accumulation of knowledge, then people who start out employing different assumptions and perspectives will eventually reach the same conclusions. If so, then approaching a longstanding subject from an evolutionary perspective will merely affirm what has already been discovered.

It would be wonderful if science and scholarship were so simple that people quickly converge on the same conclusions, no matter what their starting position.

Unfortunately, anyone familiar with actual science and scholarship knows that this is not always the case (Kuhn 1970). The human-related disciplines are famously fragmented and isolated from each other. If they have not converged, there is little reason to expect convergence with an explicitly evolutionary perspective.

It is interesting to compare the diversity of thought in the human-related academic disciplines with biological diversity at a large spatial and temporal scale. Biological populations diverge whenever gene flow is disrupted, which can happen by virtue of geographical isolation or because of traits that prevent individuals from mating, even when they are mingling with each other. The disruption of gene flow generates hundreds of species and subspecies in island archipelagos such as the Galapagos Islands studied by Darwin and the Malay Archipelago studied by Wallace.

Communication is the analog of gene flow for academic disciplines. In the absence of communication, they can be expected to diverge from each other, as surely as species on islands. Before long they will be making different assumptions, coining different terms, and forming associations among terms that amount to mutually incomprehensible languages.

As an instructive example, the Walrasian core of neoclassical economics is based on the assumption that individuals maximize their *absolute* utilities. Natural selection favors traits that maximize *relative* fitness, which cause individuals to survive and reproduce *better than others*, not in any absolute sense. The choice of assumptions is not arbitrary; if people are motivated to increase their relative welfare rather than their absolute welfare, then this must be reflected in economic theory and policy. Walras and his contemporaries had no way of knowing that one of their foundational assumptions was at odds with evolutionary theory. Subsequent economists operating within the neoclassical paradigm could have questioned one of their foundational assumptions on their own, but for the most part they didn't. Only recently have economists such as Robert Frank (2011) begun to challenge the assumption of absolute utility maximization at a foundational level by employing an explicitly evolutionary perspective.

To summarize, most academic disciplines result in the accumulation of at least some durable knowledge. In these cases, an explicitly evolutionary perspective will merely affirm what has already become well established. In many other cases, however, smart people employing the tools of science and scholarship do not quickly converge upon the same conclusions, regardless of their starting points. When we start thinking about academic thought as a form of cultural evolution, sharing some of the same properties as biological evolution, then divergence among disciplines is an inevitable consequence of isolation. Communication across disciplines is required to prevent this from happening, and effective communication requires a common theoretical language. The disciplines that comprise the biological sciences are even more diverse than those comprising the human-related sciences, but they are much better integrated, thanks to the common theoretical framework provided by evolutionary theory. There is nothing preventing the human-related disciplines from becoming integrated in the same way.

Reason #2: The concept of design long predates the concept of evolution. The fact that an object or process is well designed for a purpose can be established without knowing about the designing process. An insect that mimics a leaf is well designed to avoid detection by predators. Who cares if it is a product of evolution or a supernatural agent? Similarly, if a corporation or market process functions efficiently, who cares if they are products of biocultural coevolution?

Reasoning on the basis of design is so powerful, and we are intuitively so good at it, that it is a likely candidate for a genetically evolved adaptation. We employ it all the time in everyday life, especially when interpreting each other's behavior. We also employ it erroneously all the time, as when we agonize over why a natural disaster happened, as if there must be a reason beyond purely physical causes. Belief in supernatural agents is often attributed to our wanton tendency to think in terms of agency, even when it isn't justified (Atran 2002; Boyer 2001).

If we have correctly inferred the purpose of an object, process, or agent, then we can proceed to reason about it intuitively without explicit reference to evolution as the designing process—but that is a big "if". If we have inferred the wrong purpose or if there isn't a purpose, then we have embarked on a long road to nowhere and it's not easy to find our way back.

It is helpful to remember the history of creationism as an example of design thinking gone wrong (Numbers 2006). Before Darwin, most scientists regarded the natural world as suffused with purpose and design, based on the concept of a benign creator. Their theory of the designing process enabled them to make correct inferences about design some of the time (e.g., the heart functions as a pump) but not others (e.g., apparent cruelty in nature has a benign purpose, even though it is inscrutable to us). Darwin's theory of evolution was revolutionary precisely because if offered a different conception of the designing process, which made a big difference in the interpretation of design. Darwin's theory made sense of both the previously correct inferences (e.g., about the heart functioning as a pump), and resolved the previous paradoxes (e.g., cruelty is an expected outcome of natural selection).

The need to know about the designing process to correctly infer the presence and absence of design is a complicated business, even for the evolutionist (Wilson 2007). The design of sexual ornaments was a puzzle for Darwin until he formulated the concept of sexual selection. Creationist theories assumed that nature is well designed at all levels—for groups, species, and ecosystems no less than individuals. It has taken a long time for evolutionists to establish that design should be expected at a given level only when special conditions are met—and that these conditions sometimes even fail at the individual level (e.g., intragenomic conflict; Wilson 2004). Then there is the concept of evolutionary mismatch, in which design can only be understood in reference to a past but not the present environment (Lloyd, Wilson, and Sober 2011). The fact that evolution is a historical process gives biological design a Rube Goldberg quality, unlike what a god or an engineer might create. Even examples of biological design that seem obvious today, such as the beaks of the finches on the Galapagos Islands, required decades of hard work to establish as adaptations that evolved by natural selection (Wilson 1998). The so-called "Adaptation War" that Stephen Jay Gould and Richard Lewontin started in 1979 with their famous article titled "The Spandrels of San Marco and the Panglossian Paradigm: A

Critique of the Adaptationist Programme" was all about correct and incorrect uses of design thinking within evolutionary biology.

Against this background, it is unreasonable to think that intuitive design thinking is good enough for the study of human-related subjects. Even without the pitfalls associated with creationism, secular theories of human action are littered with false inferences about design that have led down long roads to nowhere, from which we still need to recover. The assumption of neoclassical economic theory that people are designed to maximize their absolute utilities has already been discussed. The widespread economic assumption that design at the individual level (e.g., the pursuit of self-interest) straightforwardly results in design at the societal level (e.g., well-functioning economies) is profoundly mistaken from an evolutionary perspective (Gowdy 2004; Wilson 2004). As a third example, risky adolescent behavior is an important public policy issue, even if it is seldom considered from a formal economic perspective. The main paradigm for thinking about risky adolescent behavior treats it as a pathological outcome of child development in harsh environments; in other words, a breakdown of design. An alternative paradigm, better informed by evolution, treats risky adolescent behaviors as well adapted for short-term survival and reproduction in harsh environments, with pathological consequences for long-term individual and societal welfare (Ellis et al. 2011).

To summarize, *intuitive* inferences about design often depart from *evolutionary* inferences about design. A mistaken inference about design leads to line of inquiry that, like creationism, is a long road to nowhere. An explicitly evolutionary perspective is needed to make correct inferences about design.

Reason #3: A reasonable research strategy is to study what is, without worrying much about how it got that way. After all, something like the brain is available to be studied in minute detail, whereas how it got that way is more speculative. Why speculate when we can study the real thing?

This statement can be true in a limited sense. All of Tinbergen's questions can be studied independently, including questions about proximate mechanisms. Insofar as science involves division of labor, individual scientists can spend their entire careers studying proximate mechanisms without thinking about the other three questions. This is true for the biological sciences, no less than human-related topics. According to one distinguished colleague of ours (personal communication): “Some researchers only care about proximate mechanisms. They don’t care about ‘why’ but rather about ‘how’. This is why a molecular biologist could be a creationist, for instance.”

The example of a creationist molecular biologist perfectly illustrates how a reason for ignoring evolution can suffice for a small minority of individuals but fail miserably for a field as a whole. If all molecular biologists were creationists, that would be a disaster. If all biologists were creationists, that would be more disastrous still. Yet, the issue before us is whether entire human-related subjects such as psychology, economics, or education, need to be approached from an evolutionary perspective. The argument that *everyone* can restrict themselves to proximate mechanisms fails as miserably for these broad fields of inquiry as for molecular biology and biology as a whole.

Moreover, the study of proximate mechanisms is always founded upon a set of assumptions about function or lack of function. The only reason that a creationist can function as a biologist is if the function (or lack of function) of the particular mechanism being studied has been correctly inferred. You can’t ask a good “how” questions unless you are in the ballpark of the right “why” question.

To illustrate this point with a biological example, some bird species are genetically adapted to migrate south during the winter. The proximate mechanisms that enable them to do this include the ability to memorize the night sky as nestlings. Other bird species are genetically adapted to overwinter in cold climates. The proximate mechanisms that enable them to do this include the ability to memorize hundreds of locations where food has been stored. Imagine that you are given a bird species to study without being told anything about its ecology or migratory habits. How many decades would it take you to discover its particular adaptations, just by studying its brain? This is why asking “how” and “why” questions in conjunction with each other, along with phylogenic and developmental questions, is so essential for evolutionary biology as a whole—and just as essential for human-related subjects.

The human-related disciplines abound with examples of "how" questions founded upon the wrong "why" questions. Consider a recent article titled "Why do humans reason? Arguments for an argumentative theory", by Hugo Mercier and Dan Sperber (2011), published the commentary journal *Behavioral and Brain Sciences*. We cannot improve upon their language:

> How do humans reason? Why do they reason? These two questions are mutually relevant, since the mechanisms for reasoning should be adjusted to its function. While the how-question has been systematically investigated…there is very little discussion of the why-question. How come? It may be that the function of reasoning is considered too obvious to deserve much attention. According to a long philosophical tradition, reasoning is what enables the human mind to go beyond mere perception, habit, and instinct.

Mercier and Sperber propose that human reasoning abilities evolved largely for the purpose of producing and evaluating arguments in communication. This provisional answer to the why-question makes sense of empirically documented phenomena that appear anomalous and paradoxical against the background of different answers to the why-question that have guided philosophical inquiry on reasoning for centuries and scientific research for decades. The lively peer commentary that follows their target article reinforces the fact that you can't ask a good "how" question if you're not asking the right "why" question. And you can't ask the right "why" question without seriously consulting evolutionary theory.

Reason #4) *All branches of knowledge should ideally be consistent with each other, but every branch need not be consulted for the study of any particular branch. Evolutionists rarely feel the need to consult quantum physics, and perhaps evolution rarely needs to be consulted for the study of many traits, in humans and nonhumans alike.*

It is true that each of Tinbergen's questions can be studied in isolation, as we have just stressed in our discussion of proximate and ultimate causation, but the essence of his classic article was to show that they are best studied in conjunction with each other.

Specialization can certainly be warranted for individuals, but it's hard to imagine a sizeable subject that wouldn't benefit from having all four questions addressed. This is just as true for the subjects associated with economics and public policy as for the biological sciences and human-oriented academic disciplines.

Conclusion: Putting the Evolutionary Toolkit to Work

The best way to demonstrate the utility of the evolutionary toolkit is by putting it to work on specific case studies. Fortunately, this is not a future prospect but is already in progress. Dozens of scientists are already using evolutionary theory in the same way that it is used in the biological sciences to address issues that are centrally relevant to economics and public policy. They come from a melting pot of academic disciplines, illustrating the kind of spontaneous integration made possible by a common theoretical framework. While sizeable in terms of numbers, they are still a tiny fraction of the economics and public policy community. Moreover, the theoretical framework that they represent is obscured by the complex history of evolution in relation to human affairs, resulting in a diversity of associations, some positive and others negative, but all of them falling short of the fully rounded "four questions" approach that is employed in the biological sciences. The purpose of this article, and the special issue of *JEBO* that it introduces, is to bring the modern evolutionary paradigm to the attention of the larger economics and public policy community.

Acknowledgements

This article and special issue of JEBO is based on a collaborative project between the Evolution Institute and National Evolutionary Synthesis Center to integrate evolution and economics. The project involves an advisory group of over forty scientists and scholars from across disciplines, from which participants for a sequence of workshops are drawn.

Literature Cited

Atran, S. (2002). In Gods we Trust: The evolutionary landscape of religion. Oxford: Oxford University Press.

Beinhocker, E. D. (2006). Origin of Wealth: Evolution, Complexity, and the Radical Remaking of Economics. Cambridge, MA: Harvard Business School Press.

Boyer, P. (2001). Religion Explained. New York: Basic Books.

Carniero, R. (2003). Evolution in Cultural Anthropology: a critical history. New York: Westview Press.

Cox, M., Arnold, G., & Villamayor-Tomas, S. (2010). A review of design principles for community-based natural resource management. Ecology and Society 15.

Dobzhansky, T. (1973). Nothing in biology makes sense except in the light of evolution. American Biology Teacher, 35, 125-129.

Ellis, B. J., Del Guidice, M., Dishion, T. J., Figueredo, A. J., Gray, P., Griskevicius, V., et al. (2011). Evolution and Risky Adolescent Behavior. Developmental Psychology, in press.

Ellis, B. J., McFadyen-Ketchum, S., Dodge, K. A., Pettit, G. S., & Bates, J. E. (1999). Quality of early family relationships and individual differences in the timing of pubertal maturation in girls: A longitudinal test of an evolutionary model. Journal of personality and social psychology, 77, 387-401.

Frank, R. (2011). The Darwin Economy: Liberty, Competition, and the Common Good. Princeton: Princeton University Press.

Gluckman, P., Beedle, A., & Hanson, M. (2009). Principles of Evolutionary Medicine. New York: Oxford University Press, USA.

Gluckman, P., & Hanson, M. (2004). The Fetal Matrix: Evolution, Development, and Disease. Cambridge, UK: Cambridge University Press.

Gould, S. J., & Lewontin, R. C. (1979). The spandrels of San Marco and the panglossian paradigm: A critique of the adaptationist program. Proceedings of the Royal Society of London, B205, 581-598.

Gowdy, J., & Seidl, I. (2004). Economic man and selfish genes: the relevance of group selection to economic policy. Journal of Socioeconomics, 33, 343-358.

Gowdy, J., & Van den Bergh (2003). The microfoundations of macroeconomics: an evolutionary perspective. Cambridge Journal of Economics, 27, 65-84.

Hodgson, G. M. (1993). Economics and Evolution. Cambridge, UK: Polity Press.

Hodgson, G. M. (2007). Taxonomizing the Relationship between Biology and Economics: A Very Long Engagement. Journal of Bioeconomics, 9, 169-185.

Hodgson, G. M., & Thorbjorn, K. (2010). Darwin's Conjecture: The Search of General Principles of Social and Economic Evolution. Chicago: University of Chicago Press.

Hofstadter, R. (1959/1992). Social Darwinism in American Thought. Boston, MA: Beacon Press.

Holden, C., & Mace, M. (2009). Phylogenetic Analysis of the Evolution of Lactose Digestion in Adults. Human Biology, 81, 597-619.

Ingram, C. J. E., Elamin, M. F., Mulcare, C. A., Weale, M. E., Tarekegn, A., Raga, T. O., et al. (2007). A novel polymorphism associated with lactose tolerance in Africa: multiple causes for lactase persistence? . Human Genetics, 120, 779-788.

Jackson, J. A., Friberg, I. M., Little, S., & Bradley, J. E. (2008). Review series on helminths, immune modulation and the hygiene hypothesis: Immunity against helminths and immunological phenomena in modern human populations: coevolutionary legacies? Immunology, 126, 18-27.

Kuhn, T. S. (1970). The structure of scientific revolutions (2nd ed.). Chicago
: University of Chicago Press.

Leonard, T. C. (2009). Origins of the myth of social Darwinism: the ambiguous legacy of Richard Hofstadter's Social Darwinism in American Thought. Journal of Economic Behavior and Organization, 71, 37-51.

Lloyd, L., Wilson, D. S., & Sober, E. (2011). Evolutionary Mismatch and What To Do About It: A Basic Tutorial. Evolutionary Applications (in prep).

Mercier, H., & Sperber, D. (2011). Why do humans reason? Arguments for an argumentative theory. Behavioral and Brain Sciences, 34, 57-111.

Nelson, R. R., & Winter, S. G. (1982). An Evolutionary Theory of Economic Change. Cambridge, MA: Harvard University Press.

Numbers, R. L. (2006). The Creationists: From Scientific Creationism to Intelligent Design (Expanded Edition). Cambridge, MA: Harvard University Press.

Ostrom, E. (1990). Governing the commons: The Evolution of institutions for collective Action. Cambridge, UK: Cambridge University Press.

Ostrom, E. (1992). Crafting Institutions for Self-Governing Irrigation Systems. San Francisco: Institute for Contemporary Studies.

Ostrom, E. (2005). Understanding Institutional Diversity. Princeton: Princeton University Press.

Richards, R. J. (1987). Darwin and the emergence of evolutionary theories of mind and behavior. Chicago: University of Chicago Press.

Sober, E. (1984). The nature of selection: evolutionary theory in philosophical focus. Cambridge: Bradford/MIT.

Solow, R. M. (2004). Progress in Economics since Tinbergen. De Economist, 152, 159-160.

Swallow, D. M. (2003). Genetics of lactase persistence and lactose intolerance. Annual Review of Genetics, 37, 197-219.

Tinbergen, N. (1963). On aims and methods of ethology. Zeitschrift für Tierpsychologie, 20, 410-433.

Turchin, P. (2003). Historical Dynamics: Why States Rise and Fall. Princeton: Princeton University Press.

Turchin, P. (2005). War and Peace and War. Upper Saddle River, NJ: Pi Press.

Veblen, T. (1898). Why is Economics not an Evolutionary Science? . Quarterly Journal of Economics, 12, 373-397.

Wilson, D. S. (1998). Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society of London, Series B, 353, 199-205.

Wilson, D. S. (2002). Darwin's Cathedral: Evolution, Religion and the Nature of Society. Chicago: University of Chicago Press.

Wilson, D. S. (2004). The New Fable of the Bees. In K. R. (Ed.), Advances in Austrian Economics (Vol. 9, pp. 201-220). Greenwich CN: JAI Press.

Wilson, D. S. (2007). Evolution for Everyone: How Darwin's Theory Can Change the Way We Think About Our Lives. New York: Delacorte.

Wilson, D. S. (2011). The Neighborhood Project: Using Evolution to Improve My City, One Block at a Time. New York: Little, Brown.

Wilson, D. S., Hayes, S. C., Biglan, A., & Embry, D. (2011). Evolving the Future: Toward a Science of Intentional Change. Behavioral and Brain Sciences, submitted.

Witt, U. (2003). The Evolving Economy: Essays on the Evolutionary Approach to Economics. Aldershot: Edward Elgar.

Witt, U. (2008a). Recent Developments in Evolutionary Economics. Aldershot: Edward Elgar.

Witt, U. (2008b). What is specific about evolutionary economics? Journal of Evolutionary Economics, 18, 547-575.