Population Games and Evolutionary Dynamics

Article *in* The American Mathematical Monthly · April 2012

DOI: 10.4169/amer.math.monthly.119.04.352

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REVIEWS

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Population Games and Evolutionary Dynamics. William H. Sandholm. MIT Press, Cambridge, MA, 2011, xxv + 589 pp., ISBN 978-0-262-19587-4, $65.

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An economist and a biologist walk into a bar. No joke here—the two have lots to talk about. In fact, there's an entire journal devoted to *Economics and Human Biology*, and, of course, biotechnology is big business. As the conversation deepens, more commonalities emerge. Both fields share an avid interest in evolutionary processes, and the phrase "survival of the fittest," first coined by the philosopher-economist Herbert Spencer to describe Charles Darwin's theory of natural selection, has also been used (some would say abused) to justify an unregulated competitive marketplace.

But what's math got to do with it? Both economists and biologists are interested in studying how interacting populations (of humans, animals, cells, machines, etc.) behave. In particular, they share a predilection for mathematical models of situations where the consequences of individual actions are impacted by the actions taken by others. Game theory is the mathematical framework developed to study such strategically *interdependent* interactions.

Classical game theory (CGT) assumes players are purely rational agents, acting solely to maximize their own self-interest (payoffs or utilities). The traditional solution concept of CGT is the Nash equilibrium (NE): each individual plays a strategy that is the best response, given the strategy choices made by all the other players in the game. Nash equilibria have been used to both describe and predict how people do behave, and prescribe how they *should* behave, when confronted with situations analogous to the game being studied. One of the most frequently studied games, prisoners' dilemma (dubbed the e. coli of game theory), encodes many situations where the good of the individual is in conflict with what is best for the collective (tragedy of the commons). However, behavioral and experimental economics and psychology have demonstrated that actual human behavior often deviates from this model. The equilibria in prisoners' dilemma, as well as the ultimatum and dictator games all predict and recommend that players act selfishly. But in practice, we often don't. How, then, can we account for the observed altruistic, self-sacrificing, and charitable behaviors?

The predictions of any model are only as good as the foundation on which it is built—its assumptions. Many have found the assumptions of static game theory hard to swallow. The concept of homo economicus—the "rational man"—has been critiqued, as well as the assumptions of complete information and equilibrium knowledge. Complete information means that all players know what strategies are available (the strategy set) and what payoffs result from each strategy profile (the particular combination of strategies chosen by each player). Equilibrium knowledge assumes each player is

http://dx.doi.org/10.4169/amer.math.monthly.119.04.352

able to anticipate what strategies their opponents will choose (based, in turn, on their assumption that all players are rational maximizers).

In reality, most of us lack the ability and resources to arrive at an optimal solution. As even cursory introspection will reveal, we are only partially rational—our choices are also often influenced by emotional and other extra-rational considerations. Even when this is not the case, perfectly rational decisions might not be feasible for many other reasons. Information may be limited rather than complete. The finite amount of time needed to make decisions in the face of extremely complex situations and high deliberation costs may also result in a less than perfectly rational decision. To address these realities, Herbert Simon introduced bounded rationality as an alternative basis for modeling decision-making [**3**]. This sparked a flurry of research studying the decision-making procedure itself.

Another departure from the emphasis on equilibrium solutions and perfectly rational players (and the subject of the book under review), is evolutionary game theory (EGT). EGT considers populations of large numbers of decision-makers, where the frequency with which a particular decision is made can vary in time. In these so-called *population games*, as we "evolve" from a static to a dynamic theory, we relinquish the notion that it is safe to ignore what happens away from equilibrium. We also abandon all hope of players capable of perfect or even bounded rationality. In order to determine when a particular equilibrium will actually be observed in nature, we employ the mathematical tools of local stability analysis to examine what happens when small local disturbances perturb a system away from equilibrium and ascertain whether the system will bounce back, and equilibrium be restored. But this analysis says nothing about how equilibrium is established in the first place.

Evolutionary game theory shifts the focus from Nash equilibria and rationality to disequilibrium behavior and the process by which agents adjust their behaviors in response to the present strategic environment. This shift leads to a new set of questions. Instead of asking "Who chose strategy i?" we ask "How many chose strategy i?" and "What happens to the payoff of strategy j players if some agents switch to strategy i?" Sandholm offers a comprehensive treatment of the methods used to study dynamic models of population games, and provides techniques to answer these questions and a host of other concerns raised by the strong assumptions about rationality and agents' knowledge required by traditional (static) game theory.

The development of EGT was originally inspired by problems in biology. In the early 1970s, a novel approach was developed and disseminated by John Maynard Smith, whose creative insights initiated an innovative and fruitful mathematical framework to study evolution. As the mathematical evolutionary biologist Richard Lewontin wrote in a tribute to him,

> [John] Maynard Smith saw that a major remaining problem in evolutionary theory was to explain the evolution of characteristics whose reproductive advantage or disadvantage to an individual depended on the response of other individuals. . . . Maynard Smith realized that this class of evolutionary problem could be approached through game theory. His invention of the concept of an Evolutionar[il]y Stable Strategy created a new and lively branch of theoretical studies of evolution. [**1**]

An evolutionarily stable strategy (ESS) is analogous to the classical game theoretic concept of a NE. They are similar, but not identical: every ESS corresponds to a NE, but there exist NE that are not ESS. A strategy is said to be evolutionarily stable if an entire population following that strategy cannot be invaded (i.e., dominated or conquered) by a small group following a different strategy. Whereas the NE relies on the cognitive capacities of the players, the ESS is motivated in an entirely different fashion. In the context of EGT, the players are individuals (humans, genes, viruses, plants, animals) with heritable strategies (alleles, phenotypes, traits). They have no control or choice over the strategy that they play. Indeed they may not even be capable of being consciously aware of the game. Instead of the one-shot or repeated games of CGT, EGT assumes a repeated random pairing of agents who play their inherited strategy, not influenced by any reasoning process or history of previous play (myopic behavior). While the NE is defined on strategy sets with each player choosing a strategy, the ESS is defined in terms of the strategies themselves. Instead of modeling the actions of *individual agents*, EGT investigates the spread and evolution of *inherited strategies* (genotypes, phenotypes, behaviors) in populations (species, societies). The payoffs are in terms of Darwinian fitness, measured in reproductive success. Successful strategies increase in frequency within the population.

In the late 1980s, economists adopted these game-theoretic models of natural selection. While biologists study populations of interacting agents whose different genetic programs lead to varying levels of reproductive success, economists are interested in the behavior of large populations of strategically interacting agents who occasionally reevaluate their choices in light of current payoff opportunities. Rather than using reproductive success, the economic models increase frequencies of strategies via revision protocols: agents periodically switch strategies following a defined procedure (e.g. imitating successful strategies). By the mid-1990s, the term “evolutionary” had been generalized from the narrow Darwinian sense of survival of the fittest to refer to processes that change gradually (evolution, not revolution).

The dynamic models of population games considered by Sandholm are related to, but different from, those developed by Maynard Smith. The evolutionarily stable strategy is replaced by the notion of an evolutionarily stable state in the dynamical system. Whereas the earlier models considered single populations who chose from the same strategy set, population games generalize to *societies* consisting of one or more populations of agents. The agents in each population are indistinguishable—each has the same role in the game, the same strategy set, and the same preferences. The preferences are encoded in a *payoff function*, which depends not only on the agents’ own strategy, but also takes into account the frequency distributions of strategies in each population. The collective behavior in a population game is described by the *social state* which gives the observed distribution of strategy choices for each population. For finite populations with finite strategy sets, the social state is represented by a vector with a finite number of components.

Population Games and Evolutionary Dynamics focuses attention on applications in economics and other social sciences with only a cursory glance at the biological applications that inspired the field. But the text is useful for students and researchers in any field that would benefit from models of repeated strategic interactions in large populations of small anonymous agents. By saying an agent is “small” we mean that her choices don’t have a large impact on other agents’ outcomes.

The evolutionary approach to population game dynamics is based on two assumptions—inertia and myopia. Inertia means that agents are not continually updating their choices, but rather reevaluate and consider switching strategies only at discrete random intervals (determined by a stochastic alarm clock called the “Poisson alarm clock”). Myopia means the agents revise their choices based only on current behavior and payoff opportunities. They do not factor in beliefs about future play, possible punishment, reputation, or other mechanisms that are important in repeated play of static games (e.g., iterated prisoners’ dilemma). These two assumptions mutually reinforce each other. When opponents' behavior changes slowly (inertia), it makes sense to only consider current conditions (myopia), since strategies that look good now are probably going to remain appealing for a while.

The *population game* is the strategic environment, defining the interaction that is to recur. A *revision protocol* is a set of rules telling agents when and how to change strategies. Mathematically, it is a function whose arguments are the current payoffs and social states, which returns a conditional switch rate, telling agents when and how to update their strategies over time. In other words, the revision protocol tells those agents playing strategy i who are considering changing strategies, how frequently they should switch to strategy j. Together, a population game F and a revision protocol ρ define a stochastic evolutionary process. Shifting viewpoint, he demonstrates how each revision protocol ρ can be used to define a map from population games to differential equations, yielding a deterministic evolutionary dynamic. One feature of the book that is very satisfying is the way it unifies under a single canopy both deterministic and stochastic models, and demonstrates how both deterministic and stochastic evolutionary game dynamics are branches of the same tree and can be derived from a single root.

A compelling criticism that has been leveled at evolutionary as opposed to equilibrium analysis of games—a weakness of bounded rationality as well—is that there are a host of possible and equally plausible assumptions one could make about how individuals make decisions. Once we make the move from the traditional assumptions of rationality and equilibrium, how do we decide which alternative is best suited for the application at hand? In response to this critique, Sandholm defines three classes of games (potential games, stable games and supermodular games), each with a set of constraints which embody different applications. Next he considers various collections or families of revision protocols, each family reflecting a different style of decision-making. He then proves that many results are robust within a range of decision-styles (specified revision processes) and states:

> When conclusions hold under any number of protocols sharing a certain family resemblance, one can argue that they are not artifacts of a particular choice of functional forms but of more fundamental assumptions about how agents make decisions. (p. 148)

William Sandholm is an economics professor at the University of Wisconsin in Madison, but to judge by this text, he would be equally at home in a mathematics department. His treatment is mathematically rigorous and demanding, including theorems and proofs. Although he believes the text to be accessible to senior undergraduate majors (I presume in economics), I would dispute this for mathematics and a fortiori economics majors, unless they are very advanced undergraduates. Appendices are included for each chapter, and actually comprise one-quarter of the book. These supplementary materials on calculus, convex analysis, matrix analysis, dynamical systems, probability theory and stochastic processes do offer a good review if one has already seen the topics, but I did not feel that taken together they could stand alone as an "independent introduction to the methods of dynamical modeling," as the author claims. The book is replete with beautiful color figures of phase diagrams illustrating the evolutionary dynamics using geometric methods of analysis, created using cool open source software available from the author's website.

Taking a page from the students (usually nonmajors) who always want to know "what's this stuff good for?" I wonder what these models can tell us that is important. My own interest in EGT has been as a tool to probe the tough question of the evolution of morality. In a world of selfish genes ruthlessly seeking progeny, how do we account for altruism, self-sacrifice, charity, and even a yen for fairness? In support of the cynical viewpoint, models demonstrate that one freeloader can invade a population of cooperators. However, it is also the case that a group of cooperators can take over from a population of defectors. What conditions are necessary to support a cooperative, caring society? Mechanisms such as kin selection, forms of reciprocity and group selection have been proposed to explain how competition could masquerade as cooperation in special situations (see [**2**]).

Using this approach we have "saved the phenomenon"—the assumption that we are self-interested maximizers. However, as I always tell my students, when observed behaviors are not consonant with a model's predictions, the first thing to check are the assumptions. One likely suspect to investigate is the prevailing wisdom that we are by nature competitive beings looking out for number one. Indeed, recent research in neuroscience has revealed underlying mechanisms such as mirror neurons, which help explain the origins of empathy. These discoveries lend credence to an alternative assumption that we are, in fact, as hard-wired to cooperate as we are to compete.

The story we tell about evolution is important because it fuels our beliefs about what kind of world is possible. If we believe that morality evolves as a byproduct of selfishness, and that all our behavior is motivated by a brutish nature red in tooth and claw, then it is no surprise that we see endless war, growing income inequity, environmental degradation and a host of other ills. On the other hand, if we believe that our biology supports mutuality and an instinct to live by the golden rule, and if we believe we can choose to consciously evolve in the direction of greater cooperation, then the possibility exists that nations can beat their swords into plows and we can learn to live together, finding less destructive ways to resolve our conflicts.

Are we evolving towards a more fair, caring and sharing world? What would it take to ensure that there will be progeny—biologists, economists, mathematicians and politicians to ponder these questions. Can the mathematical framework of EGT help us? I think game theory can serve as a powerful instrument for examining social dynamics. It can give us insights into possible futures, and offer us a laboratory for exploring the consequences of a variety of assumptions, choices, and societal structures. As my friend and mentor, Phil Straffin so aptly summarizes the merits of game theoretic analysis:

> The goal in the study of social interactions cannot be simple answers. I think it should be insight: new ways of analyzing, organizing and appreciating human experience. Game theory has been, and gives every indication of continuing to be, a powerful tool for the generation of insight. [**4**, p. 215]

Let us hope for the sake of our children and the next seven generations, that we use these insights wisely.

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