Game Theory in Cultural Evolution

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The purpose of this paper is to review the key contributions of game theory to the field of cultural evolution, focusing particularly on interfaces between cultural evolution and economics. Because many readers may not be familiar with the interdisciplinary field of cultural evolution, I begin with a brief orientation to this field as a scientific enterprise and then highlight the important ways that game theory has been deployed in both theoretical and empirical research within the field, noting spillovers and interactions with economics.

The field of cultural evolution

The academic label "cultural evolution" only emerged in the last decade to delineate a cluster of related lines of interdisciplinary research that draws heavily on anthropology, biology, psychology and economics as well as a broad swath of other fields. The field now has its own society along with an emerging repertoire of theoretical and empirical methods, which includes tools drawn from economics and psychology as well as anthropology and evolutionary biology (Henrich et al. 2004; Ensminger and Henrich 2014; Schulz et al. 2019). Foundational works include theoretical treatises by two duo, Boyd and Richerson and Feldman and Cavalli-Sforza, as well as others (Pulliam and Dunford 1980; Cavalli-Sforza and Feldman 1981; Lumsden and Wilson 1981; Boyd and Richerson 1985; Durham 1991). For recent reviews, see Mesoudi (2011), Henrich (2016), Boyd (2017) and Laland (2017). I also recommend Nunn's (2021) chapter in *Historical Economics*, which gathers a number of insights and approaches from the cultural evolutionary literature and translates them for economists.

Theoretically, this field's point of departure is the assumption that humans can be modeled as adaptive learners who rely heavily on various forms of social learning—on learning from other people using a broad range of psychological mechanisms, including those glossed as 'imitation.' These learning mechanisms permit individuals to acquire ideas, beliefs, strategies, values, preferences (e.g., both food and mate preferences), motivations (e.g., fairness with strangers), decision-heuristics and judgment biases. Notably, because this field digested a large body of empirical research on social learning at its founding, much of it done in the 1970s in psychology (Bandura 1977; Rosenthal and Zimmerman 1978; Birch 1981), theorists have generally assumed that individuals could acquire motivations and preferences (e.g., food preferences) from others via imitation—endogenous preferences. From this gateway, theoretical work has gone in three directions.

1. *Cultural evolution*: First, the process of cultural evolution itself can be modeled by looking at the outcomes of such individual-level learning processes in populations over time, and often over generations—because social learning creates a form of intergenerational inheritance. This work has focused on the emergence of sociological phenomena like social norms, cooperation, social classes, ethno-linguistic groups and innovation, among other topics. Game theory naturally entered as researchers sought to construct models that combined learning and social interaction. Cultural evolution considers both the dynamics of these evolutionary process as well as their equilibrium states (or lack thereof). The equilibrium concepts used by cultural evolutionists emphasize dynamic stability (often Evolutionary Stable Strategies, following Maynard Smith

(1982)) and both analytical and simulation models are used, often in a complementary fashion. Many simple models take the form of payoff-biased imitation (replicator dynamics), but theorists also study continuous trait models and models that include vertical transmission (copy parents), prestige biased transmission (copy who others are copying), conformist transmission (copy the majority or plurality) and the use of CRedibility Enhancing Displays (CREDs: actions speak louder than words)—see Acerbi, Mesoudi and Smolla (2020) for a recent review of some formalizations. Below, I will elaborate primarily on the use of game theory in understanding cultural evolution.

This work developed in parallel with important work on evolutionary game theory within economics (Weibull 1995; Fudenberg and Levine 1998; Young 1998), though in my view it benefited from a richer engagement with anthropology and psychology, a greater willingness to deploy numerical and simulation techniques in modelling, and the requirement to micro-found its assumptions about individuals' learning abilities in evolutionary theory—see next.

2. *Evolutionary foundations of learning*: Second, the particular learning abilities that individuals are assumed to possess can be micro-founded by asking how natural selection might have shaped human minds genetically to permit them to most effectively (adaptively) learn from others, given the serious energetic and processing constraints imposed by our species phylogenetic history. This has permitted researchers to both make bottom-up predictions about how infants, children and adults should learn as well as by providing a theoretical foundation for what is assumed in building models of cultural evolution. These models have explored when and why individuals should rely on non-payoff-based forms of learning, including conformist transmission (Henrich and Boyd 1998; Kendal, Giraldeau, and Laland 2009; Nakahashi, Wakano, and Henrich 2012) and parent-child transmission (McElreath and Strimling 2008). This approach leads researchers to assume that learners and actors are rather constrained in both the information available to them and their information processing abilities.

   Taking an evolutionary approach to the origins and nature of people's learning abilities has also encouraged researchers to consider how our species' social instincts, such as kin-based altruism, incest aversion and prestige psychology, might influence the formation of institutions (Henrich, Chudek, and Boyd 2015; Henrich 2020).

3. *Culture-gene coevolution*: Finally, because this approach focuses attention on the interaction between genetic and cultural evolution, there's a large body of formal theoretical work, begun in the 1970s, that examines the interaction between our genetic and cultural inheritance streams (Boyd and Richerson 1976; Feldman and Cavalli-Sforza 1976; Aoki 2001). Today, drawing on the growing body of evidence derived from studying the human genome, the case that culture has driven much of our species genetic evolution is now central to our understanding of human evolution and contemporary genetic variation (Laland, Odling-Smee, and Myles 2010; Richerson, Boyd, and Henrich 2010; Henrich 2016; Boyd 2017; Laland 2017).

I'll now review some of the major contributions associated with the use of game theory in cultural evolution with an emphasis on exchanges with economics.

Theoretical Contributions

This review covers four main topics (1) equilibrium selection and the role of intergroup competition, (2) large-scale cooperation and mechanisms for sustaining costly social norms, (3) the emergence of castes,

ethno-linguistic groups and honor cultures, and finally (4) endogenizing preferences (also called "values" or "types").

Equilibrium selection and intergroup competition

A central difference between the application of game theory within the fields of cultural evolution and economics is the question of equilibrium selection (Henrich 2004; Richerson et al. 2016). Both evolutionary and classical game theory often produce multiple stable equilibria (Fudenberg and Maskin 1986; Boyd and Richerson 1990; Weibull 1995; Fudenberg and Levine 1998; Young 1998) and cultural evolutionary game theory produces even more stable equilibria when non-payoff-based transmission mechanisms are included (e.g., conformist transmission (Henrich and Boyd 2001) and credibility-enhancing displays (Henrich 2009)).

My sense is that economists see this plethora of equilibria as a 'bug' (an annoying modeling issue) while cultural evolutionists see it as a 'feature.' That is, cultural evolutionists see the emergence of multiple stable equilibria as telling us something about the world: dynamic and often gradual learning processes occur simultaneously in different groups or populations resulting in different stable outcomes. The variation we observe around the world and back into history represents different stable equilibria or cultural evolutionary trajectories toward different equilibria. Some equilibria may either favor greater success in competition with other groups—e.g., via warfare (Boyd and Richerson 1990), attracting more migrants (Boyd and Richerson 2009) or differential copying (Boyd and Richerson 2002), etc.—or they may be less vulnerable to shocks or drift (e.g., larger basins of attraction (Kendal, Feldman, and Aoki 2006)). Over the long-run, these processes tend to favor those behavioral equilibria that foster success in intergroup competition, often leading to stable equilibria that generate higher average payoffs.

When economists began drawing ideas from the field of cultural evolution and collaborating with cultural evolutionists (Henrich et al. 2001a; Boyd et al. 2003; Fehr and Henrich 2003; Henrich et al. 2003, 2004), intergroup competition as an equilibrium selection mechanism played a central role (Bowles and Gintis 1998, 2004a; b, 2011; Fehr, Fischbacher, and Gächter 2002; Gintis 2003, 2006; Bowles 2005, 2006; Bernhard, Fischbacher, and Fehr 2006; Choi and Bowles 2007).

Origins of costly social norms, including cooperative ones

Much work in cultural evolution is focused on understanding how humans are different from other animals (Richerson and Boyd 1998; Bowles and Gintis 2011; Boyd, Richerson, and Henrich 2011; Turchin 2015). As a consequence, a central research line has been to explain our species' ability to cooperate in large-groups with non-kin and sometimes in non-repeated interactions. As a result, much theoretical work has focused on modeling the evolution of cooperation using the *n*-person Prisoner's Dilemma. The game seemed particularly well-suited to the small-scale, residentially-fluid, acephalous communities in which our species likely evolved (Smith et al. 2018b). Early theoretical work suggested that unlike in the dyadic version of the Prisoner's Dilemma, strategies that relied on reciprocity and/or kinship (Axelrod and Hamilton 1981; Axelrod 1984) in the *n*-person game were not likely to sustain cooperation among hundreds or thousands of individuals (i.e., the scales observed among foragers). Moreover, even when reciprocity and/or kinship could sustain cooperation theoretically, the predicted patterns didn't match those observed in many hunter-gatherer contexts (Axelrod 1986; Joshi 1987; Boyd 1988; Hill, Barton, and Hurtado 2009; Hill and Hurtado 2009; Henrich 2016), where little reciprocity was expected in practice and cooperation often involved non-kin (Hill et al. 2011). Animated by this challenge, a large body of later work can be understood as providing a variety of alternative mechanisms for creating

stable equilibrium near full cooperation, including those based on peer punishment, positive indirect reciprocity (and linked games), negative indirect reciprocity and signaling.

Crucially, while this work was initially focused on explaining cooperation, the results of these models consistently suggested that these mechanisms could sustain costly norms regardless of any benefits delivered to others or the group as a whole. This was taken by many cultural evolutionist—including me (Henrich 2004)—to suggest that these mechanisms might explain the plethora of costly but non-cooperative and even maladaptive norms found across human societies—canonical examples include funerary rites that entail the consumption of the brains of dead relatives (leading to the transmission of a deadly prion disease), female genital cutting, foot binding, skull deformation and a variety of food taboos (Edgerton 1992; Brown and Feldman 2009; Majid 2015; Vogt et al. 2016).

The role of diffuse or peer punishment

The most important early model of the evolution of large-scale cooperation, using the *n*-person Prisoner's Dilemma, studied the impact of punishing strategies on the emergence of cooperation: Boyd and Richerson (1992) found that costly equilibria, including cooperative ones, could be sustained via diffuse punishment if punishers used a meta-punishing strategy in which they punished non-punishers. That is, meta-punishing strategies punish not only non-cooperators but also anyone who fails to punish when they are supposed to (the punishment of non-punishers). However, whenever such cooperative equilibria existed, there were also stable equilibria for full defection with no punishment.

Later work built on this by looking for ways to alleviate the need for the (arguably) implausible meta-punishing strategy. Let's consider four approaches. First, Henrich and Boyd (2001) demonstrate that if learners rely on a small amount of conformist transmission—an evolvable bias to copy the majority or plurality—in addition to pay-off biased imitation, stable cooperative equilibria can emerge without the need for meta-punishing strategies. Specifically, when a population has cooperators and punishers who only defect or fail to punish due to errors, the differences between the payoffs to behaving prosocially (cooperating or punishing) vs. free-riding (defecting or not punishing) declines geometrically as one moves from cooperation to the punishment of non-cooperators and further up the hierarchy of punishment (e.g., the punishment of those who fail to punish those who fail to punish non-cooperators). This means that even an arbitrarily small (but non-zero) amount of conformist transmission can stabilize punishment at some finite level in the hierarchy. Once punishing is stable at a higher level, this will then stabilize punishing strategies at lower levels and eventually cooperation. The upshot is that the combination of conformist transmission and punishing strategies generates multiple stable equilibria. Henrich and Boyd then argue that intergroup competition will favor the cooperative equilibrium over the defecting equilibria with lower average payoffs.

Second, Boyd et al. (2003) reveal the synergies between cooperation, punishment and intergroup competition. Intergroup competition can sustain punishing strategies (without the meta punishing assumption) and in turn, punishment sustains cooperation. Notably, Guzman et al. (2007) show that in the model explored by Boyd et al. selection will favor the emergence of conformist transmission alongside payoff-biased transmission—theoretically justifying Henrich and Boyd's assumption (although see Van Cleve 2016).

Finally, to offset the cost of diffuse or third party punishment, some cultural evolutionary models have considered games in which punishment could act as a signal of an otherwise hidden inclination toward

cooperativeness or trustworthiness (Gintis, Smith, and Bowles 2001; Jordan et al. 2016). Here, individuals signal their social-behavioral qualities by punishing non-cooperators (or any norm violator), which both sustains costly norms (including larger scale cooperation) and promotes beneficial future interactions for the signaler.

Finally, signals can be used to coordinate punishment and sustain cooperation. In this model, after a norm violation occurs punishers signal their intent to punish and then punish if enough others also signal their punitive intentions (Boyd, Gintis, and Bowles 2010). If too few individuals signal, punishers withhold their sanctions. By coordinating punishment and compelling defectors into cooperation, this system can guarantee that punishers tend to end up in cooperative groups, and when they don't, they can still avoid the costs of punishment.

Positive and negative indirect reciprocity

Large-scale cooperation can also be sustained by reputational systems, often termed *indirect reciprocity*, that tie different kinds of social interactions together via a shared roster of who is in good or bad standing. Notably, while standard versions of indirect reciprocity can sustain cooperation in dyads, these models don't readily extend to explain larger-scale cooperation (Boyd and Richerson 1989; Leimar and Hammerstein 2001). However, indirect reciprocity models do better when a two-person game is linked via reputation to the *n*-person interaction. In a classic model (Panchanathan and Boyd 2004), individuals experience two kinds of interactions: an *n*-person Prisoner's Dilemma and a dyadic mutual aid interaction. Individuals decide whether to help based on their partner's contribution to the public good (e.g., paying taxes). If a player defects in the public good, their partner can abstain from helping them in the dyadic interaction when they are in the role of 'donor' (without themselves getting a bad reputation for it). Essentially, the withdrawal of aid in the dyadic helping interaction, which benefits the person freed from the costs of helping, is used to sanction non-contributors to the public good.

Focusing on negative indirect reciprocity and motivated by ethnographic observations of village-level cooperation in the South Pacific (Henrich and Henrich 2014), Bhui et al. (2019) have constructed a model that links an *n*-person Prisoner's Dilemma with a dyadic exploitation game, where individuals have a chance to harm another individual for a benefit (e.g., theft). Strategies that only harm individuals with a bad reputation can sustain stable equilibria in which most individuals cooperate and don't harm others. Bad reputations are acquired by harming those with good reputations and by failing to cooperate in the *n*-person Prisoner's Dilemma. Ethnographic reports suggest this may be a common mechanism to sustain costly social norms in small-scale societies, where diffuse or third-party punishment are rare. The dynamics of this model could be described as "ostracism," potentially creating the "outlaw" situation in which individuals are no longer protected from exploitation by others.

Currently, many cultural evolutionists would argue that empirically different stabilizing mechanisms and combinations of these—signaling, punishment and reputation (indirect reciprocity)—are relevant in different societies and contexts. For example, some societies engage in diffuse or third-party punishment while others do not (Henrich et al. 2006), suggesting that the use of punishing strategies is itself culturally evolved. This is a significant step, since initially these were thought of as alternative hypotheses to explain human cooperation. This empirical inference is consistent with research that deploys economic games across societies—see below.

Castes, ethnic groups and honor cultures

Theorists have deployed a version of the battle of the sexes game, a simple coordination game and the hawk-dove game within a cultural evolutionary context to illuminate, respectively, the emergence of stratified social classes or castes, symbolically-marked ethnic groups and 'cultures of honor.'

Recurrently, across continents, social classes or castes have emerged in many societies, usually a few millennia after the origins of agriculture (but not always). To address this, Henrich and Boyd (2008) studied how economic interactions in a battle of the sexes payoff structure involving two 'cultural subpopulations' (the subpopulations are where learning occurs) might lead to stable equilibria in which members of one subpopulation generally played the high payoff strategy (and usually received the higher payoff) while members of the other subpopulation generally played the lower-payoff strategy. They also consider the impact of intergroup competition on the long-run equilibria. The results give the conditions that favor the emergence of social stratification, which depend on the surplus generated, the rate of adaptive change, and the degree of mixing between the cultural subpopulations. The analysis also suggests that intergroup competition will favor an equal division of the surplus—see Turchin (2009, 2010, 2015) for work exploring the tension between the forces created by elite extraction and intergroup competition (in economics, many models of political economy ignore intergroup competition entirely).

Across all regions of the globe, human societies form ethno-linguistic or tribal groupings. These groups are generally symbolically marked by different languages or dialects as well as markers of dress, adornment and greeting customs. Such markers have substantial impacts on who associates with whom in a variety of ways, including in marriage, trade and war, and they are generally associated with an array of stable and enduring social norms. To explain the origins of this common sociological pattern, McElreath et. al. (2003) studied the impact of interactions in a simple two-person coordination game among individuals in a structured population. Individuals learned strategies for interaction within their home subpopulation but then interacted either within their subpopulation or with members of other subpopulations. During cultural learning, individuals acquire both a marker trait (e.g., dialect) and social practice (e.g., pay dowry, not brideprice) based on their model's payoffs. The results show that chance variation in ethnic markers can be harnessed as a cue of unobservable norms (marking the strategies likely to be used in the coordination game). The cultural evolution process then (often) produces groups marked by observable traits (e.g., dialect) that are strong predictors of non-observable social norms, allowing individuals to avoid coordination failures. Economists and cultural evolutionists have teamed up to test this model by creating a laboratory simulation of the process (Efferson, Lalive, and Fehr 2008) that confirms the basic findings of the model.

In light of the pattern produced by cultural evolution, the authors consider if natural selection will favor a bias to both preferentially learn from, and interact with, those who share one's marker trait. When cultural evolution favors the emergence of marked groups that share norms (the behavior used in the coordination game), natural selection will favor a learning bias that cues off of symbolic markers, like language or dialect. Interestingly, later work confirmed the existence of the predicted psychological bias in young children and infants (Shutts, Banaji, and Spelke 2010; Kinzler, Corriveau, and Harris 2011; Kinzler, Shutts, and Spelke 2012)

In societies known for their 'culture of honor' men react aggressively to any threats to their independence and property (which they perceive as including their wives and daughters) and women

celebrate those traits in men. Anthropologists have long documented these societies ethnographically but psychologists didn't begin to systematically explore the behavioral consequences of honor cultures until the 1990s (Nisbett and Cohen 1996). Recently, economists have explored the impact of honor cultures on murder rates in the U.S. (Grosjean 2014) and on warfare in Africa (Moscona, Nunn, and Robinson 2017, 2020). To develop a theory for this common sociological phenomena, McElreath (2003) deployed a Hawk-Dove payoff structure to explore why, when and how cultural evolution might create cultures of honor. In this simple model, individuals from an infinite population are selected at random to interact in a HD payoff structure and this interaction repeats with a fixed probability. Individuals possess noisy information on the reputation or standing of their opponent/partner that they can use in choosing whether to fight or split a resource. The results highlight how the value of the resources, the quality of reputational information, and factors like the ecology and population size might influence when and where we see the motivations, norms and strategies associated with honor cultures. Recent work by economists (Cao et al. 2021) using newly available datasets confirm several of McElreath's predictions.

Endogenizing preferences and modeling culture

Both the formal machinery and empirical findings of cultural evolution strongly point to the importance of what economists call 'endogenizing preferences.' Of course, this is an old idea: Bowles (1998) lays out a vision for this by drawing heavily on cultural evolutionary theory, citing the foundational work I discuss above, and anticipates many subsequent developments in the social sciences, emphasizing the role of social norms, cultural transmission, conformist transmission, norm internalization and the impacts of markets on psychology (including on preferences) as well as cultural differences in personality (lately, a hot topic outside of economics). In a footnote, Bowles even anticipates cultural variation in the endowment effect based on market integration—a speculation later confirmed empirically by Apicella et al. (2014).

Today, when modeling culture or endogenizing preferences, economists frequently reference models by Bisin and Verdier (1998, 2000). Notably, however, Bisin and Verdier explicitly point out that they are building on the work of cultural evolutionists, generally citing the "seminal" work of Boyd and Richerson and Cavalli-Sforza and Feldman (Bisin and Verdier 2001: 301), but then depending on the paper, they also reference work by Bowles and Gintis within the domain of cultural evolution.

Picking up this line of work, Francois and Zobojnik (2005) endogenize preferences and explore the emergence of local social norms that influence the operation of formal institutions, leading to distinct and stable effects on welfare. Building on this, recent modeling efforts that integrate cultural evolution with existing approaches to political economy, rooted in strategic decision-making, have further enriched this integration by showing how preferences ("values") interlock and coevolve with formal institutions to create distinct cultural evolutionary trajectories and often substantial persistence (Besley and Persson 2019).

Empirical contributions related to game theory

Beginning in the 1990s, work in the nascent field of cultural evolution began an exchange with economics, particularly behavioral economics (although today, the strongest connections are with development economics, political economy and economic history). Tools drawn from behavioral economics were deployed to test theoretical ideas from cultural evolution and long-running collaborations began to enrich both fields. As the 21st century dawned, work drawing on this

collaboration began to be published in leading journals within economics (Fehr and Gächter 1998; Fehr and Gächter 2000; Henrich 2000; Henrich et al. 2001), although more commonly it found its way into general scientific journals like *Science* and *Nature* with much larger and broader impacts (Fehr and Gachter 2002; Boyd et al. 2003; Fehr and Fischbacher 2003a; Fehr and Rochenbach 2003; Henrich et al. 2005a; Silk et al. 2005; Bernhard, Fischbacher, and Fehr 2006; Bowles 2006; Henrich et al. 2006; Choi and Bowles 2007; Efferson, Lalive, and Fehr 2008). Interpreting the empirical results of behavioral game theoretical experiments, often conducted in diverse populations from around the world (including among both children and chimpanzees), these papers introduced and began to test numerous ideas and concepts developed theoretically in the modeling literature discussed above. This work immediately began to appear in textbook treatments of both behavioral economics and microeconomics (Camerer 2003; Bowles 2004).

There were three key empirical contributions that emerged initially from this interaction: (1) costly punishment as a potential mechanism to explain cooperation in humans, (2) the breath of behavioral variation across populations in game theoretic experiments like the Ultimatum Game (and others), and (3) the importance of endogenizing preferences given the variation in game play across societies and the existing empirical evidence that people can acquire preferences via observational learning.

Costly punishment

As noted, in 1992 Boyd and Richerson had modeled costly punishment as one mechanism for sustaining cooperation in an *n*-person Prisoner's Dilemma. Early experiments by Fehr and Gächter (2000, 2002) provided an important and powerful initial demonstration of the power of diffuse costly punishment in sustaining cooperation, at least in the laboratory. The evidence suggested that Swiss students were willing to pay costs to punish free-riders and this could increase cooperation under many conditions. In developing this work, and in considering what it might mean for economic and evolutionary thinking, Fehr and colleagues developed the concept of *strong reciprocity* (Gintis 2000; Fehr, Fischbacher, and Gächter 2002) and *Homo reciprocans* (Fehr and Gächter 1998; Bowles and Gintis 2002) as well as a number of new experiments to explore these concepts, including the Third-Party Punishment Game (Fehr and Fischbacher 2003b). These findings and formulations propelled a cottage industry of empirical work on social preferences but also immediately posed a theoretical question for those interested in evolution: why would people be willing to engage in this 'altruistic punishment'; where did this 'strong reciprocity' come from (Gintis 2000; Fehr and Henrich 2003; Bowles and Gintis 2004b, 2011)?

Culture matters

At the same time these ideas about costly punishment were developing, an interdisciplinary team of anthropologists, psychologists and economists began conducting behavioral experiments in diverse societies around the world (key economists included Bowles, Gintis, Fehr, Eckel and Camerer). Circling the globe from New Guinea and Indonesia to Tanzania and Siberia, the team conducted Ultimatum Games and other experiments among populations of hunter-gatherers, herders, slash-and-burn horticulturalists, sedentary farmers and urban dwellers. The first phase focused primarily on using the Ultimatum Game (Henrich et al. 2001b, 2004, 2005b) but a second project replicated and extended this prior project using the Dictator, Ultimatum (strategy method) and Third-Party Punishment Games (Henrich et al. 2006, 2010; Ensminger and Henrich 2014). In my experience, many economists are familiar with the first phase, published in the AER (Henrich et al. 2001a) and BBS (Henrich et al. 2005b), but not with the second phase, published in *Science* (Henrich et al. 2006, 2010).

These results highlighted three important empirical facts that drove subsequent research in a few areas:

(1) Substantial variation exists across human populations in how people play these games even when large stakes are used and great efforts ensure that people comprehend the instructions, payments, etc. My colleagues and I have made the case that this is because the experiments tap different social norms in different places (Henrich et al. 2005b). This work (1) inspired more such comparative projects (e.g., Herrmann, Thöni, and Gächter 2008; Lowes et al. 2017; Falk et al. 2018; Smith et al. 2018a; Valencia Caicedo 2018), both within economics and beyond, (2) motivated much work on culture and social norms within economics (e.g., Nunn 2009; Alesina and Giuliano 2015; Nunn and De La Sierra 2017), and (3) led to behavioral game experiments becoming a routine tool for both development economists and anthropologists (Tracer 2003; Gurven 2004; Cronk 2007; Voors et al. 2012; Cassar, Grosjean, and Whitt 2013; Bauer et al. 2014; Kosfeld and Rustagi 2015; Lightner and Hagen 2021).
(2) The canonical predictions from classical game theory (assuming folks are income maximizers, etc.) fail everywhere, but in different ways in different places. The main exception to this comes from work among chimpanzees, where the canonical predictions are strikingly accurate in many experiments (Silk et al. 2005; Jensen, Call, and Tomasello 2007a; b; Vonk et al. 2008). Since chimpanzees are smart but don't have social norms, this fits the interpretation offered by our team.
(3) Across both phases of this enterprise, a community's degree of market integration was associated with higher offers in our one-shot bargaining experiments—a fact consistent with the venerable *Doux Commerce* hypothesis. In the second phase, we also showed that participation in a world religion was associated with higher offers; and, with data on the prevalence of second- and third-party punishment, we found that small communities showed little willingness to engage in any sort of punishment. This motivated more empirical work, both within and outside of economics, on how market integration and religion might affect preferences or at least game behavior (Rustagi, Engel, and Kosfeld 2010; Siziba, Bulte, and Siziba 2012; Cecchi and Bulte 2013; Gurven et al. 2015; Kosfeld and Rustagi 2015; Purzycki et al. 2016; Lang et al. 2019; Baldassarri 2020; Lightner and Hagen 2021)

Intergroup competition selects among equilibria

Economists have contributed a few approaches that illuminate the role of intergroup competition. First, experimentalists have built on the tradition of putting groups into competition with each other within the laboratory context using behavioral experiments such as the public goods game (Bornstein and Erev 1994; Bornstein 2000). In one instructive experiment, Gürerk et al. (2006) created multiple groups who could select to play either a regular linear, repeated (finite), public goods game or one with peer punishment. After each round, players could choose to move to the other group. Most people made the wrong choice by selecting the group without punishment (little foresight). Cooperation levels immediately began to decline in the group without punishment and gradually everyone migrated to the group with punishment—a process captured by this cultural evolutionary model (Boyd and Richerson 2009). Punishment continued to sustain cooperation even as the reluctant migrants entered the group. Later such laboratory experiments have revealed how intergroup competition can endogenously generate cooperative institutions (Fehr and Williams 2018).

Complementing this laboratory work with natural experiments, Francois, Fujiwara and van Ypersele (2018) show the power of intergroup competition to drive up generalized trust. In their first study, they show how the deregulation of the U.S. banking sector, which began in different states at different times

for idiosyncratic reasons, increased competition among firms and gradually drove up trust levels (based on the 'trust question'). Second, using panel data from Germany, they showed that when people moved from less competitive to more competitive sectors of the economy, their trust levels increased while when they moved from more competitive to less competitive sectors, their trust levels declined (again, measured using the 'trust question'). Finally, working in the laboratory, they show how competition increases cooperative contributions in social dilemmas and that this can be measured using the trust question.

Finally, an emphasis on intergroup competition suggests that humans may be sensitive to conflict and violence in predictable ways. By studying post-conflict societies using both surveys and behavioral games, economists and cultural evolutionists have teamed up to show how the experience of conflict influences social behavior (Bellows and Miguel 2009; Blattman 2009; Blattman and Annan 2010; Cassar, Grosjean, and Whitt 2013; Bauer et al. 2014, see review in 2016) and religious commitments (Henrich et al. 2019). Bauer et al. suggest this has important implications for understanding the reconstruction of societies after long-running conflicts.

Conclusion

By providing a language for thinking systematically about different kinds of social interactions, tools from game theory have permitted substantial progress, both empirically and theoretically, in the new field of cultural evolution. These developments have both influenced, and been influenced by, a rich and ongoing interaction and exchange between economists and the cadre of anthropologists, evolutionary biologists and psychologists that have laid the foundations for a new and fully interdisciplinary approach to *Homo sapiens*.

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