

# Cooperation versus Competition

Martin A. Nowak and Karl Sigmund  
With an Introduction by Martin L. Leibowitz

## Introduction

This article is admittedly different from the standard *Financial Analysts Journal* fare, in that it does not directly focus on financial markets. It represents a new direction toward understanding the fundamental dynamics of market behavior—competition and cooperation among individuals who possess limited information—including conditions in which equilibrium can emerge from these dynamics. A new understanding of fundamental market dynamics may be an especially important goal these days, a time when the standard efficient market model has shown itself to be, at best, incomplete.

When this work was first presented by Martin Nowak at the Institute for Quantitative Research in Finance, it received high accolades.<sup>1</sup> Nowak is a leading academic theorist in the field of mathematical biology who has recently relocated from Oxford, United Kingdom, to Princeton, New Jersey, to create a new initiative in theoretical biology at Princeton's Institute for Advanced Study. His co-author of this piece, Karl Sigmund, is one of the founders of evolutionary game theory.

Game theory, the approach used in the article, allows analysts to study imperfect market situations characterized by small numbers of players, limited information, hidden actions, opportunities for adverse selection, or incomplete contracts. It also enables examination of nonmarket interactions, such as principal-agent relationships. Game theory has been applied by researchers to banking and other financial and regulatory situations in which a cooperative equilibrium appears (or fails to appear) through reciprocal interactions among participants. Nowak and Sigmund use dynamic, stochastic versions of the commonly used Prisoner's Dilemma game to analyze the evolution of cooperation and competition among large numbers of individuals.

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We hope this article can play a role in stimulating the financial community to consider new approaches that might lead to deeper conceptual knowledge of market behavior.

—Martin L. Leibowitz

## Cooperation versus Exploitation

The principle of give-and-take, or reciprocity, pervades human society. It is older than markets and trade. All members of a household are engaged in a ceaseless, mostly unconscious, bartering of services and goods. Economists have become increasingly fascinated by these exchanges—so have ethologists, who have documented many comparable instances in groups of chimpanzees and other primates. Charles Darwin himself was well aware of the role of reciprocity in human evolution. Writing in *The Descent of Man* (1871), he stressed that

the small strength and speed of man, his want of natural weapons etc. are more than counter-balanced by his . . . social qualities, which led him to *give and receive aid* from his fellow men [italics added].

Obviously, this Darwinian man is a far cry from the Hobbesian savage leading a life that is "solitary, poor, nasty, brutish, and short."<sup>2</sup> Nevertheless, a number of Darwin's early followers emphasized the ferocious aspects of the struggle for survival—to such an extent that the Russian prince Peter Kropotkin felt compelled to write a book to refute them.<sup>3</sup> In *Mutual Aid*, hailed by the *London Times* as "possibly the most important book of the year" (it was 1902), he drew a vast fresco of cooperation in action among Siberian herds, Polynesian savages, and medieval guilds. Kropotkin's claim to fame rests on his role as chief ideologue of anarchism, but his dabbling in natural history was no mere hobby: Someone bent on getting rid of the State needed to show that human cooperation was not imposed from top down by an iron-fisted authority but had origins rooted in Darwinian evolution.

In a way, this program of refutation has succeeded far beyond what Kropotkin could ever have foreseen. A wealth of studies in anthropology and primatology point to the overwhelming

role of reciprocal help in early hominid societies. Textbooks on animal behavior are filled with examples of mutual aid that range from grooming, feeding, teaching, and warning to helping in fights and joint hunting. In ecology, symbiotic associations are increasingly seen as fundamental. Biologists find examples of cooperation at the levels of cells, organelles (organ-like cell parts), and even molecules.

But at the same time, the ubiquity of cooperation seems to have become ever more paradoxical. The Russian anarchist failed to see how threatened cooperation is by exploitation. What prevents mutualists from turning into parasites? Why should anyone share in a common effort rather than cheat the others? Natural selection puts a premium on individual reproductive success. How can natural selection shape behavior that is "altruistic," in the sense that the behavior benefits others at the expense of one's own?

Researchers have explored two main approaches to this question—kin selection and reciprocal aid. They are not mutually exclusive, but they are sharply distinct.<sup>4</sup> Kin selection is rooted in genetics. If a gene helps promote the reproductive success of close relatives of its bearer, it helps promote copies of itself. Within a family, a good turn is, in this sense, its own reward. But a good turn to an unrelated fellow-being must be *returned* to pay off.

Reciprocal aid—defined as the trading of altruistic acts in which benefit is larger than cost, so that a net gain results—is essentially an economic principle. It works less directly than kin selection and is, therefore, more vulnerable to abuse. Two parties can strike a mutually profitable bargain, but each might gain still more by withholding his or her own contribution. In modern society, an enormous apparatus of law and order ensures that this temptation to cheat will remain, in general, resistible. But how can reciprocal altruism work in the absence of such authoritarian institutions, so despised by Kropotkin's anarchists?

To highlight the conundrum, in 1971, the U.S. sociobiologist Robert Trivers, now at Rutgers University (and, fittingly, a former lawyer), borrowed a metaphor from game theory that had been known since the early 1950s as "the Prisoner's Dilemma." (See also Trivers 1985.) It is an outrageously simple game. The two players have only to decide whether they wish to cooperate or not. If both cooperate, they receive a reward of 3 points each. If both defect (by not cooperating), they receive 1 point each. If one player defects and the other cooperates, then the defector receives 5 points whereas the player who opted to cooperate receives 0 points.

Will you cooperate? If the other player defects, you will end up with nothing. In that case, clearly, you ought to have defected. In fact, even if the other player cooperates, you should have defected because doing so would have given you 5 points instead of only 3. No matter what the other player does, your best option is to defect. So, you defect. But the other player, who is in exactly the same position, will also defect. Hence, both players will receive only 1 point each. Why didn't they cooperate?

This "game" encapsulates a conflict between what is best from an individual's point of view and what is best from a collective's point of view. This conflict endangers almost every form of cooperation, including trade and mutual aid. Forget about the points. Just remember that the "reward" for mutual cooperation is higher than the "punishment" for mutual defection, but a one-sided defection yields—as "temptation"—somewhat more than the reward for cooperation, which leaves the exploited cooperator with a "sucker's payoff" that is even lower than the punishment points. This rank ordering of the payoff values—from temptation (5) via reward (3) and punishment (1) down to the sucker's payoff (0)—implies that your best move is to defect, irrespective of the co-player's move—a conclusion that leads inexorably to mutual defection.

Most people feel uneasy with this conclusion. In experiments, people often do, in fact, cooperate—their motivations being feelings of solidarity or selflessness. And in real business life, defection is relatively rare, thanks partly to the pressure of society. But forget for the moment all social or emotional aspects and view the game not in the context of foresight and rationality but in a strictly Darwinian setting, where every form of payoff—be it calories, mates, or safety from predators—is ultimately converted into a single currency: offspring.

Let us perform a thought experiment and consider an entire population consisting of preprogrammed players—mere automata. Each automaton is firmly wedded to one strategy and will either always cooperate or always defect. The automata engage in a round-robin tournament: Each one is matched against every other one for one round of the Prisoner's Dilemma. During the tournament, the automata pile up points. For each automaton, the total payoff depends on the co-players encountered and, therefore, on the composition of the population, but a defector will always earn more than a cooperator. At the end, the automata reproduce by turning their accumulated points into automata of their own kind—defectors or cooperators—which make up the next generation. This second generation's members will engage in a round-robin

tournament and get paid in offspring, and so on through the generations. In this caricature of a biological setup, where the payoff is number of offspring and strategies are inherited, the outcome is obvious: Defectors will steadily increase in frequency from one generation to the next and eventually swamp the population.

## Direct Reciprocity

Among the several ways to escape from the Prisoner's Dilemma, the most obvious one is simply to repeat the game. In many societies, the same two individuals interact not once but frequently. A person will think twice about defecting if it makes her or his co-player decide to defect on the next occasion *and if such an occasion is likely to occur*. Assume that there is a fixed probability that the game will be repeated for more rounds. For instance, assume the probability is 95 percent that the game will last, on average, for 20 rounds. But you cannot know in advance when it will stop. A strategy for such a repeated game is a program telling the player what to do in each round. It may depend on what happened in the previous rounds but cannot depend, of course, on the future.

In contrast to the one-round Prisoner's Dilemma, where only two options exist and the option to defect is always better than the option to cooperate, countless strategies exist for the *repeated* Prisoner's Dilemma, and none serves as a best response to all comers in the rounds. For instance, if your co-player decides to always cooperate, you will do best by always defecting. If your co-player decides to cooperate until you defect and then never cooperate again, you will be careful not to spoil your partnership: The temptation to cheat in one round and grab 5 points instead of 3 will be more than offset by the expected loss in the subsequent rounds, where you cannot hope to earn more than 1 point.

No hard-and-fast recipe exists for playing the repeated Prisoner's Dilemma. Success depends on the other player's strategy, which one does not know beforehand. A strategy that does well in certain environments can miserably fail in others. This absence of a best strategy in the repeated Prisoner's Dilemma is crucial to understanding the evolution of cooperation in society.

In the late 1970s, political scientist Robert Axelrod at the University of Michigan ran a contest in which the "contestants" were programs submitted by scientists containing round-robin tournaments for the repeated Prisoner's Dilemma (see Axelrod and Hamilton 1981). Axelrod ran these entries on his computer, and the winner was to be the strategy

that received the highest number of points after having played all other strategies. In principle, the complexity of a program had no upper bound, and some of the entries were fairly sophisticated. But in the end, the simplest entry won: It was a program called "Tit for Tat," which starts with a cooperative move and then always repeats the co-player's previous move. Remarkably, a TFT player, being never the first to defect and ready to follow suit as soon as the co-player switches back to cooperation, is never ahead at any stage of the repeated game. Nevertheless, a player can win the whole tournament, because the Prisoner's Dilemma is not a zero-sum game: One can make points without taking them away from others. Because of its transparency, the TFT rule frequently persuades co-players that it pays to cooperate. In the Axelrod tournaments, the TFT strategy, which had been entered by the well-known game theorist Anatol Rapoport, elicited many rewarding rounds of cooperation fairly shared with co-players, whereas these co-players among themselves were apt to get bogged down in long runs of defection.

By "winning" the round-robin tournament, TFT obtained more representatives among the next generation than did other strategies. Moreover, those programs that had cooperated with TFT tended to receive more offspring than those that had not. Therefore, the composition of the population turned still more in favor of TFT. From generation to generation, TFT shaped a more congenial environment. This outcome is quite in contrast to the fate of those strategies that ruthlessly exploited suckers and thus depleted their own resources. In Axelrod's simulations, evolution led to the establishment of a bevy of strategies that all cooperated with each other. Furthermore, clusters of TFT players could invade populations of "always defect" players and thus promote cooperation.

How general are Axelrod's simulations? Three objections come to mind. First, the entries making up the initial population were probably a good sample of expert opinion on how to play the repeated Prisoner's Dilemma but not necessarily typical for strategies likely to occur in biological communities. Second, such evolutionary chronicles ought to be provided with a steady trickle of mutations exploring the strategy space. Third, errors and uncertainties are bound to occur in true biological interactions. Only in cyberspace can a program be expected to run flawlessly. In real life, decisions are beset by mistakes in understanding and execution. Think how easy it is to spoil good feelings by heedlessly "dropping a brick" or how common to vent one's frustration upon an innocent bystander.

Indeed, the interaction of two TFT players is particularly vulnerable to errors. One inadvertent defection starts a run of alternating defections. The average payoff per round then drops drastically. Obviously, the TFT players ought to forgive occasionally—not in a predictable pattern, which would make them exploitable, but on a random basis.

This idea suggests that stochastic strategies that cooperate only with certain probabilities would be more vulnerable to error than pure TFT. Stochastic strategies would capture something of the fuzziness of real life, where individuals do not generally obey clear-cut rules but are affected by countless unpredictable factors leading not to hard-and-fast rules but only to certain *propensities* to act this way or that. One approach to such a lifelike game is to assume that these propensities depend on the co-player's previous move, which produces strategies governed by (1) the probability to cooperate after a *cooperative* move by the opponent or (2) the probability to cooperate after an opponent's *defection*. For example, for a strategy that always defects (which we will call "All-D"), these probabilities are both equal to 0. For a strategy that always cooperates (which we will call "All-C"), both probabilities are equal to 1. TFT cooperates with (almost) 100 percent probability after a cooperative move of the co-player and with 0 percent probability after a defection.

Of course, these probabilities hold if the strategies are faultlessly executed. But an error rate of 1 percent changes the propensities to cooperate—in TFT's case, for instance, to 99 percent after a friendly, cooperative move and to 1 percent after an unfriendly move by the co-player. Therefore, in the following approach, we assume that nobody is perfect and we allow only for probability values that are distinct from zero and 100 percent.

Choose at random 100 strategies, each given by a pair of probabilities.<sup>5</sup> In the beginning population, all these strategies are equally frequent. The players now engage in a round-robin tournament, each playing one repeated Prisoner's Dilemma against each other member of the population. Then, players reproduce. Their number of offspring is proportional to their accumulated payoff. The offspring inherit the parents' strategies and promptly engage in the next tournament.

Those strategies closest to All-D, which are thus least likely to cooperate, will immediately take the lead. They thrive by exploiting those players with a high propensity to cooperate after having been cheated in the previous round (the suckers). A hundred or so generations later, these suckers will have vanished from the population. Almost

every interaction now reduces to a mutual defection. This outcome is usually the final outcome of a computer simulation. The exception is those cases in which the initial sample contained a strategy very close to TFT. In these runs, the initial phase of the evolution looks precisely the same as in the All-D versus suckers evolution. Because TFT-like players do not cheat on suckers, they will do much less well than the inveterate defectors do at first. Once the suckers are disposed of, however, the game changes. The population now consists mostly of defectors relentlessly engaged in punishing each other. In their encounters with TFT players, they have an edge on them, but the edge is extremely slight because TFT players, unlike suckers, retaliate. And when two TFT players meet, they do considerably better than two defectors—in spite of occasional misunderstandings. As a result, the embattled minority of TFT-like players grows—slowly at first but with gathering momentum. Their advantage increases with each added member—quite a contrast to the fate of exploiters, who harm each other's cause. Now, the tide of defectors begins to wane. But the computer simulations show that the TFT-like strategy, whose stern retaliatory action caused this reversal of fortune, will not be the ultimate beneficiary. After eliminating the nasties and thus fulfilling its mission, TFT eliminates itself. Its very strictness, so salutary for the community, harms its own offspring. It is superseded by a much more forgiving variant: Generous Tit for Tat.

For the given payoff values, Generous TFT cooperates with 100 percent probability after a cooperative move and with 33 percent probability after a defection of a co-player.<sup>6</sup> This strategy never starts defecting except by mistake, but it is quite willing to start cooperating by extending an olive branch one out of three times.<sup>7</sup> The strategy that finally becomes established in the computer simulations will be that strategy of the original sample that is closest to Generous TFT. But—and this observation is essential—Generous TFT cannot win on its own. It needs a strategy as stern as TFT to catalyze the turn away from defection.

Next, we performed computer simulations with an extended set of strategies that based their next move on the outcome of the previous round (not the opponent's previous move but the two moves together). In these simulations, each round had the four possible outcomes—0, 1, 3, and 5 and players needed only to know their payoff to know what had happened. For example, if you gained 5 points, you knew that your co-player had cooperated while you had defected. A strategy based on the outcome of a previous round must tell a player what to do in each eventuality. Then, if stochastic

strategies are allowed again, which would mean players would respond to the four possible outcomes by smaller or greater *propensities* to cooperate, a huge array of possibilities would exist, which would be difficult to sample in a representative way. However, the job can be left to evolutionary simulations by the addition in every hundredth generation of some small amount of a new randomly selected stochastic strategy. Eventually, these mutations will cover a substantial part of the possible strategies.

In our recent simulations, we followed many such mutation-selection chronicles for millions of generations—not because we think that the emergence of cooperation needed such a huge time span (in the case of human evolution, it would take us to way before the Jurassic) but because this approach allowed statistically meaningful conclusions based on testing 100,000 mutations in each run.

In spite of the rich diversity displayed in these chronicles, they led to some simple, clear results. First, the average payoff in the population was a showpiece for *punctuated equilibrium*. Most of the time, either almost all members of the population cooperated or almost all defected. The transitions between these two regimes were usually rare and abrupt; transitions took only a few generations, whereas periods of quiescence frequently endured for millions of generations. Second, the later in the run the transition occurred, the longer it tended to last. Third, a definite trend toward cooperation was apparent. In these simulations, the longer we waited, the greater was the likelihood for a cooperative regime. But, fourth, the threat of a sudden collapse always remained.

Among cooperative populations, Generous TFT is sometimes the dominant strategy, but much more frequently, an altogether different strategy, the Pavlov strategy, dominates.<sup>8</sup> A Pavlov player cooperates after experiencing a reward or a punishment and never otherwise. After experiencing a reward for mutual cooperation (3 points each), the two players repeat the former cooperative move; after being punished for mutual defection (1 point each), they both switch to cooperation; after getting away with a unilateral defection (5 points), a player repeats the defecting move; and after being subject to the sucker's payoff for unilaterally cooperating (0 points), a player reacts by defecting. At first, this rule may seem odd: It tells you to defect if your co-player's move was different from your move in the previous round. A second glance reveals that the rule makes sense: The Pavlov rule tells you to stick to your former move if it earned you a high payoff but change your behavior if it brought you a low return.

This learning rule of win-stay, lose-shift seems to be widespread, and it works well in many other contexts. In animal psychology, for example, it is considered to be an elementary principle: One expects a rat's readiness to repeat an action to increase with the size of the reward, and one expects the rat to drop behavior that had painful consequences. The same crude principle of carrot and stick underlies most attempts to bring up children.

In the repeated Prisoner's Dilemma game, retaliation after one has been exploited is usually seen as evidence of TFT-like behavior, but it could as well be evidence of Pavlovian behavior. A society of Pavlov players is very resistant to errors. A mistaken defection between two of its members leads to one round of mutual defection and then back to cooperation. Faced with a milksop who does not retaliate, a Pavlov player will keep defecting, which makes it difficult for players who always cooperate to gain a foothold in the community. The policy in a Generous TFT society to not discriminate against suckers is a costly policy in the long run because players who do not retaliate can drift into the population and ultimately undermine cooperation by allowing exploiters to cash in.

Although Pavlov is a good strategy to prevent exploiters from invading a cooperative society, it fares poorly in a society of noncooperators. Against All-D, for instance, a Pavlovian will try every second round to resume cooperation. In the environment of Axelrod's tournaments, Pavlov would have ended close to the bottom of the competition. Pavlov's advantages show only after sterner, unyielding strategies such as TFT have paved the ground by twisting evolution away from defection. Even then, Pavlov can often be improved by a variant that is more wary of resuming cooperation after a round of mutual defection and does so only with a certain probability, which depends on the precise payoff values and the expected interaction length.

Again, how general are these results? So far, we have considered strategies based on remembering only the last round. Kristian Lindgren (1991) from Göteborg University has analyzed evolutionary chronicles among players with a longer memory. His conclusions are quite similar to the ones for one-round memory: Depending on the payoff values chosen, the eventual outcome will either be a Pavlov strategy or a strategy that resumes cooperation after *two* rounds of mutual defection. The domestic quarrel following a misunderstanding lasts a little longer in this case, but that is all. Such strategies share with Pavlov the two properties of being error correcting and sucker exploiting: An inadvertent defection between two long-memory

players is quickly redressed, but a co-player who does not retaliate is relentlessly exploited.

Therefore, we may safely conclude that the emergence and persistence of cooperative behavior is not at all unlikely, provided the players meet repeatedly, recognize each other, and remember the outcomes of past encounters (so that they can implement strategies that retaliate for defections in previous meetings). This set of restrictive circumstances should seem reasonable enough to the reader—familiar, indeed, from daily life in the home or office—but among the larger world of living things, it demands a fair degree of sophistication. For instance, a substantial region of the human brain is devoted to the task of recognizing faces, but cooperation even among simple organisms that are unlikely to possess such ability has been observed. Furthermore, the strategies discussed will work only if payoffs from future encounters are not discounted too much. Again, this phenomenon may be reasonable for many of the games humans play, but for many simpler organisms, payoffs in the form of future reproductive success are liable to be heavily discounted; if life is short and unpredictable, little evolutionary pressure exists to make long-term investments.

All these restrictions add up to the expectation that cooperation will indeed appear and persist among humans and other social animals who have the neurological apparatus required for recognizing and remembering and who play their games in settings where future rewards are not too heavily discounted. Indeed, in recent years, a variety of field observations and laboratory experiments have been reported that were intended to show that strategies are used by primates other than ourselves (and bats, and stickleback fish, and so on). Not surprisingly, given the inherent complexity of the overall situations, none of these studies—although suggestive—provides conclusive evidence that reciprocal altruism is occurring in these populations.

But what of the many simpler organisms that seem to exhibit forms of reciprocal cooperation yet clearly do not possess the attributes—recognizing fellow players, recalling past actions, and so on—that are vital to the success of the strategies discussed so far? Even for sophisticated animals, one can question whether the kind of analysis required by the strategies really applies to all circumstances in which cooperation is seen but kin selection cannot explain it. Is there another road?

## **Spatial Reciprocity**

One possible alternative explanation of the genesis of cooperation is that, in effect, players grab a set of

co-players and make sure future rounds are played with these individuals and no others. In general, this approach will be hard, but in one circumstance, it is not only easy but even automatic. If the players occupy fixed sites in some two-dimensional arena and if they interact only with close neighbors, then they will have no need to recognize and remember players because the players are fixed by the spatial geometry. On the one hand, interactions within such spatially static circumstances reduce any uncertainty about whom one will interact with. On the other hand, it severely curtails the number of possible partners.

So far, the games examined assumed that everyone interacts with everyone else or at least (and this amounts to the same thing) with a representative sample of the entire population. We now look at scenarios in which every player interacts with only a few neighbors.

Studies of "spatial games" are very recent. They give an altogether new twist to the Prisoner's Dilemma. They also can give rise to spatial patterns of extraordinary beauty and complexity.

Not surprisingly, cooperation is greater in a sedentary than in a mobile population. Defectors can thrive in an anonymous crowd, but mutual aid is frequent between neighbors. Exploitation is good only if you can get away with it, and someone who is stuck in one place cannot get away with it and must face reprisals. This barrier to exploitation is obvious enough. But in many cases, territorially structured interactions actually also promote cooperation even if no follow-up encounter is expected. A limited neighborhood makes cooperation a viable option—even for the seemingly hopeless single-shot Prisoner's Dilemma.

Consider a spatial version of the tournament with each member of the population sitting on a square of an extended chessboard. Each player is either a pure cooperator or a pure defector (no strategic niceties here). Each interacts only with the eight immediate neighbors, playing one round of the Prisoner's Dilemma with each. In the next generation, the square is inherited by whoever garnered the most points—neighbor or previous owner.

A lone cooperator will obviously be exploited by the surrounding defectors and succumb. But four cooperators in a block can conceivably hold their own, because each interacts with three cooperators whereas a defector, as an outsider, can reach and exploit two at most. If the bonus for cheating is not large, clusters of cooperators will grow. Lone defectors will always do well, however, because they will be surrounded by exploitable cooperators. But by spreading, such nasties eventually sur-

round themselves with their like and diminish their own returns.

The actual evolution of such spatial systems depends on the payoff values. Cooperators can certainly be wiped off the board, but we have frequently found regularly or irregularly shifting mosaics, with both cooperator and defector strategies being maintained. Mixtures of pure cooperators and pure defectors can coexist indefinitely in proportions that fluctuate about predictable long-term averages. This result is remarkably robust. In its essentials, it holds true for other choices of spatial lattices and neighbors (such as the four orthogonal neighbors in a square, a chessboard array, or the six nearest neighbors in a hexagonal lattice) and even for spatially irregular or random arrays; the important requirement is that a player not interact with too many neighbors.

We found the results to hold also if we relaxed the deterministic rule that the neighbor with the highest score necessarily wins (if we allowed for a degree of uncertainty in the outcome but kept the bias toward higher scores) or if, instead of updating the entire population in one step (at the end of the breeding season, perhaps), we picked sites at random and updated them one at a time. The outcome in all cases was frequently an endlessly milling spatio-temporal chaos, with clusters expanding, colliding, and fragmenting and with both nice guys and nasties persisting.

Suppose we assume that generations are synchronized, that winning is always determined by the largest score, and that the spatial array is some symmetrical lattice. Then, if we begin with a symmetrical initial configuration—which, of course, is biologically unrealistic—we find fantastic kaleidoscopes of gorgeous patterns that are suggestive of Persian carpets.

Generally, the simple rules of these spatial games define dynamics of dazzling complexity. They allow for “gliders” (patterns that wander across the board and periodically resume their former shape) and display other motifs that grow without limit and exhibit self-similar details on many scales.<sup>9</sup> Some of these features invite comparison with John Horton Conway’s Game of Life and other cellular automata, but with several interesting differences.<sup>10</sup> For one thing, in the spatial version of the Prisoner’s Dilemma (and in other spatial evolutionary games), the fate of a given site or cell depends on its neighbors’ scores—which in turn, depend on their neighbors’ scores—so the neighbors’ neighbors need to be specified. Thus, if the Prisoner’s Dilemma spatial games were expressed in the idiom of cellular automata, the transition rule for any 1 cell in, for example, the 8-neighbor case

would involve specifying the states of 25 cells. That is, the spatial version of the Prisoner’s Dilemma appears to be complicated if it is viewed as being played by conventional cellular automata. The underlying rules of the spatial games are simple and biologically motivated, however, in contrast to the Game of Life and other games of cellular automata, whose seemingly simple rules were constructed arbitrarily, after much trial and error, to generate interesting dynamics.

In short, the Prisoner’s Dilemma spatial games differ from other cellular automata games in that the rules of such games derive from already existing biological problems, but the Prisoner’s Dilemma spatial games share with these other systems the feature of having complicated dynamics. The dynamics unfolded by any one of the spatial versions of the Prisoner’s Dilemma—be they irregular patterns or symmetrical Persian carpets—may well be, in principle, unpredictable or “chaotic,” in the sense that no algorithm can possibly tell us in advance what will occur. We can only watch the arabesques unfold.

An essential outcome of such spatial structures is, in effect, the protection of diversity. These structures allow cooperators and defectors to exist side by side. In a different but related context, similar spatial structures allow populations of hosts and parasites, or prey and predators, to persist together despite the inherent instability of their interactions.

Such complex spatial structures, self-generated from simple rules, may be relevant to the dynamics of a wide variety of spatially extended systems. For example, researchers increasingly believe that many of the chemical reactions that were crucial in prebiotic evolution (evolution before the emergence of living beings) took place on surfaces rather than in well-stirred solutions. Catalyzing the replication of a molecule is a form of aid; a chain of catalysts, with each link feeding back on itself, would be the earliest instance of mutual aid. In this sense, cooperation could be older than life itself. Such cooperative chains or “hyper cycles” are always vulnerable to “cheating” molecular mutants, however, who take more catalytic aid than they give. These difficulties were thought to undercut all ideas about prebiotic evolution being based on such cooperative chains of chemical reactions, but Maarten Boerlijst and Paulien Hogeweg (1991a, 1991b) of Utrecht University have recently demonstrated by computer simulations that self-generated spatial structures akin to those just discussed can hamper the spread of cheating parasitic molecules and thus revive the possibility that life began with cooperation.

## Indirect Reciprocity

The idea of reciprocal altruism was introduced by Trivers (1971): A donor may help a recipient if the recipient is likely to subsequently return the favor. In his seminal paper, Trivers mentioned the possibility of "generalized altruism," in which the return is directed toward a third party:

Individuals . . . may respond to an altruistic act that benefits themselves by acting altruistically toward a third individual uninvolved in the initial interaction. . . . In a system of strong multiparty interactions it is possible that in some situations individuals are selected to demonstrate generalized altruistic tendencies.

Trivers stressed this possibility further in his book *Social Evolution* (1985), where he speculated that a sense of justice may evolve

in species such as ours in which a system of multi-party altruism may operate such that an individual does not necessarily receive reciprocal benefit from the individual aided but may receive the return from third parties.

Richard Alexander in his 1987 article greatly extended this idea and coined the term "indirect reciprocity" for the situation in which one does not expect a return from the recipient but from someone else. Cooperation is thereby channeled toward the cooperative members of the community. A donor provides help if the recipient is likely to help others, which is usually decided on the basis of experience (i.e., according to whether the potential recipient has helped others in the past). According to Alexander, indirect reciprocity, which "involves reputation and status, and results in everyone in the group continually being assessed and reassessed," plays an essential role in human societies. Alexander argued (convincingly, to our mind) that systems of indirect reciprocity are the basis of moral systems.

The principles of direct reciprocity are usually studied by means of repeated games (such as the Prisoner's Dilemma) between the same two players. To study indirect reciprocity, researchers can investigate situations in which the players engage in several rounds of the game but with a negligible probability of ever encountering the same co-player again. This scenario is, of course, an idealization; in human communities, both direct and indirect reciprocity occur together. In fact, Alexander stressed that "indirect reciprocity is a consequence of direct reciprocity occurring in the presence of others." But to understand the mechanism of indirect reciprocity, we eliminated direct reciprocity from the models.

In Nowak and Sigmund (1998), we analyzed populations of individuals having the option of helping one another or not as follows: Denote the

benefit of the altruistic act to the recipient by  $b$ , the cost to the donor by  $c$ , and assume that  $c < b$ . If the donor decides not to help, both individuals receive zero payoff. The payoff is measured in terms of "incremental fitness," as follows.

At birth, each player—potential donor or recipient—has an image score,  $s$ , and an initial score of 0. The score of a potential donor increases by one unit if he or she performs the altruistic act; if not, it decreases by one unit. The image score of a recipient in this exchange does not change. We consider here strategies in which donors decide to help according to the image scores of potential recipients (garnered from their times as donors). A strategy is given by an integer  $k$ : A player with this strategy provides help if and only if the image score of the potential recipient is at least  $k$ . Players who provide help must pay some cost, but they increase their score and are thus more likely to receive help in the future. During their lifetime, individuals undergo several rounds of this interaction, either as donors or as recipients, but the possibility of meeting the same co-player again will be neglected. At the end of each generation, individuals leave offspring in proportion to their accumulated payoff, and the offspring inherit the strategy of their parent.

In extensive computer simulations, we showed that even for a small number of rounds per generation, a cooperative regime based on indirect reciprocity can be stable. If one allows for mutations, then long-term cycling becomes likely. That is, cooperative populations based on discrimination according to the score of the recipient are undermined by indiscriminate altruists. Then, unconditional defectors invade—until discriminating cooperators cycle back in.

We also extended the model under a restriction that individuals could witness only a fraction of the interactions in their community and, therefore, had incomplete information about their co-player's score. The findings from the unrestricted model held. Furthermore, in our 1998 paper, we presented results from analytical investigations showing that the probability,  $q$ , that a player knows the score of another player must exceed  $c/b$  if indirect reciprocity is to work. This result is an intriguing parallel to Hamilton's Rule, the cornerstone of the kin-selection approach to altruism (see Hamilton 1996). Hamilton's Rule states that the coefficient of relatedness must exceed the cost to the donor divided by the benefit of the altruistic act to the recipient ( $c/b$ ). In this sense, indirect reciprocity differs from kin selection in replacing relatedness with acquaintanceship. If the average number of rounds per lifetime exceeds  $(bq + c)/(bq - c)$ , then cooperation based on score discrimination is evolutionarily stable.



## Final Remarks

Throughout the evolutionary history of life, "cooperation" among smaller units led to the emergence of more-complex structures (as, for example, in the emergence of multicellular organisms). In this sense, cooperation is as essential for evolution as natural selection: Cooperation generates more-complex structures, whereas natural selection chooses which of these can survive.

The turns and twists of the billion-year-old tug of war between cooperation and its bane, exploitation, have grown so complex that to expect any real-life examples to be mirrored faithfully by a simple model would be unreasonable. We have discussed two broad classes of models: Those in which individuals have strategies that encourage cooperation

and retaliate against defection based on repeated interactions, recognition of players, and remembering past encounters and those in which cooperation persists by virtue of self-organized spatial structures generated by interactions with immediate neighbors in some fixed spatial array. Both kinds of models shed oblique light on how cooperation might arise and be maintained in real-world situations.

Computer simulations of the Prisoner's Dilemma are an inescapable approach for understanding the evolution of mutual help in a Darwinian world. But in its pure forms, the Prisoner's Dilemma game is as unlikely to be found on earth as, say, frictionless motion. Like frictionless motion, however, it ought to have a place in our learning.

## Notes

1. This article was presented to the Autumn 1999 (October 17–20) meeting of the Institute for Quantitative Research in Finance (the Q Group) under the title "The Evolution of Cooperation: Direct, Indirect, and Spatial Reciprocity."
2. Thomas Hobbes, *Leviathan* (1651).
3. *Mutual Aid: A Factor of Evolution* (1902).
4. See Hamilton (1996).
5. We also choose a first move, but it plays no great role if the game is repeated often enough for mistakes to occur, because then, the initial phase will contribute little to the overall payoff.
6. This precise percentage, 33 percent, depends on the numerical details of the specified 5, 3, 1, 0 payoff scheme, but the essential outcome holds very generally.
7. Computer simulations show that a higher level of forgiveness would make the population too exploitable and a lower level would make it too vulnerable to backbiting caused by errors.
8. The name comes from the mathematicians David Kraines and Vivian Kraines of Duke University.
9. In this context, self-similarity means that patterns look similar on different spatial scales.
10. An excellent description of the Game of Life is given in *The Recursive Universe* by William Poundston (1985).

## References and Readings

- Alexander, R.D. 1979. *Darwinism and Human Affairs*. Seattle, WA: University of Washington Press.
- . 1987. *The Biology of Moral Systems*. New York: Aldine de Gruyter.
- Axelrod, R. 1990. *The Evolution of Cooperation*. London; New York: Penguin Books.
- Axelrod, R., and D. Dion. 1988. "The Further Evolution of Cooperation." *Science*, vol. 242:1385–90.
- Axelrod, R., and W.D. Hamilton. 1981. "The Evolution of Cooperation." *Science*, vol. 211:1390–96.
- Boerlijst, M., and P. Hogeweg. 1991a. "Self-Structuring and Selection." In *Artificial Life II*. Edited by C.G. Langton, Charles Taylor, J. Doyne Farmer, and Steen Rasmussen. Redwood City, CA: Addison-Wesley.
- . 1991b. "Spiral Wave Structure in Prebiotic Evolution: Hypercycles Stable against Parasites." *Physica*, vol. D48:17.
- Boyd, R., and P.J. Richerson. 1989. "The Evolution of Indirect Reciprocity." *Social Networks*, vol. 11:213–236.
- Dugatkin, L.A., M. Mesterton-Gibbons, and A.I. Houston. 1992. "Beyond the Prisoner's Dilemma: Towards Models to Discriminate among Mechanisms of Cooperation in Nature." *Trends in Ecology & Evolution*, vol. 7:202–205.
- Eigen, M., and P. Schuster. 1979. *The Hypercycle: A Principle of Natural Self-Organization*. Berlin: Springer.
- Hamilton, W.D. 1996. *Narrow Roads of Gene Land: The Collected Papers of W.D. Hamilton*. Vol. 1: "Evolution of Social Behavior." Oxford, U.K.: W.H. Freeman.
- Hofbauer, J., and K. Sigmund. 1998. *Evolutionary Games and Population Dynamics*. Cambridge, U.K.: Cambridge University Press.
- Lindgren, K. 1991. "Evolutionary Phenomena in Simple Dynamics." In *Artificial Life II*. Edited by C.G. Langton, Charles Taylor, J. Doyne Farmer, and Steen Rasmussen. Redwood City, CA: Addison-Wesley.
- May, R.M. 1987. "More Evolution of Cooperation." *Nature*, vol. 327:15–17.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge, U.K.: Cambridge University Press.
- Nowak, M.A., and R.M. May. 1992. "Evolutionary Games and Spatial Chaos." *Nature*, vol. 359:826–829.

- Nowak, M.A., and K. Sigmund. 1992. "TFT in Heterogeneous Populations." *Nature*, vol. 355:250–252.
- . 1993. "Win-Stay, Lose-Shift Outperforms Tit-for-Tat." *Nature*, vol. 364:56–58.
- . 1998. "Evolution of Indirect Reciprocity by Image Scoring." *Nature*, vol. 393:573–577.
- Pollock, G.B., and L.A. Dugatkin. 1992. "Reciprocity and the Evolution of Reputation." *Journal of Theoretical Biology*, vol. 159:25–37.
- Poundston, W. 1985. *The Recursive Universe*. Oxford, U.K.: Oxford University Press.
- Sigmund, K. 1995. *Games of Life*. Oxford, U.K.: Penguin.
- Sugden, R. 1986. *The Evolution of Rights, Co-Operation and Welfare*. Oxford, U.K.: Blackwell.
- Trivers, R. 1971. "The Evolution of Reciprocal Altruism." *Quarterly Review of Biology*, vol. 46:35–57.
- . 1985. *Social Evolution*. Menlo Park, CA: Benjamin/Cummings.
- Weibull, J.W. 1995. *Evolutionary Game Theory*. Cambridge, MA: MIT Press.
- Wilson, D.S., and E. Sober. 1994. "Re-Introducing Group Selection to Human Behavioural Sciences." *Behavioural and Brain Sciences*, vol. 17:585–654.
- Zeeman, E.C. 1980. "Population Dynamics from Game Theory." In *Global Theory of Dynamical Systems*. Lecture Notes in Mathematics, vol. 819. Berlin: Springer:472–497.