

Game Theory Analysis: Evolutionary Spatial Cooperation

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Abstract

Game theory analysis has been extensively applied in study of evolutionary cooperation where Prisoner's Dilemma proved a fascinating insight. An alternative interpretation of Prisoner's Dilemma is a pair of altruist donations. With the simple donating mechanism explained through kin selection, I compared spatial cooperation to temporal cooperation and analyzed two agent-based simulation studies. The first study added the deterministic spatial chaos model of Nowak and May (1992) with two stochastic parameters to uncover the role of group concurrency in the spatial cooperation. The second study extended the stochastic Ethnocentrism model of Hammond and Axelrod (2006a & 2006b) and discovered that kin selection beat reciprocal cooperation in that special evolutionary circumstance.

Literature Review

Evolutionary game theory and the temporal cooperation

J. von Neumann invented the modern game theory framework. He used a matrix with elements $\{p_{i,j}\}$ to describe the quantitative payoff of strategy i played by the opponent j ¹. Prisoner Dilemma is the classic game theory model for cooperation (Axelrod, 1980a, 1980b; Axelrod & Hamilton, 1981). Conventionally, D denotes the defective strategy, while

¹The general concept of game includes more than two partners with a higher dimensional payoff matrix. The condition of two partners is just a default case (von Neumann & Morgenstern, 1944).

C denotes the cooperative strategy. T (Temptation to defect) denotes $p_{D,C}$; R (Reward for mutual cooperation) denotes $p_{C,C}$; P (Punishment for mutual defection) denotes $p_{D,D}$ and S (Sucker's payoff) denotes $p_{C,D}$. The inequalities hold: $T > R > P > S$. For the following iterated cases, $T + S < 2R$ holds too.

The definition of a game is conditional on the strategy space. $\{C, D\}$ is just the simplest. Axelrod (1980a, 1980b) introduced a seminal framework termed *Iterated Prisoner's Dilemma*, in which the final payoff is the sum or average of repeated standard Prisoner's Dilemma games one step after another, with an independent ending possibility, between the same pair of partners. In such a combined game defined on a process involving simpler games, the final strategy space could be very complicated when the synthetic strategy is factually a temporal rationale of simpler strategies. It notes that a temporal rationale could be contingent upon only the past simpler strategies of the opponent, neither the current or future simpler strategies of the opponent, nor the matching temporal rationale. Even if the averaged of the payoff is random for those strategies with stochastic mechanism and the repeating probability, the final payoff matrix defined by the expected mean of the final sum is deterministic. A representative strategy space of temporal rationales was limited to one-step memory of the reaction of opponents (Nowak & Sigmund, 1992). The most famous strategy in that space is *tit for tat* (TFT), which won Axelrod's tournaments (1980a, 1980b). If the last step memory of reaction of self is added, the space will be extended to include the strategy named *Pavlov* or *win-stay-lose-shift* (Nowak & Sigmund, 1993).

TFT, Pavlov and many other possible strategies can all perform *reciprocal altruism* proposed by Triver (1971). Axelrod (1980b) summarized three traits of his champion strategy TFT. Two of them, *niceness* and *provocability*, made up Triver's sketched exemplar of reciprocal altruist strategies, named *Friedman* by Axelrod (1980a) later. Niceness means never first to defect. Provocability means to defect in next step of Prisoner's Dilemma Game as long as it gains an S payoff in the current step. Friedman never cooperates once being defected, while Pavlov defects if and only it gains an S or T payoff in the last step, and TFT defects if and only the opponent defect in the last step. One variant of TFT named

GTFT also plays nice but just defects at 50% probability whenever TFT would defect. Any reciprocal altruist strategy requires some memory of the past playing information. Comparing to spatial cooperation without past memory in following, let's name reciprocal altruism *temporal cooperation*.

The temporal cooperative strategies were introduced to study the evolution of cooperation. Offspring inherit synthetic strategies of ancestors and the payoffs between strategies decide the offspring quantities. The strategy space does not change while just the population evolves. The point in the evolutionary game theory is that the payoffs between strategies do change contingently upon the current population. The classic research question asks whether one strategy could thrive within a population dominated by another strategy (Nowak, 2006a, Chap4). Axelrod and Hamilton (1981) pointed out that TFT strategy could setup cooperation within dominating defective strategies. Nowak and Sigmund (1993) confirmed its efficiency in simulation study although they found *Pavlov* keeps cooperative population better than TFT when cooperation begins to dominate and the circumstance noises can't be ignored.

Spatial cooperation without temporally structured strategy space

It's well known that with fully mixed or totally random spatial structure, the simple defective strategy would beat the simple cooperative strategy (Triver, 1971; Nowak, 2006b). However, Nowak and May (1992) demonstrated that even the simplest strategy space of $\{C, D\}$ without any temporal structure could evolve into amazingly cooperative patterns just on a common spatial structure of lattice. The evolutionary dynamics textbook of Nowak (2006a, Section 8.7) provided two chapters for three kinds of evolving mechanisms on more abstract graphs or on more regular spatial structures, without any temporal complexity of strategy space. Their common setup assumes that each individual agent occupies its exclusive vertices and interacts only through edges. The inherited traits of agents will result in fitness payoffs for each pair of interacting individuals. The fitness payoffs of each individual are summed up to differentiate its reproductive success from others. Each offspring will still

occupy an exclusive vertex. So an evolving mechanism is factually an updating process for the traits on vertices of the graph.

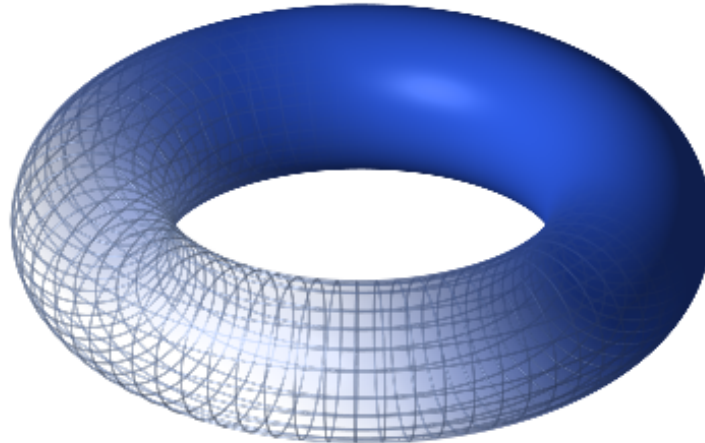
The simplest framework takes the imitation process. A vertex is to be occupied by offspring of the fittest one of those individuals on or neighboring the vertex. It also seems that one vertex is imitating the traits of its neighbor who played most successfully in fitness payoffs. However, the winning neighbor may be less successful than someone neighboring itself. So, a simple deterministic mechanism for fitness could make out temporal chaos patterns on the graph (Nowak & May, 1992). This framework could also be added stochastic element, just like our following study.

The other two mechanisms take stochastic processes in which the fitness of payoffs decides the probability of reproducing. *Birth-death* process randomly chooses one victim in the neighbors of each newly reproducing agent (Lieberman, Hauert & Nowak, 2005). The death is conditional on neighboring birth. While *death-birth* process randomly chooses the dying individual before its neighbors compete its left vertex according to fitness (Ohtsuki, Hauert, Lieberman & Nowak, 2006). The birth is conditional on neighboring death. The order of death and birth makes sensitive difference in consequences (Nowak, 2006a). The study of Hammond and Axelrod (2006a, 2006b) mainly took a death-birth process. Their immigrating procedure (2006b, Box 1, p. 934) was discarded in the following study to make the model *as simple as possible* (2006b, Footnote 1, p. 928).

Generally, evolution depends on the structure of the graph in various ways (Lieberman, Hauert & Nowak, 2005). This paper will focus cases on the regular two-dimensional lattices with the simplest types of neighborhood definition. One type is named after J. von Neumann, with edges linking the four neighbors not farther than unit distance, or the Castle's neighbors in chess (Hammond & Axelrod, 2006a, 2006b). The other type is named after E. F. Moore, with edges linking the eight neighbors not farther than $\sqrt{2}$ units distance, or the Queen's neighbors in chess (Nowak & May, 1992). To make the lattice both finite and symmetric free of boundaries, the left border and the right border could be taped to form a tube, then the top ring and the bottom ring are rolled and taped into a torus finally. On the torus, each

vertex is equivalent in structure with the same number of neighbors (Hammond & Axelrod, 2006a, 2006b).

Figure 1. Topology of Torus (<http://en.wikipedia.org/wiki/Torus>)



Kin selection and Hamilton's rule

L. Lehmann and L. Keller (2006) categorized spatial cooperation without temporally structured strategy space as kin selection (Maynard Smith, 1964) and proposed to call it altruism rather than cooperation. They tried to extend Hamilton's rule (Lehmann & Keller, 2006, Table 1) into a general framework to unify altruism of kin selection and reciprocal cooperation. Rather than pair of matching strategies in game theory, Hamilton's rule focuses on one-way donation. Nowak (2006b) utilized that one-way donation (with b fitness benefit of the donee and c fitness cost of the donator) to unify the various forms of cooperation rules. It is also not difficult to interpret the game theory payoffs as a pair of one-way donations with an interaction effect². The one-way donation framework is more general in

²Let b equates to $R - S$, c to $P - S$, and the base fitness of both participants equates to S without the c fitness to be donated or held. To donate is cooperative; to hold is defective. If $T \neq R - S + P$, it just need an interaction effect a_{bc} . The corresponding concepts in economics are utilities (von Neumann & Morgenstern, 1944), complement goods (positive interaction in utilities of two goods) and substitute goods (negative interaction). Let $a_{bc} = (T - R) - (P - S)$ and so T is decomposed into $b + c + a_{bc} + S$. For the classic example $(T, R, P, S) = (5, 3, 1, 0)$ (Axelrod, 1980a, 1980b), it describes the case donee will receive

that it does not require simultaneity or contingency.

With analysis of one-way fitness donation, Hamilton (1964) gave his seminal rule for selected altruism. In his original paper, it took up a simple form, $c/b < r(\text{Altruist, Kin})$, wherein $r(\text{Altruist, Kin})$ was the expected fraction of genes identical by descents of donater and donee. A refined version of Hamilton's rule replaced $r(\text{Altruist, Kin})$ with $(Q_d - Q_0) / (Q_\bullet - Q_0)$ (Lehmann & Keller, 2006, Table 1; Grafen, 1985). Here Q_d is probability of genetic identity between one allele sampled in the focus altruist and another sampled from its kin, which equates to Hamilton's $r(\text{Altruist, Kin})$ in haploid case. Q_\bullet is identical probability between two randomly sampled genes at the same locus in the altruist, equating to unit in haploid³. Q_0 is identical probability between one sampled in the focus altruist and another sampled from the whole population⁴, which is assumed zero in artificially extreme non-bred setup. The actual non-zero value of Q_0 will be encountered in my studies. Conventionally, the refined ratio $(Q_d - Q_0) / (Q_\bullet - Q_0)$ is still denoted r and termed *coefficient of relatedness*.

G. R. Price (1970) developed a powerful equation (Frank, 1997; Veelen, 2005) that could derive Hamilton's rule elegantly. Factually, a lot of significant topics including kin selection, group selection and Fisher's Fundamental Theorem had been derived and re-derived from Price Equation in quantitative genetics and given it a central theoretic role (Frank, 1997, 1998; Veelen, 2005). The following is a brief version to give the coefficient of relatedness in haploid case with a single gene locus, which is $(q_{kin} - \bar{q}) / (1 - \bar{q})$ with Price's random variable q denoting the frequency (within the respective individual) of the genotype shared by the donaters, named genotype A. From Price Equation $\Delta Q = \text{Cov}(z/\bar{z}, q) =$

benefit three times of the cost of the donater, and the interaction effect of receiving benefit and holding is positive. For the case of Nowak & May (1992), $(T, R, P, S) = (T, 1, \epsilon, 0)$ wherein $2 > T > 1.8$ and $\epsilon \rightarrow 0+$, the ratio of benefit to cost is infinitely large and the interaction effect is positive.

³In the usual diploid case, $Q_\bullet = (1 + F_A) / 2$ wherein F_A is Hamilton's (1972) inbreeding coefficient which was assumed zero in non-bred setup (Hamilton, 1964). Thus, Hamilton's $r(\text{Altruist, Kin}) = Q_d / Q_\bullet = 2Q_d$ for diploid organisms. It also notes that in case $F_A \neq F_B$, both Hamilton's $r(\text{Altruist, Kin})$ and the refined version of relatedness coefficient are directionally defined, i. e. $r(A, B) \neq r(B, A)$.

There is another important difference between Hamilton's original version and the refined one. Only the latter could be negative. That fact makes it possible to interpret spite through the refined rule (Hamilton, 1970; Foster, Wenseleers & Ratnieks, 2001).

⁴Including the altruist itself. The original note of Lehmann and Keller (2006, Table 1) is not precise in this detail.

$\sum_i [(z_i/\bar{z}) - 1] (q_i - \bar{q}) / N$ (see Appendix A for details), to keep the aggregate change of A-frequency free of the fitness donation, it is sufficient and necessary to let the benefit in donee, i.e. the positive change in the $(z_{donee}/\bar{z}) - 1$, and the cost of the donor, i.e. the negative change in the $(z_{donor}/\bar{z}) - 1$, inversely proportional to their respective weights $(q_{donee} - \bar{q}) / N$ and $(q_{donor} - \bar{q}) / N$. So, every one unit of benefit of kin is balanced by every $(q_{donee} - \bar{q}) / (q_{donor} - \bar{q}) = (q_{kin} - \bar{q}) / (1 - \bar{q})$ unit of cost of the altruist in fitness. The coefficient quantifies the relatedness of the kinship and provides the evolutionarily selected criterion for the altruist donating phenotype. In my following second study, this quantity is calculated and plotted.

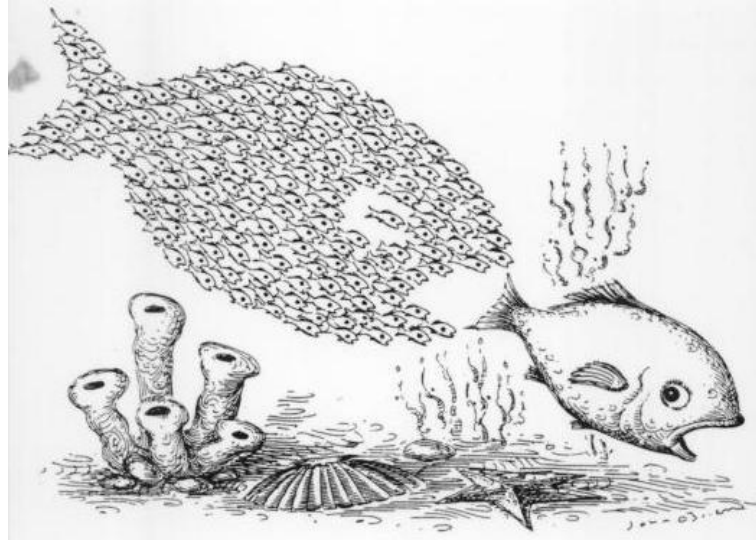
There have been more complicated generalizations of Hamilton's rule after Price Equation (Hamilton, 1970; Queller, 1985, 1992; Frank, 1998; Fletcher & Zwick, 2006), which accommodate altruist donation across species with related phenotypes and even reciprocal altruism (Trivers, 1971; Axelrod & Hamilton, 1981). Another development of Hamilton's rule (Queller, 1992; Frank, 1998; Sober & Wilson, 1998) is to unify its early rival, group selection (Wilson, 1975; Traulsen & Nowak, 2006) while when Maynard Smith proposed the term *kin selection* (1964) at the time of Hamilton's work (1964), the efforts were just to distinguish it from confusion with the denial group selection⁵.

The ubiquity of kin selection makes it too difficult to give quantitative evidences of pure group selection. However, the group structure is often implicated in kin selection model when the average kinship is defined without complicated assumption of developed kin recognition. The repeated interaction between agents is usually limited to short distance and small spatial domain occupied by the same family, group, etc. It is a key fact that reproduction performs locally and most offspring are nurtured by parents in the same place. Generally for simple agents, the neighborhood is a more operative element than kinship. Such a context encourages the research on the cooperation mechanism dependent on spatial

⁵Dawkins (1999) differentiated two types of group selection theories. One emphasized the organization and interaction within a holistic replicating group and played down roles of gene or individual. This theory is sharply criticized by neo-Darwinism standing a gene-central opinion. The other, also termed multilevel selection theory, or multilevel vehicle selection in books of Dawkins, endeavors to resolve group fitness into individual fitness with quantitative models (Wilson, 1975) and empirical data (Wilson & Holldobler, 2005; Traulsen & Nowak, 2006).

structure.

Figure 2. Hamilton's Rule and Social Evolution (Frank, 1998)



Spatial viscosity

There is a similar rationale of Hamilton's rule for fitness donation on the lattice. The local way of asexual reproduction makes individuals more frequently interact with peers taking the identical traits. With gene-central view, the only difference between the simulated agents on vertices and the conventional organisms is that the gene of the former performs only functionally without a molecular media like cistrans. Here it is a little difficult but not necessary to distinguish genotypes from phenotypes, as long as the phenotypes are replicators as precise as ordinary genotypes. Whether they are tags or strategies, they are replicators⁶ (Dawkins, 1999, Chap. 5).

There has been a proposed rule for cooperation on graph similar to Hamilton's rule (Ohtsuki, Hauert, Lieberman & Nowak, 2006; Nowak, 2006b), in the form $b/c > k$ wherein

⁶Only one exceptional attribute copied in spatial cooperation will render difficulty. That is the quantitative spatial position inherited in any descendant from its ancestors. It is copied precisely and with constantly mutated small bias. That difficulty would give rise to two issues. One is the historical controversy between biometrician and the new Mendelian (Frank, 1998, section 2.1). The other is the natural impossibility of absolute distinction between the environment and the subjective agent (Simon, 1996), which is relative to but not within this paper.

k is simply the number of edges of each vertex, or degree. The result depends on two presumptions. One is the specially defined *death-birth* process for reproduction. The other presumption is that the c and b are both required just slightly marginal to the base fitness, which termed *weak selection* (Nowak, 2006a). The rationale emphasizes that there are many factors other than selection to affect the competition. However, that should introduce significant disturbance into the base fitness while it is modeled to be strictly stable to make the rule. The connection in depth between the two limitations is that the specialty of reproducing rules heavily relies on the stability of base fitness. That specialty should cast some uneasiness on the comparison between k and the reciprocal of relatedness coefficient in Hamilton's rule (Ohtsuki, Hauert, Lieberman & Nowak, 2006).

Ohtsuki, Hauert, Lieberman & Nowak (2006) stated that k , the number of edges for each vertex, is *an inverse measure of social relatedness, or social viscosity*. Social viscosity reflects the extent to which neighborhood could be treated as kinship, relying on the local way of reproduction, or the limited dispersal of offspring from parents (Hamilton, 1964, 1972; van Baalen & Rand, 1998; West, Pen & Griffin, 2002). On lattice, k of Moore neighborhood is 2 times of von Neumann neighborhood, while the neighboring radius of the former is $\sqrt{2}$ times of the latter. Similarly, $\sqrt{k}/2$ could be viewed as the interacting radius on lattice⁷.

West, Pen & Griffin (2002) reviewed that the competition as well as the cooperation both positively correlate to social viscosity. They pointed out that viscosity increases the local average of kinship (a within-group version of Q_0 in relatedness coefficient), which decreases the locally defined relatedness. Le Galliard, Ferriere & Dieckmann (2005) also proved altruism could be positively correlated to mobility in certain case of coevolution of these two traits, which is on coincidence with the earlier report of West, Murray, Machado, Griffin & Herre (2001) as competition and viscosity are just respectively the inverse measures of altruism and mobility. These results conflicting with the conventional conclusion of viscosity remind again that the concrete rule of system could be sensitive. In study of Hammond and Axelrod (2006a) within a death-birth process, the bigger k or the lower viscosity, the lower

⁷ $\sqrt{(k+1)/\pi}$ could be used in case of a general plane.

donating level in the finally evolved population, which is in coincidence with conventional expectations. It may involve the fact that only the fitness near the borders between groups affects the reproduction. To understand that mechanism, let's review the key difference between deterministic evolutionary dynamics and stochastic evolutionary dynamics of finite population with constant upper bound of size.

Drift and Moran process

A real population is finite and evolves in a stochastic⁸ process termed *Moran process* (Nowak, 2006a, Chap. 6), which is a type of the general birth-death (without order limitation of birth and death) processes with some absorbing states, or population fixations. In a fixation, a population reaches stable and is taken over homogeneously. Other former rivaling genotypes all go extinct. Before reaching a fixation, Morgan process just randomly walks forward or backward in a population space. The mutation is treated exogenous. If there is no selection in the Moran process, it is called drift. In drift, each individual shares the same probability to take over population with its offspring finally. For a single one, the probability is $1/N$ where N is the invariant population size. $1/N$ is also the criterion to judge whether a genotype is selected or not. M. Kimura (1968) calculated the mean time of the neutral mutation to take over population, and then compared it with empirical data. It was amazing that most genetic evolution at the molecular level proved to be neutral without selection. The neutral selection discovery justified the theoretical assumption of weak selection. With that assumption, evolutionary game payoff only marginally influences the fitness, which is defined now through the ratio between the conditional probabilities of respective directions of population stepping. With large population size, an elegant $1/3$ law was discovered that if the basin of attraction of one strategy is shorter than $1/3$, its rival is selected, which predicts that TFT strategy could easily be selected by weak selection in population of defectors (Nowak, Sasaki, Taylor & Fudenberg, 2004).

Although weak selection is fruitful in theories, in agent-based simulation, the strong

⁸The deterministic model of spatial cooperation of Nowak & May (1992) should be better interpreted as a special stochastic Moran process on finite population space with unit conditional stepping probability.

selection setup of Hammond & Axelrod (2006a, 2006b) is more efficient to simulate the final domination of some strategy. The mutation rate is not too small which make the population neither likely to reach nor to stay at fixation. Agent-based simulation acts as an exploring tool to touch heuristic facts while theoretical models could analyze and conclude finally. So, this paper will not report quantitative statistics if the qualitative differences have highlighted the rationale enough.

There are various available platforms for agent-based simulation of finite population dynamics research. Netlogo system (Wilensky, 2006b) has been applied in the course in Northwestern University for years, which gave it sound tests and prepared a rich library of examples. The examples are useful for both tutorial and academic aims. Another advantage is its base of Java language (Sun Microsystems Inc., 2006), which makes it free of operational systems and provides online applets directly. Moreover, its interface is so easy to manipulate that lecturers are best to distribute it as a fascinating educational toy across various sciences. While the main limitation of Netlogo is its efficiency that is not enough to large scale simulating computation.

Simulation Studies

First study: spatial viscosity and group concurrency

In this study I added two probability parameters to the model of Nowak & May (1992). The theme in this study is spatial viscosity, or more specially, the group concurrency of spatial cooperation. The space was a 99×99 square-lattice torus⁹ of cooperators except one defector on the central square. Each square on torus is symmetrically same, so it is convenient to choose the defector to be in the center on the box representing the torus. The interacting radius is $\sqrt{2}$, of Moore neighborhood. It notes that the agent on its square will also interact with itself. So, there are 9 interactions for each agent in each generation, just like the original paper. The payoff is according the original setup, $(T, R, P, S) = (1.9001, 1, 0.01, 0)$,

⁹In the figure 3 of the original paper (Nowak & May, 1992), it was box rather than torus. But they reported that simulation on torus gave similar results.

which makes it impossible for any defector to score a total same to any cooperator. After all interactions complete, each agent has its total score. For each given agent A , the agent scoring the highest within the neighboring 3×3 squares of A , denoted by B , will reproduce a descendant and the descendant will occupy the square of A in the next generation. Then, each square would be occupied by some descendant in the next generation when all agents in this generation will die out to leave the squares. Some agents reproduce many descendants while some reproduce none. The color for each type of square is same to that in the original paper. Blue denotes occupied by cooperators both in last and current generation. Red, by defectors both in last and current. Yellow, by a last cooperator and a current defector. Green, by a last defector and a current cooperator. It is subtle that a reproducing agent may not occupy its square with a descendant of itself. That is, the reproduction and dispersal synchronize¹⁰ for all agents before the ancestors all die out in next generation. A typical replicate of the original simulation on the torus is depicted as following. To play it online, see Appendix B for links. The applets are outputted by Netlogo (Wilensky, 2006b). Their codes in Netlogo are also listed along. See also their ancestors (Wilensky, 2002, 2006a) in Netlogo Model Library, which are granted for academic aims in distribution of Netlogo.

The two boxes on the bottom are the new parameters this paper added. One is the probability for a cooperator to successfully replace a defector. The other is the probability for a defector to successfully replace a cooperator. It is interesting that the dynamics are very sensitive to the former probability while almost insensitive to the latter one. Let's examine case of each pair of probability parameters in following. To play it online, click SETUP-ONE button at first¹¹, then click GO FOREVER button to see the dynamics.

The (100%, 100%) case is just a replicate of the original study of Nowak and may. I listed it to compare the other cases reported in this study. The extreme case of (100%, 1%) does not improve the ratio of cooperation even with 1% probability of defector's reproducing.

¹⁰The Netlogo's Models Library provided a similar model (Wilensky, 2002) with the mistake in this detail. To verify it, run its online applet with a symmetric starting setup with extreme 99.9% initial-cooperation to set just one defector, and the see the mistaken asymmetric result.

¹¹The RANDOMIZE button will set the starting status with the percentage of INITIAL-COOPERATION randomly, rather than the single defector starting status in examples in this paper.

While 15% probability of cooperator's failure in reproducing significantly make cooperators extinct in 500 steps. If the failure probabilities of both cooperators and defectors lower to 10%, the spatial chaos could hold again, with a little lower ratio of cooperation than the deterministic case.

Figure 3. Torus replicate of spatial chaos of Nowak & May (1992)

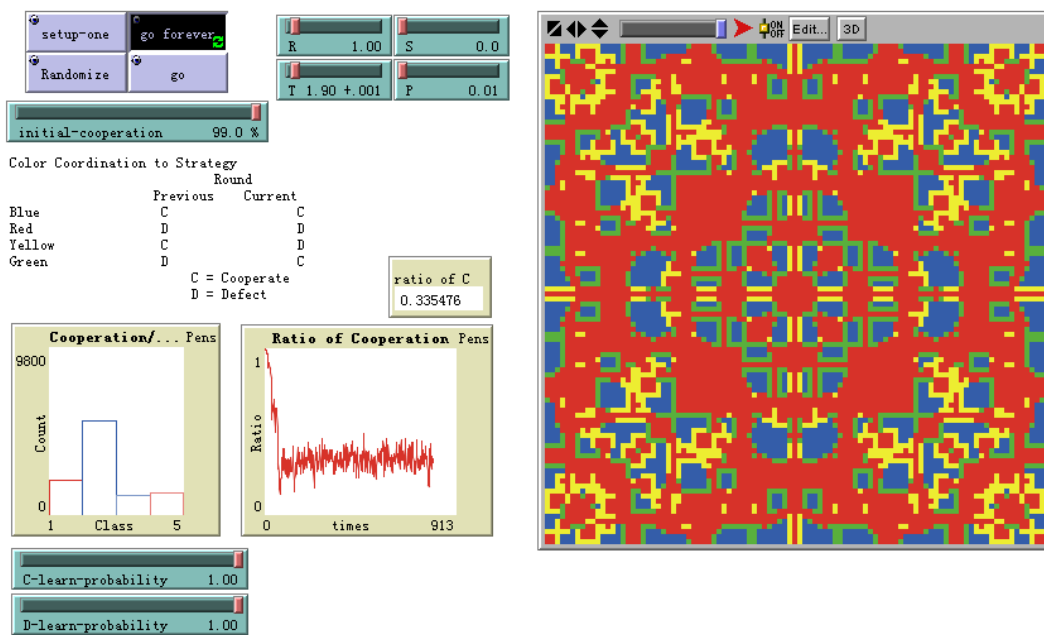


Figure 4. 1% probability for defectors to replace cooperators while 100% for cooperators to replace defectors

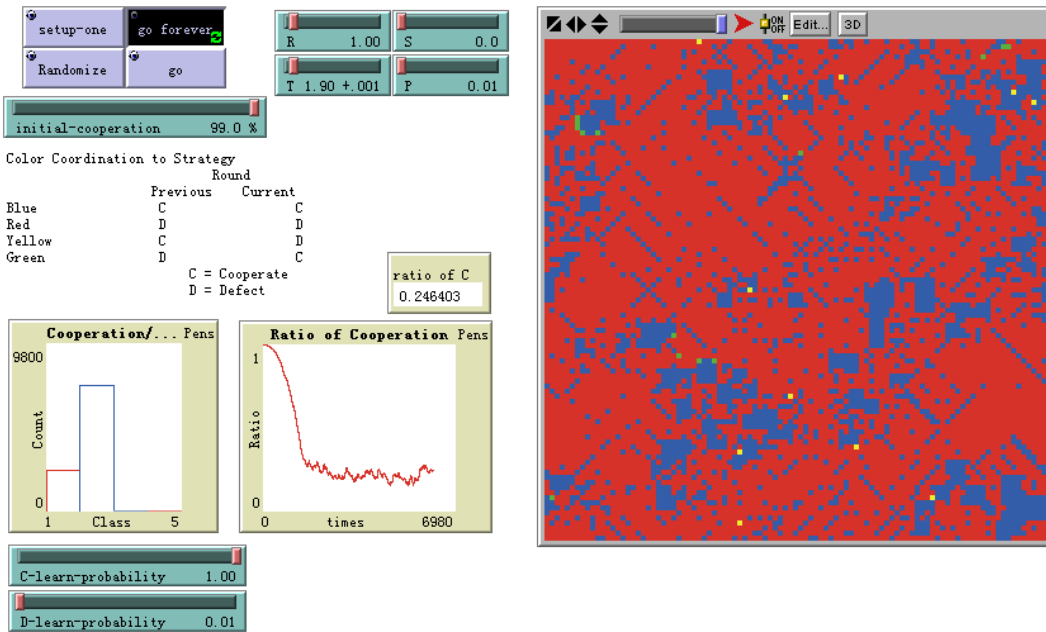


Figure 5. both 85% probabilities for defectors to replace cooperators and for cooperators to replace defectors

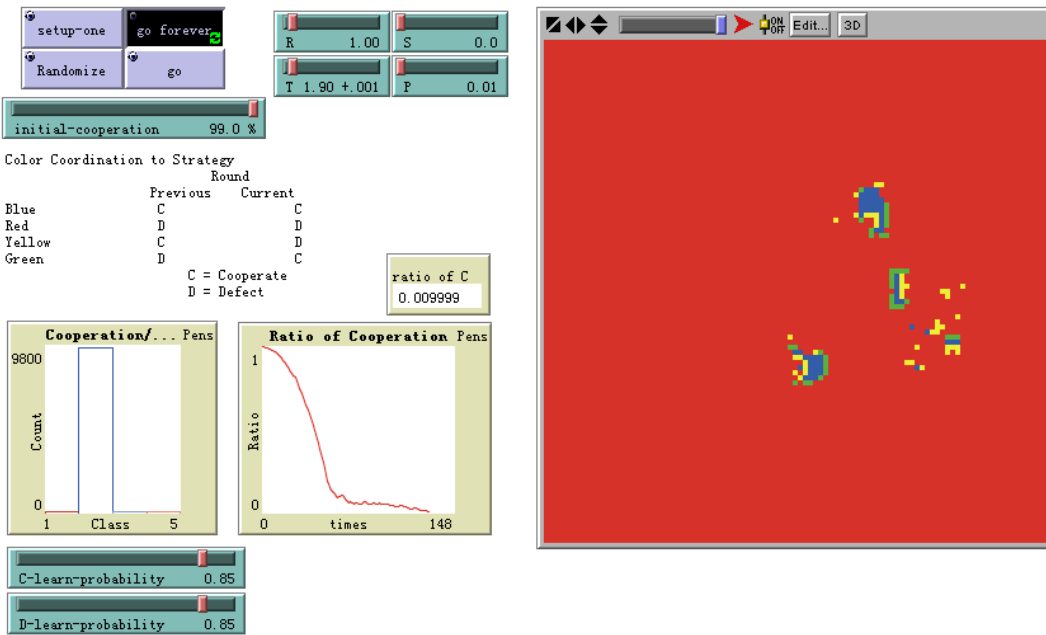
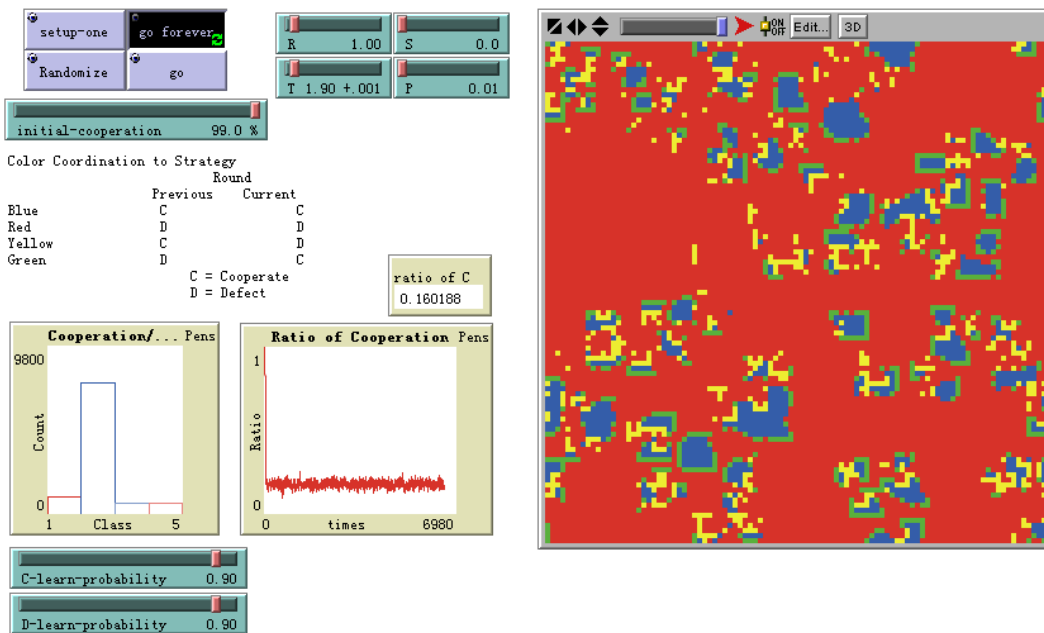


Figure 6. both 90% probabilities for defectors to replace cooperators and for cooperators to replace defectors



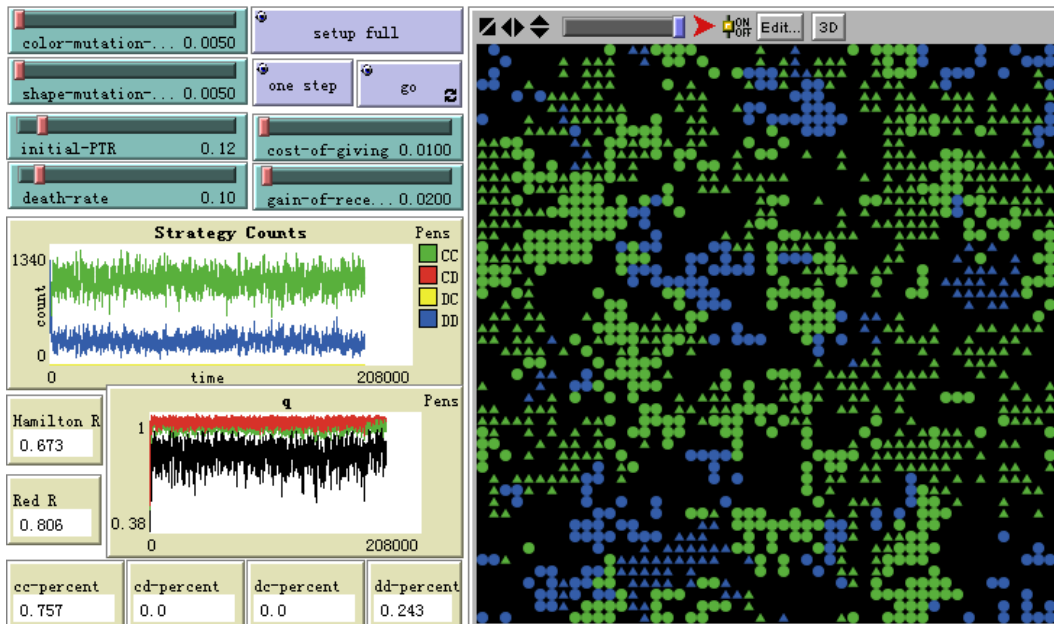
Second study: spatial kin recognition beats temporal reciprocal memory

This simulating study is developed from the papers of Hammond & Axelrod (2006a, 2006b). The space is 50×50 lattice torus. Each square contains one agent. A random starting status will not affecting the dynamics in long term, as the mutation rate of every reproduction is constant as .005. Each agent holds a strategy trait, cooperative (altruist) or defective (free rider). A cooperative agent will donate to its 4 von Neumann neighbors. Each donation will benefit the donatee b unit of fitness with $c = 1\%$ fitness cost in donater. The updating rule is as following. First, each agent faces a death rate 10% constantly. Dying agents leave the square. Second, each living agent's fitness is updated as initial, 12%. Third, each cooperative agent donates to each of its neighbors. Finally, agents are reproducing according the probability equating to their fitness. If there is a blank neighboring square, the offspring will live there, or the offspring will die. The reproducing order of agents is random.

In the diagram (see also Appendix B), the box CC-PERCENT indicates the global ratio of the altruists in last 100 generations. To play the applet, click the SETUP FULL at first then click GO. When b is 2%, $b/c = 2$, the ratio of altruists will easily exceed .70 in long term.

The black line in the following diagram plots the quantity of \bar{q} in relatedness coefficient $(q_{kin} - \bar{q}) / (1 - \bar{q})$ for altruist green agents. The green line (labeled with q) plots q_{kin} for altruist green agents. The box *Hamilton R* denotes the averaged relatedness coefficient for altruist green agents in last 100 generations. It reported that the green line was higher than the black line steady and *Hamilton R* box showed a figure larger than $c/b = 0.5$.

Figure 7. Altruists (in Green) vs. Free Riders (in Blue)



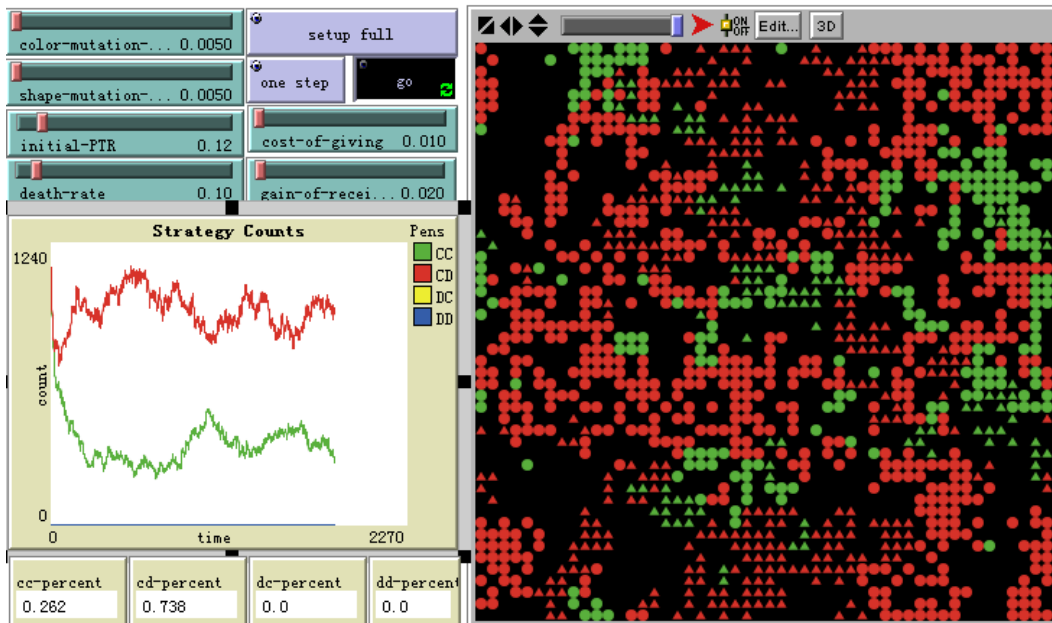
This is a typical social viscosity example. However, if there is one more trait, the situation will be complicated. Notes that there have been two shapes¹² in agents on the torus. One is circle and the other is triangle. The red line in the last diagram labeled

¹²In the original paper, the trait is color. As colors are used in the diagram, this paper used color to indicate the strategy of each agent.

with q plots the q_{kin} for those green agents if they would only donate to neighbors with the identical shape. The box *Red R* denotes the corresponding relatedness coefficient for those green agents if they take the imaginary ethnocentrist strategy. It reported that the red line was higher than the green line and the *Red R* box showed a figure larger than that in *Hamilton R* box.

In the following diagram, there are altruists and ethnocentrists. The ethnocentrists only donate to agents with a same shape, no matter what color (what strategy) the donatees are in.

Figure 8. Ethnocentrists (in Red) vs. Altruists (in Green)



In the diagram, the box *cd-percent* indicates the global ratio of the ethnocentrist in last 100 generations. When b is 2%, $b/c = 2$, the ratio of altruists will easily decrease to less than 0.30 in long term. If calibrate the *shape-mutation-rate* slider to 0.5, the ethnocentrists then change to donaters with half donating probability. Then *cc-percent* reach 0.70.

The study is extended as following to see how temporal strategies play on spatial cooperation. The torus is extended to 100×100 . There are seven strategies. Besides egoist,

ethnocentrists, and altruist, the yellow agents are those just donating to agents in different shape. These four are simple strategies without temporal memory. The brown ones are TFT agents. TFT agents will remember the last action of each of the neighbors in 4 directions respectively, and reply them just the same in current action. GTFT agents will remember the last action in a probability of 50%. NTFT agents are factually the same of altruists. TFT, GTFT have temporal memory but can't recognize the shapes of neighbors. The other four types of agents can't remember but can recognize. The mutation rates are .001. In fact there are many types of mutation. Besides that of shape, of color, the mutations of remembering vs. recognizing and the mutation across strategy types are both 0.001. The b is set to be 2%. After 100,000 generations, ethnocentrists that than TFTs or GTFTs, are observed to dominate the population.

Figure 9. Ethnocentrists (in Red) vs. TFT (in Brown)

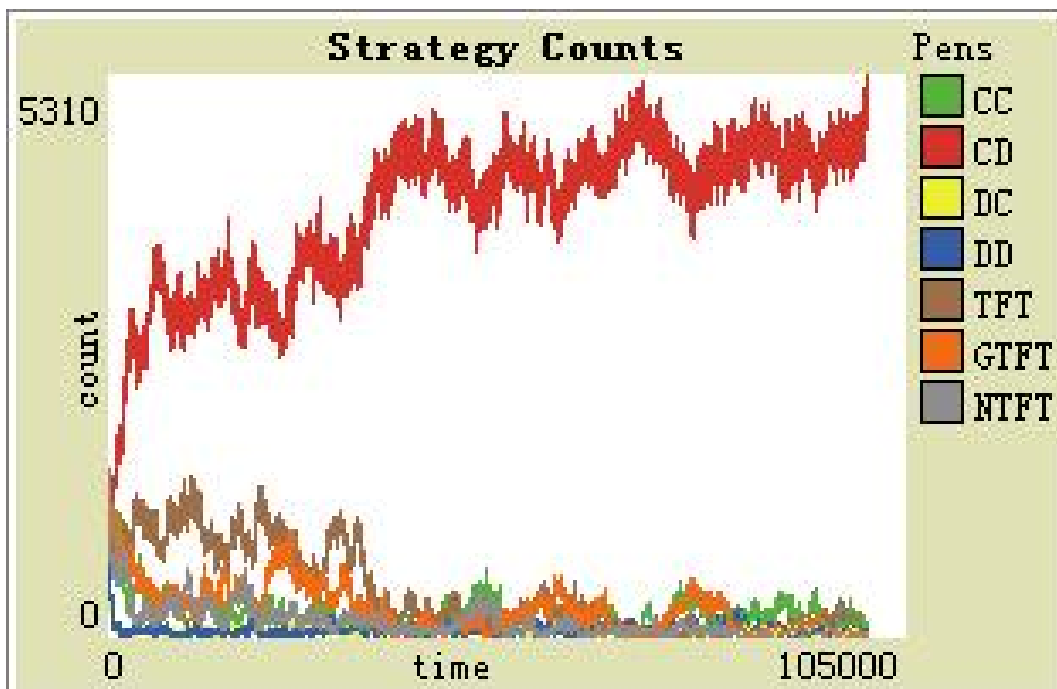
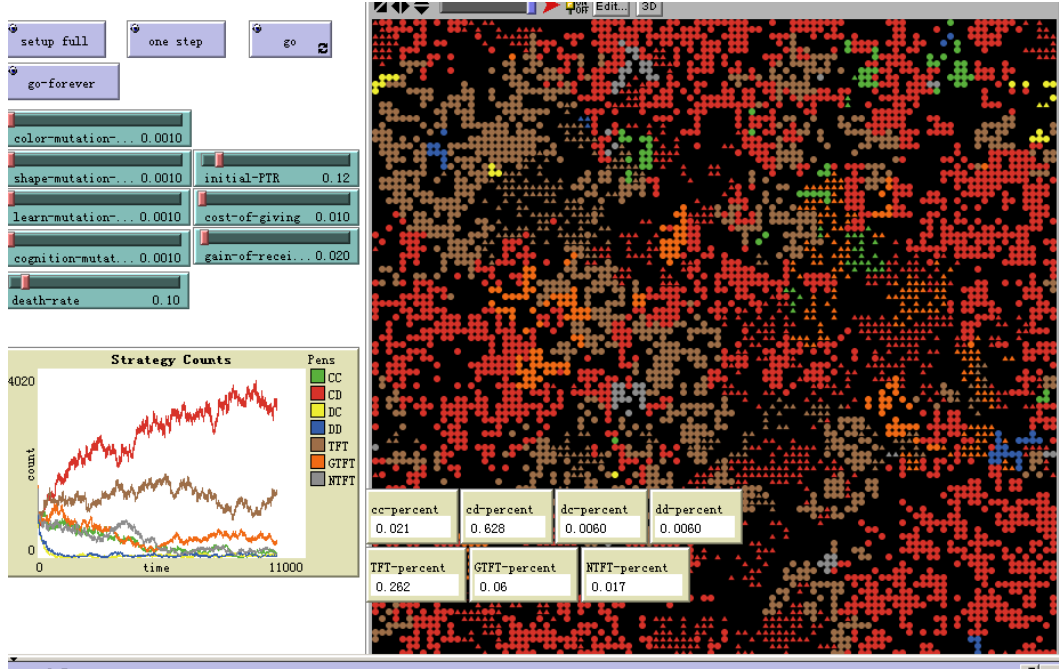


Figure 10. Ethnocentrists (in Red) vs. TFT (in Brown), at the 11,000th generation



Discussion

Social viscosity and group concurrency

The higher probability of cooperators's success in replacing, the more regular borders between defectors and cooperators are kept. In the spatial cooperation, what makes difference is the difference between the set of cooperators supporting one cooperator on border, and the set of cooperators donating defective rivals of that cooperator. A regular border with short interacting radius could keep the difference to favor the cooperator on border, while an irregular border would lower the difference or even reverse the difference to disfavor the cooperator on border. The more irregular the border is kept, or the smaller difference to support the cooperator on border, the higher b/c ratio is required. Let s denote the number of supporting cooperators, d denote the number of cooperators denoting to rivaling defectors. With assumed symmetry, there are also about d defectors interacting with the cooperator on border. $[s(b - c) - dc] / (db) > 1 \Leftrightarrow b/c > (s + d)/(s - d)$ is another criterion for cooperating selection. For example, in case of \sqrt{k} equating to the average distance

between two distinct groups of cooperators, $(s + d)/(s - d)$ would increase to infinity.

Viscosity on spatial cooperation heavily consists in the regularity of the borders between two groups. An irregular border would make more defectors surrounded by cooperators, which would significantly increase $(s + d)/(s - d)$, then lower cooperation ratio. From skin to great wall, a shared mechanism of regularity of borders supports cooperation. On the contrary, invading defectors favor an irregular border. Even a significantly lower successful probability of replacing never impairs their final success.

Defectors compete by individuals while cooperators by regular groups. The higher the probability of successful cooperative replacing is, the more group concurrency cooperators share. On spatial cooperation, donating agents should be treated as many irrational limbs of a rational assemble. In the other study we see how rational individuals with temporal memory are defeated by these irrational limbs with partial kin recognition on spatial cooperation.

Spatial kin recognition beats temporal reciprocal memory

It is interesting that Hammond and Axelrod proposed two very different approaches to explain their identical simulating experiment. One (2006a) relies on kin selection and armpit¹³ effect while the other takes Ethnocentrism (2006b) as a basic mechanism without any reference to kin selection.

In the first replicate in this paper, the result could be explained by social viscosity. Some altruists play the suckers in the Prisoner's Dilemma and die out, and other altruists play cooperators and thrive. Viscosity makes those fortunate cooperators neighboring each other. The evolved population gives a rather big conditional probability for the neighbors to share the same trait of strategy. Hamilton's rule then is applied. The indirect result is that there at the same time evolves a bigger probability for the neighbors to share the same trait of shapes than with different shapes, although shapes do not involve the interaction. In the second replicate in this paper, red groups perform as cooperative as the green groups

¹³For a real armpit case in biology, see the study of Mateo and Johnston (2000).

in within-group kin selection. Moreover, red agents on the group borders outperform green agents generally because the identity in shape trait is high positively correlated to the identity in strategy traits. For green agents, although in q_{kin} they are significantly lower than the red agents, in \bar{q} they are lower than the red agents too. When the \bar{q} of red agents reach some high value, the relatedness coefficient would be low and frequencies of agent colors will arrive stability¹⁴.

The reciprocal altruism is beaten by spatial kin selection in the last simulation. That is not an obviously expected result. The memory vs. recognition competing remains an open problem because we have not explored the more extended strategy space including WSLS (Nowak & Sigmund, 1993). Limited to the current results, there are some preliminary propositions. First, on the plane, generally, recognizing ability would be selected over the remembering ability. Second, even in the error free environment (Nowak & Sigmund, 1992), TFT may not default be the best choice. Third, the spatial kin selection is not based on individual rationality. Or the wisdom is in the assembled group rather than in the simple individual (Simon, 1996).

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¹⁴In the green vs. blue case, the quantity in the box *Hamilton R* is still bigger than the ratio of $\frac{c}{b} = 0.5$. The reason is the green will mutate into blue with the same rate as the reverse. More offspring of green agents mutates as there are more parent agents in green. To balance the mutation, the coefficient should be kept a little higher than the theoretic value 0.5.

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Appendix A: Price Equation (Price, 1970)

$$Q_1[\text{gene A's global freq}] = \frac{\sum q_i[\text{gene A's freq within individual } i]}{N} = \bar{q}$$

$$\begin{aligned} & Q_2[\text{gene A's global freq in the next generation}] \\ = & \frac{\sum g'_i[\text{number of gene A in } i\text{'s successful gametes}]}{\sum z_i[\text{number of } i\text{'s successful gametes}]n_G[\text{gametic ploidy}]} \\ = & \frac{\sum z_i n_G q'_i[\text{gene A's freq within } i\text{'s successful gametes}]}{\sum z_i n_G} \\ = & \frac{\sum z_i q'_i}{N\bar{z}} \\ = & \frac{(\sum z_i q_i) + (\sum z_i \Delta q_i)}{N\bar{z}} \\ = & \frac{E(zq) + E(z\Delta q)}{\bar{z}} \\ = & \frac{\text{Cov}(z, q) + E(z)E(q)}{\bar{z}} \\ = & \bar{q} + \frac{\text{Cov}(z, q) + E(z\Delta q)}{\bar{z}} \end{aligned}$$

$$\begin{aligned} \Delta Q &= Q_2 - Q_1 = \frac{1}{\bar{z}} (\text{Cov}(z, q) + E(z\Delta q)) \\ &= \text{Cov}\left(\frac{z}{\bar{z}}, q\right); \text{ if and only } z \text{ is not correlative to } \Delta q \\ &= \beta_{zq} \sigma_q^2 \frac{1}{\bar{z}} \\ &= \rho_{zq} \sigma_z \sigma_q \frac{1}{\bar{z}} \\ &= \sum_i \left(\frac{z_i}{\bar{z}} - 1\right) \left(\frac{q_i - \bar{q}}{N}\right) \end{aligned}$$

Appendix B: Online Javalets and Original Netlogo Codes with Help

Viscosity simulation

http://lxxm.com/t/netlogo/Naure359_29_826-829.withTwoProb.html

http://lxxm.com/t/netlogo/Naure359_29_826-829.withTwoProb.nlogo

See also the example provided by Netlogo (Wilensky, 1992).

Spatial kin selection

<http://lxxm.com/t/netlogo/Ethnocentrism.G-B.html>

<http://lxxm.com/t/netlogo/Ethnocentrism.G-B.nlogo>

<http://lxxm.com/t/netlogo/Ethnocentrism.R-G.html>

<http://lxxm.com/t/netlogo/Ethnocentrism.R-G.nlogo>

<http://lxxm.com/t/netlogo/Ethnocentrism.EthnocentricVSTFT.html>

<http://lxxm.com/t/netlogo/Ethnocentrism.EthnocentricVSTFT.nlogo>

See also the example provided by Netlogo (Wilensky, 1996b).