

Collective Evolutionary Dynamics and Spatial Reciprocity under the N-Person Snowdrift Game

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Abstract. The evolution of cooperation has been gathering increasing attention during the last decades. Most of the times, cooperative behavior involves more than two individuals, and the N-person Prisoner's Dilemma, which is the most studied generalized social dilemma in this context, not always manages to capture those situations that often occur to humans. In such cases, the N-person Snowdrift Game (NSG) often provides an adequate alternative. Here we show, making use of the NSG, how spatial populations affect the average levels of cooperation, when compared with the results obtained under conventional evolutionary game theory, that is, for well-mixed populations.

Keywords: Cooperation, Evolution, Evolutionary Game Theory, Diversity.

1 Introduction

Cooperation is on the basis of some of the major transitions in evolution [1]. Genes cooperate to form cells, which in turn cooperate to form multi-cellular organisms; individuals cooperate to form groups and societies, and human culture is a cooperative process. To understand how cooperative behavior emerges and evolves is therefore a quest which has received growing attention during the last decades, and to which Evolutionary Game Theory (EGT) [2, 3] has been able to provide fundamental insights [2-15]. One-shot, symmetric 2-person games are the traditional approach adopted to investigate the emergence and evolution of cooperation; however, one cannot ignore that many real-life situations are actually associated with collective action based on joint decisions made by groups involving more than 2 individuals. There are many examples, in our everyday life and throughout our history, where instances of N-person games are, or have been, at stake. The effort to protect the Earth's environment, on which every single "player" has to make a choice whether to adopt a more conscious behavior or not; the sharing of common resources among different countries; the participation in open source projects; the payment of taxes and social welfare; etc..., the examples abound. Furthermore, and very commonly,

performing a given task which is beneficial to an entire group requires the cooperation of several individuals of that group, who often share the workload required to perform that task. In this case, the N-person generalization of the so-called Snowdrift Game provides suitable description [16].

In its 2-person version, two individuals are driving on a road which gets blocked by a snowdrift. To proceed with their journey home, the snow must be removed, and this removal may or may not be done: if no one shovels, no one gets home; if the two drivers cooperate and shovel, both get home, each one sharing the workload of shovelling the snow. If only one driver decides to shovel, both get home despite one driver incurring the entire cost of snow shovelling. If we define the benefit of getting home as b and the cost of removing the snow as c , then if both drivers cooperate and shovel, each gets $b - c/2$. If both defect, no one gets anything (or goes home) $- 0$. If one cooperates and the other defects, the Cooperator (C) gets $b - c$ whereas the Defector (D) gets b . Assuming, as usual, that the benefit is greater than the cost (i.e., $b > c$), we get a payoff ranking characteristic of a chicken, hawk-dove or snowdrift dilemma [2, 17, 18]. The N-person generalization of this dilemma is immediate. In keeping with the previous example, we can imagine that the snowdrift occurs at a cross-road where N drivers meet. Again, all want to go home (getting all the same benefit b), but perhaps not all are willing to shovel. If all shovel, then each gets $b - c/N$. But if only $k > 0$ individuals cooperate, each gets $b - c/k$ while those who defect get home without shoveling (and hence get b).

Our goal on this paper is to understand the impact of the structure of the population on the outcome of cooperation on a simple model of the N-person Snowdrift Game. In the framework of EGT, populations are conventionally modelled as *infinite* and *well-mixed* (each and every individual is equally likely to interact with everyone else). We will explore the consequences of each of these assumptions, and ultimately show how structured populations generally lead to higher levels of cooperation at low costs, inhibiting cooperation at high costs, raising new and exciting questions.

This work is organized as follows: on sections 2 and 3 we explain in further detail the model at study and some background on this topic regarding well-mixed populations, respectively; and on section 4 we present the results obtained for structured populations. Finally on section 5 we discuss the results obtained and highlight some future lines of study.

2 The Model

As referred to above, two types of strategies are considered: Cooperators (C, individuals that are willing to pay a certain cost so that the benefit is obtained) and Defectors (D, who do not contribute at all). The payoffs are as follows [19]:

$$\begin{aligned}
P_c(k) &= b - k \quad k \in [1, N] \\
P_D(k) &= \begin{cases} 0 & k = 0 \\ b & k \in [1, N-1] \end{cases}
\end{aligned} \tag{1}$$

, where n is the number of cooperators in the group of N individuals including the one concerned, c is the cost, and b is the benefit obtained by each individual of the group, regardless of her strategy, when the task is performed, with $b > c$ (throughout the manuscript, we take $b = 1$). From this definition one concludes that a single cooperator is able to afford the benefit. This is the simplest case, on which we will be focusing on this work; interesting results also arise when more than one cooperator is necessary to be able to attain the benefit - that is, a higher threshold is introduced [16].

3 Background on Well-Mixed Populations

Well-mixed populations (the so-called mean-field approximation in Physics) constitute the simplest approach possible to this problem, for which analytical results can be obtained. The individual fitness of an individual is the result of averaging over all possible groups of size N ; as a consequence, all cooperators have the same fitness, the same happening with all defectors. Evolution is implemented by means of the replicator equation [3],

$$\dot{x} = x(1-x)(f_C(x) - f_D(x)). \tag{2}$$

, where x stands for the fraction of Cs on the population, and $f_C(x)$ and $f_D(x)$ correspond to the average fitness of Cs and Ds for that x , respectively. Strategies' evolution follows the gradient of natural selection determined by the relative fitness difference.

At this point, a distinction has to be made, between *infinite* and *finite* populations. In *infinite* populations the sampling is binomial, and consequently the average fitness of cooperators and defectors in the population is, respectively, given by

$$\begin{aligned}
f_C(x) &= \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} P_C(k+1) \\
f_D(x) &= \sum_{k=0}^{N-1} \binom{N-1}{k} x^k (1-x)^{N-1-k} P_D(k)
\end{aligned} \tag{3}$$

Solving (2) for the steady state $\dot{x}=0$ on the N-person Snowdrift Game, one obtains [19]

$$\frac{c}{b}(1-x^*)^N + Nx^*(1-x^*)^{N-1} - \frac{c}{b} = 0, \quad (4)$$

which can be solved numerically for arbitrary N , leading to the results shown in Figure 1. It shows us that smaller groups are more advantageous for cooperation, since the equilibrium abundance of cooperators decreases with increasing group size N and decreasing benefit-cost ratio c/b .

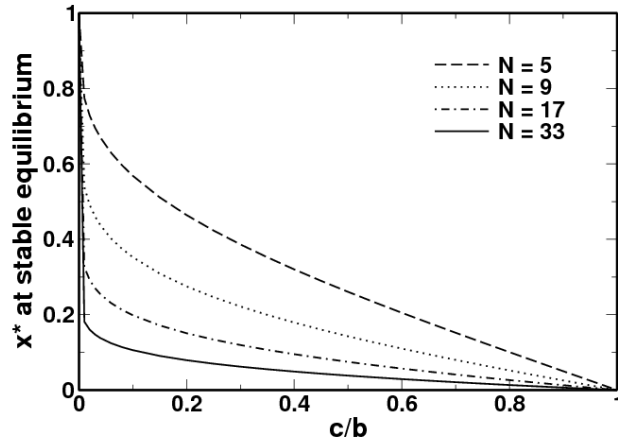


Fig. 1. Fraction of cooperators x^* at the stable equilibrium, as a function of c/b , for different group sizes, in infinite well-mixed populations. One observes that the bigger the group, the smaller the equilibrium fraction of cooperators, for the same ratio c/b .

However, the *infinite* assumption is one that certainly is not compatible with the real world. EGT on a finite population (of size Z) introduces some modifications: the fraction of cooperators is no longer a continuous variable, but varying in steps of $1/Z$; and sampling of individuals is no longer binomial, following now a hypergeometric distribution:

$$f_c(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k-1}{j} \binom{Z-k}{N-j-1} P_c(j-1) \quad (5)$$

$$f_D(k) = \binom{Z-1}{N-1}^{-1} \sum_{j=0}^{N-1} \binom{k}{j} \binom{Z-k-1}{N-j-1} P_D(j)$$

Following the conventional approach, we compute the fraction of cooperators in the population after a transient period of evolutionary dynamics of the population. The fitness of individual i is given by the accumulated payoff resulting from all the games in which she participates. Strategy evolution is implemented via the pairwise comparison rule [20-22]: in each time-step, an individual (A) is selected at random from the population to revise her strategy, comparing her accumulated payoff with one of her neighbors (B) also randomly chosen. Individual A adopts the strategy of B with a probability given by the ubiquitous Fermi expression from statistical physics

$$p = [1 + e^{-\beta(f_B - f_A)}]^{-1} \quad (6)$$

, where f_A and f_B are the fitness of individuals A and B respectively, and β , which in physics corresponds to an inverse temperature, denotes here the intensity of selection. For $\beta \ll 1$ selection is weak, and in the limit on infinite populations (that is, $Z \rightarrow \infty$), one recovers the replicator equation. Increasing β increases the intensity of selection, reaching pure imitation dynamics whenever $\beta \gg 1$.

When one performs evolutions on large yet finite well-mixed populations, the agreement is, as expected, almost perfect. Only small discrepancies can be observed for the higher and lower values of c/b , due to the finiteness of the population. This effect disappears once sufficiently big populations are considered (on this type of processes, for $Z = 10^4$ convergence to the infinite population case is excellent).

One can also define the probability to increase and to decrease the number k of cooperators in the population by one, at each time-step:

$$T^\pm(k) = \frac{k}{Z} \frac{Z-k}{Z} \frac{1}{1 + e^{\mp \beta(f_c(k) - f_d(k))}}. \quad (7)$$

The first term relates to the probability of selecting a cooperator, the second one to the probability of selecting a defector, and the last to the take-over probability, taking into account the average payoffs of cooperators and defectors for that specific k . For arbitrary β , the quantity corresponding to the right hand side of the replicator equation, which specifies the gradient of selection, is given by

$$g(k) \equiv T^+(k) - T^-(k) = \frac{k}{Z} \frac{Z-k}{Z} \tanh \left\{ \frac{\beta}{2} [f_c(k) - f_d(k)] \right\}. \quad (8)$$

The right-hand side of $g(k)$ is similar to the replicator equation, only that the pairwise comparison leads to the appearance of the hyperbolic tangent of the fitness difference, instead of the fitness difference. This has implications in the characteristic evolutionary times, which now depend on β , but not in what concerns the roots of

$g(k)$. Also, adoption of this specific social learning hypothesis, combined with the finite population size, means that internal equilibria are no longer possible: the evolutionary dynamics will only stop whenever the system reaches one of the two absorbing states, full cooperation or full defection. Hence, the sign of $g(k)$, which indicates the direction of selection, is important in that it may strongly influence the evolutionary time required to reach any of the absorbing states.

For well-mixed populations, calculating $g(k)$ is generally straightforward, as every C will have the same fitness, the same happening with every D . In structured populations this property no longer holds, and the task of computing $g(k)$ becomes considerably harder. Here we shall compute $T^+(k)$ and $T^-(k)$ at a mean-field level, that is, we compute the average frequency of transitions increasing (and decreasing) the number of cooperators for each random configuration with kN cooperators.

4 NSG on Structured Populations

Real world populations have yet additional degrees of complexity. For instance, individuals do not potentially interact with everyone else in the population, but only with a limited number of neighbors. Graph theory constitutes a natural and very convenient framework to describe population structure: individuals are placed on the vertices of a graph, whose edges define the existence of interaction between them.

In network structured populations, each individual has z social ties, which means her payoff is determined by the $z + 1$ games she participates in: the one centered on herself, and also those centered on her neighbors [14], as depicted on Figure 2.

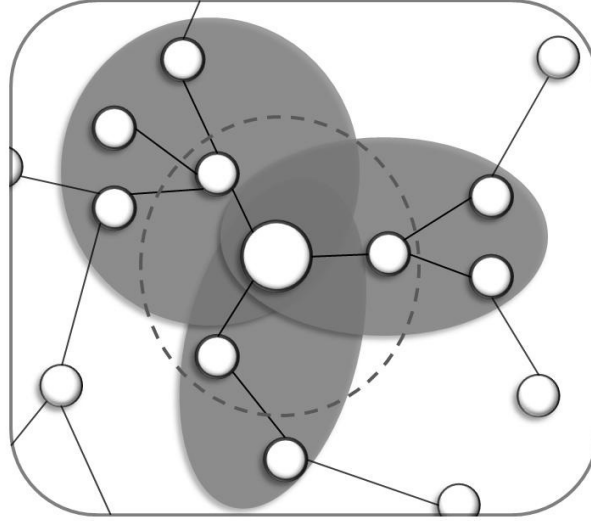


Fig. 2. In this example, the focal individual (largest sphere) has $z = 3$ social ties, and therefore her payoff is determined by the participation on the game centered on herself (grey dashed line) and the games centered on her neighbors (grey shaded shapes), in a total of 4 games.

On this work we will focus on homogeneous networks, and particularly on regular ones. On the other hand, a regular network can be understood as some form of spatial organization, leading to a process known as “spatial reciprocity”.

Figure 3 shows the gradient of selection defined in equation (8) for some values of the ratio c/b , as well as the comparison between the coexistence points obtained in this way and those corresponding to infinite, well-mixed populations.

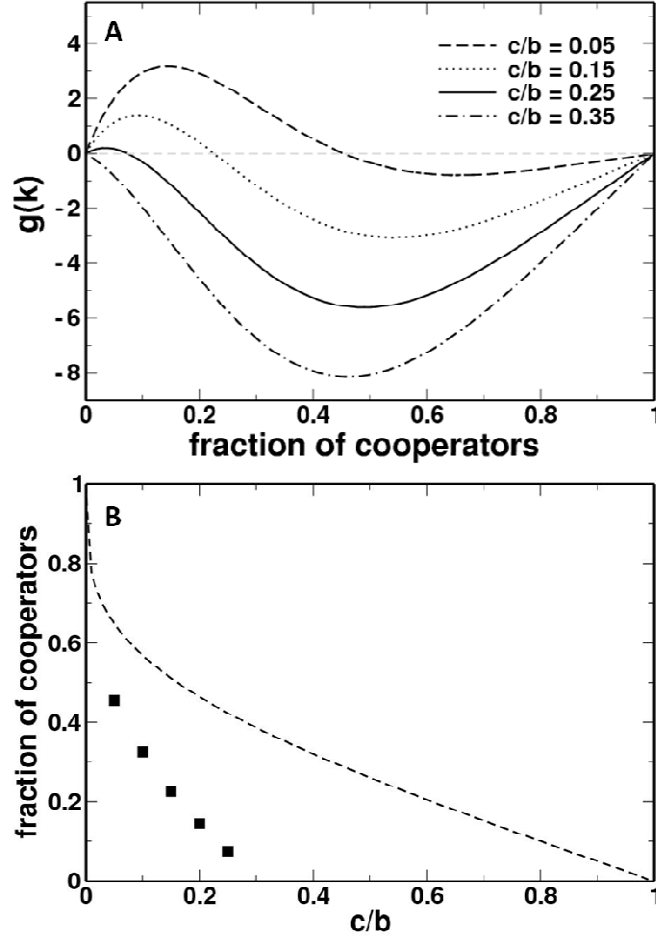


Fig. 3. A. Gradients of selection $g(k)$ for NSG on a regular network for some values of the ratio c/b . **B.** Comparison of the coexistence points (full circles) obtained in A (depicted by full squares) with those associated with well-mixed populations (dashed line). **Parameters:** $Z=1000$, $z=4$, $b=1.0$, $\beta=1.0$

Unlike what happens in the infinite population case, now the mean-field gradients show the occurrence internal coexistence-like points up to $c/b = 0.3$. One observes that these points differ significantly from the analytical results previously obtained, suggesting that the evolutionary dynamics of the NSG under spatial reciprocity differs significantly from that in infinite, well-mixed populations. For $c/b > 0.3$, the gradient is always negative, showing that, at a mean-field level, cooperators do not stand a chance.

The fact that the calculations of the gradients are mean-field in nature points to the qualitative nature of these results. Therefore, one might expect that, qualitatively, cooperators will stand a chance for $c/b < 0.3$, whereas beyond this regime defectors will win the evolutionary race.

Figure 4 shows the evolution of cooperation under spatial reciprocity for the NSG.

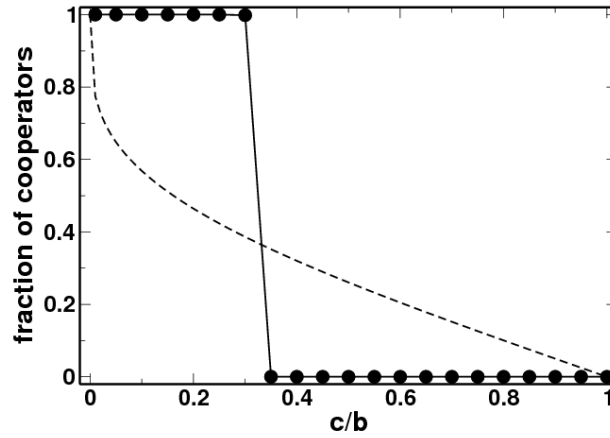


Fig. 4. Average level of cooperation, as a function of c/b , under spatial reciprocity for NSG, for group size $N = 5$ (depicted by solid circles), compared with the correspondent result for well-mixed populations. One observes that cooperation is favored for low values of the cost, being inhibited for large values. **Parameters:** $Z=1000$, $z=4$, $b=1.0$, $\beta = 1.0$

Similar to what has been obtained for the 2-person SG [18] cooperation is favoured for low values of the cost while it is inhibited for large values. The solid circles were obtained by averaging over 2000 generations, after a transient period of 10^5 generations, and each circle corresponds to an average over 10^3 runs. These results, in turn, are qualitatively similar to those one obtains by plotting the fraction of times the population converges to full cooperation for a given value of the cost-to-benefit ratio (not shown).

In order to understand better the origin of this result, we focus on a particular value of $c/b < 0.30$, and follow the time evolution of the fraction of cooperators, starting from two different initial conditions – above and below the coexistence point $x_{coexistence}$ obtained for the same value of c/b in the infinite, well-mixed case (dashed line in Figure 3b).

In Figure 5 we start from a population of 1% and 70% of cooperators respectively, randomly distributed in the network, and allow the system to evolve 10^5 time-steps. In all our simulations we adopted asynchronous update in populations of size 10^3 and

connectivity $z = 4$; each dot corresponds to an average over 1000 runs (as stated, we set $b = 1$ in all simulations, such that the only game parameter is the ratio c/b).

Figure 5A shows that, although the final outcome is the same (the population is heading to the absorbing state of full cooperation), the dynamic behavior observed throughout evolution is quite different. While for $x < x_{coexistence}$ the fraction of cooperators increases right from the start, for $x > x_{coexistence}$ it starts by first decreasing, increasing only after a considerable amount of generations. What is the mechanism responsible for the decrease of the number of cooperators? To answer this question, let us define the fraction of links between individuals playing strategies i and j as:

$$\phi_{ij} = \frac{\sum_{i=1}^z \#ij \text{ links}}{Zz/2} \quad (9)$$

where $Zz/2$ is the total number of links of the network and i and j is either C or D.

Figure 5B shows the average time evolution of these quantities when starting with a fraction of cooperators $x > x_{coexistence}$, along with the above defined quantities. Analysis of these results shows that isolated cooperators are the ones specifically being eliminated, i.e., cooperators and defectors on the population organize themselves increasingly more in an *assorted* manner – individuals that adopt a certain strategy are not isolated but organized in such a way that have at least one neighbor following the same strategy. This is corroborated by the several curves shown: ϕ_{CC} increases slightly, accompanied by a sudden decrease of ϕ_{CD} , representing the self-organization of cooperators and defectors; the maximum “saturation value” reached by ϕ_{DD} corresponds to the moment in which cooperators are less represented in the population. For these values of c/b , regular structures can, therefore, be favorable for cooperation under the NSG, potentiating the self-organization of the population towards the full cooperation absorbing state.

As $c/b > 0.3$, cooperators no longer resist the increased capacity of assortment exhibited by defectors, and indeed in the majority of cases the population evolves into full defection.

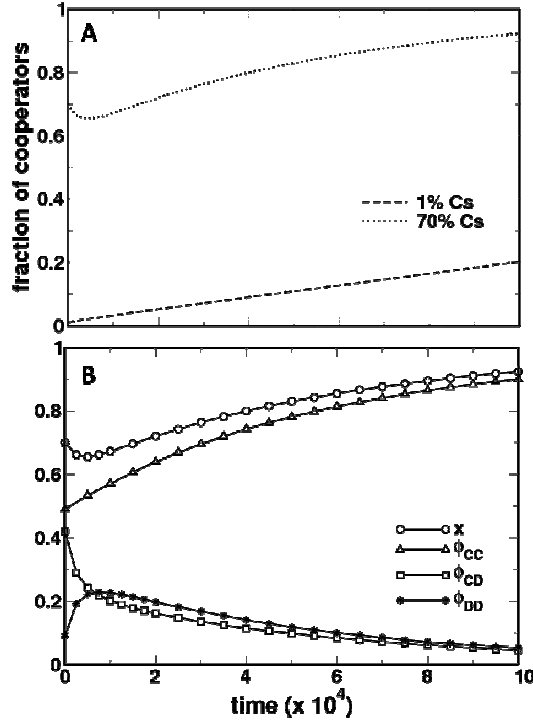


Fig. 5. A. Fraction of cooperators (x) as a function of time steps, starting above $x_{coexistence}$ (70% of cooperators) and below it (1% of cooperators). **B.** x , ϕ_{CC} , ϕ_{DD} and ϕ_{CD} as a function of time, starting from 70% of cooperators, for regular networks. **Parameters:** $Z=1000$, $z=4$, $b=1.0$, $c=0.15$, $\beta=1.0$

5 Discussion

The present study puts in evidence the impact of regular structures on the evolution of cooperation making use of a model of collective cooperation based on the N-person SG. We have shown that, below a critical cost-to-benefit ratio, regular networks facilitate cooperation, by enhancing the self-organization of the population regarding the distribution of strategies. This capacity of self-organization of cooperators breaks-down as one surpasses this critical cost-to-benefit ratio, which we have shown can be qualitatively associated with the mean-field value of the gradient of selection numerically computed for the structured population.

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References

1. Maynard-Smith, J. and E. Szathmáry, *The Major Transitions in Evolution*. 1995, Oxford: Freeman.
2. Maynard-Smith, J., *Evolution and the Theory of Games*. 1982, Cambridge: Cambridge University Press.
3. Hofbauer, J. and K. Sigmund, *Evolutionary Games and Population Dynamics*. 1998, Cambridge, UK: Cambridge Univ. Press.
4. Axelrod, R. and W.D. Hamilton, *The evolution of cooperation*. Science, 1981. **211**(4489): p. 1390-6.
5. Boyd, R. and P.J. Richerson, *Culture and the Evolutionary Process*. 1985: University of Chicago Press).
6. Skyrms, B., *The Stag Hunt* Proceedings and Addresses of the American Philosophical Association, 2001. **75**(2): p. 31-41.
7. Macy, M.W. and A. Flache, *Learning dynamics in social dilemmas*. Proc Natl Acad Sci U S A, 2002. **99** Suppl 3: p. 7229-36.
8. Hammerstein, P., *Genetic and Cultural Evolution of Cooperation*. 2003, Cambridge, Massachusetts: MIT Press.
9. Nowak, M.A., et al., *Emergence of cooperation and evolutionary stability in finite populations*. Nature, 2004. **428**(6983): p. 646-50.
10. Skyrms, B., *The Stag Hunt and the Evolution of Social Structure*. 2004: Cambridge University Press.
11. Santos, F.C. and J.M. Pacheco, *Scale-free networks provide a unifying framework for the emergence of cooperation*. Phys Rev Lett, 2005. **95**(9): p. 098104.
12. Ohtsuki, H., et al., *A simple rule for the evolution of cooperation on graphs and social networks*. Nature, 2006. **441**(7092): p. 502-5.
13. Santos, F.C., J.M. Pacheco, and T. Lenaerts, *Evolutionary dynamics of social dilemmas in structured heterogeneous populations*. Proc Natl Acad Sci U S A, 2006. **103**(9): p. 3490-4.
14. Santos, F.C., M.D. Santos, and J.M. Pacheco, *Social diversity promotes the emergence of cooperation in public goods games*. Nature, 2008. **454**(7201): p. 213-6.
15. Pacheco, J.M., F.L. Pinheiro, and F.C. Santos, *Population structure induces a symmetry breaking favoring the emergence of cooperation*. PLoS Comput Biol, 2009. **5**(12): p. e1000596.
16. Souza, M.O., J.M. Pacheco, and F.C. Santos, *Evolution of cooperation under N-person snowdrift games*. Journal of Theoretical Biology, 2009. **260**(4): p. 581-588.
17. Sugden, R., *The Economics of Rights, Co-operation and Welfare*. 1986, Oxford UK: Blackwell. 191.

18. Hauert, C. and M. Doebeli, *Spatial structure often inhibits the evolution of cooperation in the snowdrift game*. Nature, 2004. **428**(6983): p. 643-646.
19. Zheng, D.F., et al., *Cooperation behavior in a model of evolutionary snowdrift games with N-person interactions*. Europhysics Letters, 2007. **80**: p. 18002-18006.
20. Traulsen, A., M.A. Nowak, and J.M. Pacheco, *Stochastic dynamics of invasion and fixation*. Phys Rev E Stat Nonlin Soft Matter Phys, 2006. **74**(1 Pt 1): p. 011909.
21. Traulsen, A., M.A. Nowak, and J.M. Pacheco, *Stochastic payoff evaluation increases the temperature of selection*. J Theor Biol, 2007. **244**(2): p. 349-56.
22. Traulsen, A., J.M. Pacheco, and M.A. Nowak, *Pairwise comparison and selection temperature in evolutionary game dynamics*. J Theor Biol, 2007. **246**(3): p. 522-9.
23. Ohtsuki, H., M.A. Nowak, and J.M. Pacheco, *Breaking the symmetry between interaction and replacement in evolutionary dynamics on graphs*. Phys Rev Lett, 2007. **98**(10): p. 108106.