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Effects of neighbourhood size and connectivity on the spatial Continuous Prisoner's Dilemma

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Abstract

The Prisoner's Dilemma, a two-person game in which the players can either cooperate or defect, is a common paradigm for studying the evolution of cooperation. In real situations cooperation is almost never all or nothing. This observation is the motivation for the Continuous Prisoner's Dilemma, in which individuals exhibit variable degrees of cooperation. It is known that in the presence of spatial structure, when individuals "play against" (i.e. interact with) their neighbours, and "compare to" ("learn from") them, cooperative investments can evolve to considerable levels. Here, we examine the effect of increasing the neighbourhood size: we find that the mean-field limit of no cooperation is reached for a critical neighbourhood size of about five neighbours on each side in a Moore neighbourhood, which does not depend on the size of the spatial lattice. We also find the related result that in a network of players, the critical average degree (number of neighbours) of nodes for which defection is the final state does not depend on network size, but only on the network topology. This critical average degree is considerably (about 10 times) higher for clustered (social) networks, than for distributed random networks. This result strengthens the argument that clustering is the mechanism which makes the development and maintenance of the cooperation possible. In the lattice topology, it is observed that when the neighbourhood sizes for "interacting" and "learning" differ by more than 0.5, cooperation is not sustainable, even for neighbourhood sizes that are below the mean-field limit of defection. We also study the evolution of neighbourhood sizes, as well as investment level. Here, we observe that the series of the interaction and learning neighbourhoods converge, and a final cooperative state with considerable levels of average investment is achieved.

Keywords: Prisoner's Dilemma; Continuous; Spatial; Lattice; Network

1. Introduction

The origin of cooperation is a fundamental problem in evolutionary biology. Cooperation is essential in the functioning of almost every known biological system (Hamilton, 1964a, b; Trivers, 1971; Dugatkin, 1997). For example, according to Eigen and Schuster (1979), Michod (1983), and Maynard Smith and Szathmáry (1995), early replicating molecules may have cooperated to form larger entities which could encode more information. Also, the transition from free-living single-cell protists to multicellular organisms seems to have depended on cooperation (Maynard Smith and Szathmáry, 1995; Buss, 1997).

It is however, difficult to explain why individuals should cooperate. In the traditional Prisoner's Dilemma (PD) model of cooperation, defecting individuals always have a higher fitness than cooperators. Cooperation is not an evolutionary stable strategy, because it can be invaded by defectors. Hence, the emergence of

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cooperation is generally assumed to require repeated play (with memory) and strategies such as Tit for Tat, or "tags" (Axelrod, 1984; Guttman, 1996; Lindgren and Nordahl, 1994; Miller, 1996). The work of Nowak and May (1992) showed that placing ensembles of cooperators and defectors on a lattice generates changing spatial patterns, in which both cooperators and defectors persist indefinitely. The introduction of spatial structure changes the picture from the mean-field result in which defection always wins to a final state with both cooperators and defectors present. Similar results were obtained by Epstein (1998), who introduced the Demographic Prisoner's Dilemma, in which the individuals have a fixed strategy (which is their phenotype), but are placed in a spatially structured lattice world. Epstein (1998) found that regions of cooperation persisted in this spatial model. The studies of Nakamaru et al. (1997), Iwasa et al. (1998), Nakamaru et al. (1998), and Irwin and Taylor (2001) showed that spatially structured models, such as the lattice model, produce the clumping of the cooperative players, and then enables them to invade a population of defectors, but the spatial structure also encourages the evolution of spiteful behaviour. These models consider the invasiveness and stability of fully developed, highly cooperative interactions.

The gradual evolution of cooperation from an initially selfish state represents a more plausible evolutionary scenario. It is then more natural to consider models in which several degrees of cooperation are possible (Doebeli and Knowlton, 1998; Roberts and Sherratt, 1998; Wahl and Nowak, 1999a, b; Szabó and Hauert, 2002a, b; Killingback and Doebeli, 2002). When we take into account the possibility of variable levels of cooperation, we can study the crucial issue of how cooperation can gradually evolve from a non-cooperative initial state. Roberts and Sherratt (1998) considered a "raise-the-stakes" strategy for the iterated PD, and showed that it invades and is stable against a number of alternative strategies. Doebeli and Knowlton (1998) considered interspecific symbiosis in the context of iterated asymmetric PD, and concluded that such interactions could increase in extent and frequency if the populations are spatially structured. In this model, strategies with very low levels of cooperation can gradually evolve to much more cooperative strategies. The end result is a high degree of mutualism between pairs of interacting individuals that belong to different species.

Killingback et al. (1999) extended the classical PD, introducing a model of cooperation which is based on the concept of investment, and develops further the ideas of Doebeli and Knowlton (1998). This evolutionary game is called Continuous Prisoner's Dilemma (CPD). Killingback et al. (1999) showed that intraspecific cooperation easily evolves from very low levels, and is sustained, with fluctuations, at relatively high levels, when the game is played in spatially structured populations. Killingback et al. (1999) assume that individuals play against their immediate neighbours, and also compare their payoffs to those of the same individual neighbours. It is important to know how robust are the results obtained by Killingback et al. (1999) when these assumptions are relaxed, i.e. when individuals are allowed to play against more distant neighbours (than their nearest ones), and then compare their payoffs to those of a different group of neighbours, which may be larger or smaller than the ones included in the first interaction neighbourhood. Also, Killingback et al. (1999) conjecture that clustering is the mechanism that allows the establishment and maintenance of a cooperative state. To investigate the validity of this hypothesis, we studied the behaviour of the CPD game on different topologies, such as networks with different clustering properties.

2. The basic model: the CPD

The CPD game between two individuals is based on the assumption that each of them makes an investment (which can take any non-negative real value). Making an investment I has the effect of reducing the fitness of the individual who makes it by "the cost" $C(I)$ and increasing the fitness of the beneficiary by "the benefit" $B(I)$. So, if two individuals 1 and 2, play against each other and make investments I_1 and I_2, the payoff of 1 is $B(I_2) - C(I_1)$ and that of 2 is $B(I_1) - C(I_2)$. Possible benefit and cost functions are shown in Fig. 1. Cost and benefit functions of this type are typical of what might be expected in a real biological situation, such as those discussed by Hart and Hart (1992) and Wilkinson (1984). The common feature of the functions $C(I)$ and $B(I)$ is that $B(I) > C(I)$ for a range of the argument $0 < I < I_{max}$ (for $I > I_{max}$ the cost is higher than the

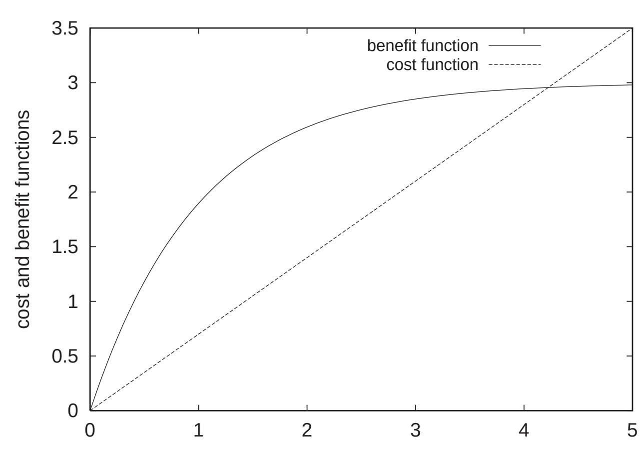

Fig. 1. Possible benefit and cost functions for the CPD game.

benefit, so it does not make sense for a player to invest an amount higher than I_{max}). Limiting the investment levels to just a pair of investment amounts would bring us back to the standard PD.

In the absence of an additional structure, i.e. in the mean-field approximation, or the well-mixed system, the zero-investment strategy is again the winning one. Starting at any level, investments will gradually evolve to zero, since the defectors will benefit from the investment of the cooperators without bearing the costs. Using adaptive dynamics, one can see that the zero investment strategy is the evolutionary stable strategy.

3. CPD in a lattice

Killingback et al. (1999) introduced spatial structure into the model, following the general approach of spatial evolutionary game theory (Axelrod, 1984; Nowak and May, 1992; Killingback and Doebeli, 1996). The individuals are placed in the cells of a 2D square lattice. Each individual makes an investment, and interacts with the individuals within a Moore neighbourhood of hers. A Moore neighbourhood of, e.g. size one, includes a cell's eight immediate neighbours: north, northeast, east, southeast, south, southwest, west, northwest, i.e. a "ring" of "thickness" one neighbour in all directions; that of size 2 will include all individuals within a "ring" of "thickness" two neighbours in all directions, etc. In this paper, we will refer to the thickness of the interaction neighbourhood as the *neighbourhood parameter*. The individual will get payoffs as prescribed by the rules of the game, when playing against each of the neighbours within her interaction neighbourhood. Her fitness is then the sum of the payoffs she gets from playing against all her neighbours. (In the process, the fitness of the neighbours is calculated too, as the sum of the payoffs they get from playing against the individuals within their own interaction neighbourhoods.) She then compares her payoff to those of the individuals within her learning neighbourhood, whose size (thickness) may be the same or different from that of the interaction neighbourhood. In traditional spatial evolutionary game theory, this distinction between the individual's interaction and learning neighbourhood is not made, silently assuming that they are the same. In this paper, we will refer to the thickness of the learning neighbourhood as the *dispersal parameter*. Our focal individual then identifies the neighbour with the highest fitness, and adopts that neighbour's strategy, by changing the amount of her investment to that of the neighbour's. At this stage the investment level of the player can be mutated at a fixed probability. This corresponds to an economic scenario in which the agents learn (with occasional errors) from their more successful partners, or to an evolutionary scenario in which the more successful phenotypes replace the less successful ones (with mutations). Every few generations the average investment per individual is calculated.

Killingback et al. (1999) simulated the CPD game in a square lattice with neighbourhood sizes for both interacting and learning (i.e. both the neighbourhood and dispersal parameters) set to one. They observed that the average investment increases from an almost zero starting value, to a significant final level of investment. Its average value for a cost function $C(I) = 0.7 \times I$ and benefit function $B(I) = 8(1 - e^{-I})$, in a 70×70 lattice, with periodic boundary conditions, is around 1.05. (The probability of mutations is set to 0.01, and they follow a Gaussian curve with centre at the individual's investment value, and width 10% of its peak.) The average investment amount is maintained close to 1.05 by the dynamics of the spatial system. It is smaller than the maximum investment I_{max}, but much larger than the initial maximum investment amount of 0.0001. The key factor that causes a state with considerable average investment levels to be established is the fact that higher investing individuals benefit from clustering together (Killingback et al., 1999). This result agrees with those of Nakamaru et al. (1997), Iwasa et al. (1998), Nakamaru et al. (1998), and Irwin and Taylor (2001).

We introduced "real-time" evolution as follows: every individual gets her own "clock" which tells her when to "wake up", look around, play against the neighbours within the interaction neighbourhood, compare her payoff to that of the neighbours within the learning neighbourhood, and revise her strategy. The "wake up" times are generated as $-\ln(rn)$ where rn is a random number with uniform distribution in [0,1], which guarantees that the events are independent (Gibson and Bruck, 2000). (This corresponds to asynchronous updating, but with a different distribution of "wake up" events.) We use the same lattice size, cost and benefit functions, and mutation rate as Killingback et al. (1999). After a sufficiently long time (which is of the order of 2000–3000 generations), the ensemble again reaches a state with a considerable degree of cooperativity, and the average investment level is about the same as that obtained by Killingback et al. (1999). A typical evolutionary outcome is shown in Fig. 2 (top graph).

Here, we can take a moment to discuss the role of mutations. The top graph in Fig. 2 corresponds to a very high mutation rate of 5%, with Gaussian distribution; the width of the Gaussian is set at 10% of its height. In Fig. 2, in the bottom graph, we show a time series obtained for a mutation rate of 0.5%, width of the Gaussian is 1% of its height. It is clear that the mutation rate does not determine mean value of the average investment in the steady state reached by the system; it rather influences how fast the steady state is reached (occasional "kicks" by mutations help the average

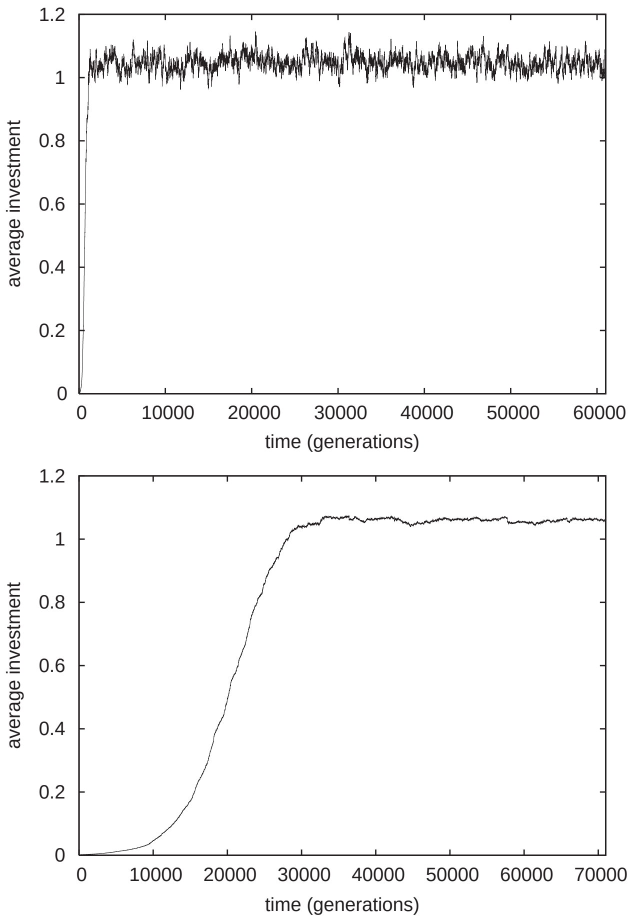

Fig. 2. The evolution of average investment with time when we only consider the nearest neighbours for interaction-control run. The top graph shows a time series obtained for a high mutation rate of 5%, the bottom graph corresponds to a mutation rate of 0.5%.

investment grow quickly), and the magnitude of fluctuations in steady state.

One general question is: what amount of spatial structure do we need (i.e. how big can neighbourhood sizes become) before we reach the mean-field (all defection) situation? Keeping a Moore-type of neighbourhood, with the neighbourhood and dispersal parameters equal to each-other (for the moment), we consider the cases where an individual plays against everybody within a neighbourhood of radius 2 (24 individuals), 3 (48 individuals), 4 (80 individuals), and so on. The rules of the game, the cost function, benefit function, mutation rate, and width of the Gaussian mutation curve, are kept fixed and equal to those used by Killingback et al. (1999). For each case, we averaged over 500 realisations of the system, and report results obtained on a 70×70 lattice, unless otherwise stated.

For neighbourhood and dispersal parameters equal to 2 (i.e. a neighbourhood that includes 24 individuals, as opposed to 8 for neighbourhood parameter 1), the final average investment value is very close to that obtained when those parameters are 1. When we increase the neighbourhood and dispersal parameters to 3, the final average investment drops to around 0.85, and it drops even further to about 0.6 for parameters' values equal to 4. For larger lattice sizes we get similar values of average investment in the steady state. Some typical runs are shown in Fig. 3 for lattice size 70×70.

The picture changes qualitatively when the neighbourhood and dispersal parameters become 5. Even though we start with a relatively large initial investment, the final average investment is extremely small (about 0.04, as opposed to 0.6 for a size four neighbourhood), and can occasionally drop to zero under the influence of even moderate fluctuations. This is shown in Fig. 4. The gradual drop in the value of average investment as we increase the neighbourhood size is typical for non-equilibrium-phase transitions. For larger lattice sizes we get similar results for the average investment, but, as expected, the fluctuations are lower. We can then state that at this neighbourhood size we have reached the mean-field limit, i.e. the picture we would obtain in absence of a spatial structure altogether (which for the CPD corresponds to a state of pure defection, as discussed above). The value of the neighbourhood and dispersal parameters for which the mean-field limit is reached was found to be independent of the lattice size, at least for reasonably large lattices (the meaning of "reasonably large" will become clear in the next paragraph). The immediate neighbourhood comprises about 100 individuals, while the extended one (the neighbours of the neighbours) comprises about 300. Furthermore, the results were independent of the choice of the boundary conditions; they hold also when periodic boundary conditions are not used (and the last row cells have only five neighbours, as opposed to eight

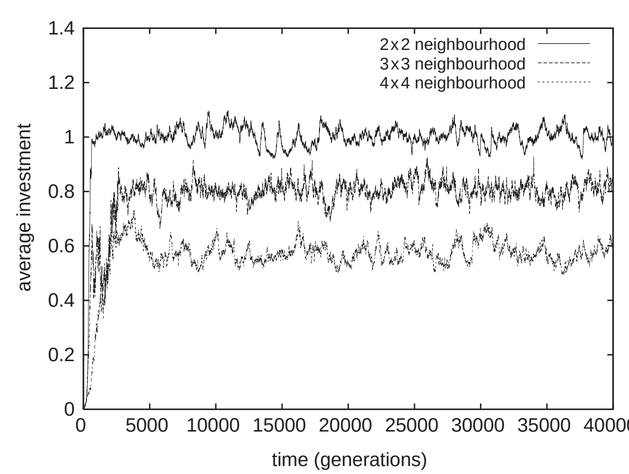

Fig. 3. Average investment vs. time for the cases when we consider more than one neighbour, here the neighbourhood and dispersal parameters are equal and vary from 2 to 4.

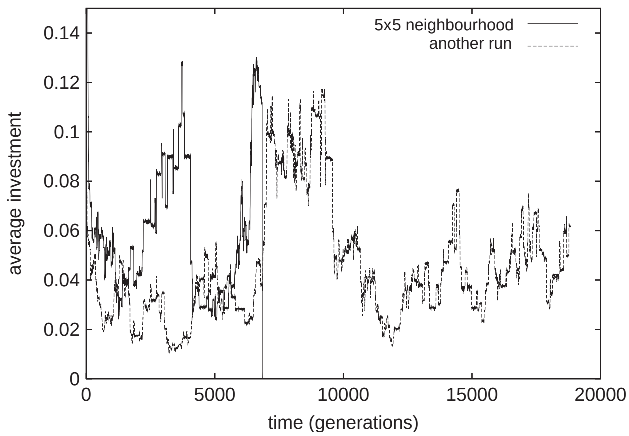

Fig. 4. In the case when the neighbourhood and dispersal parameter become 5, we are at the mean-field limit.

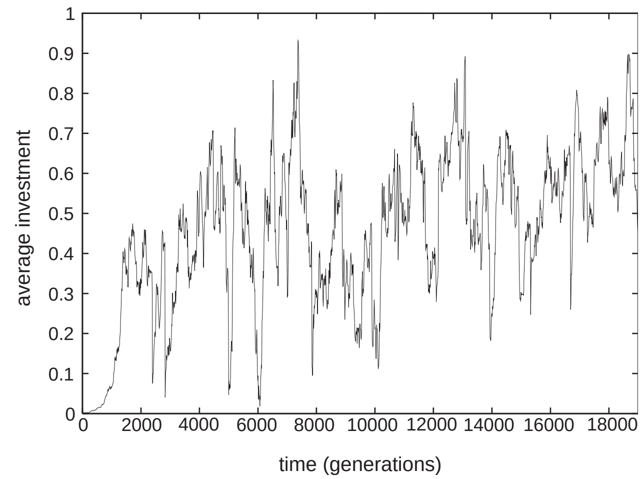

Fig. 5. The evolution of average investment with time in the case when both the neighbourhood and dispersal parameters are 4, but the lattice size is 30×30. Note the huge fluctuations, which bring the investment very close to zero as a result of mutations.

the other cells have, for a size one neighbourhood, and similarly for other neighbourhood sizes).

Let us now examine the role of the ratio of the neighbourhood size to lattice size. In Fig. 5, we show a time series of average investment for the case when both the neighbourhood and dispersal parameters are 4, and the lattice size is 30×30. It is important to note that for smaller lattices the size of fluctuations can become comparable to the average investment amount, even when the latter is considerably above zero, and often a mutation is enough to bring the average investment amount to zero. The average investment does come ‘‘dangerously’’ close to zero a few times in Fig. 5, and we observed it drop to zero in many other runs not shown here. So, if the lattice is too small, the fluctuations are enormous, and one might be misled by the result of a particular simulation. (For non-equilibrium-phase transitions like this one, physicists scale the average investment with the lattice size, but this goes beyond the purpose of the present paper.) The 70×70 lattice size we worked with (most of the time) is large enough to keep the fluctuations moderate, but also small enough to allow our simulations to run within reasonable times. We can conclude, based on our simulations, that the neighbourhood size for which we achieve the mean-field limit is about 5, and does not depend on the lattice size (at least for reasonably large lattices), contrary to the expectations of Killingback et al. (1999). The larger neighbourhood sizes ‘‘expose’’ the players that sit close to the borders of the square to a larger number of defector ‘‘outsiders’’, whose easily earned large payoffs might ‘‘tempt’’ our players. The numbers of these ‘‘tempters’’ only depend on the neighbourhood size. However, the lattice size influences a very important factor, the size of the fluctuations, which can make or break the fate of the cooperative state.

4. Variable neighbourhood size, the role of information, and evolution

The above results were obtained when the size of the interaction neighbourhood was the same as that of the learning neighbourhood. It is interesting to investigate what happens when this requirement is relaxed, and the neighbourhood and dispersal parameters are allowed to be different from each-other. For this purpose, we simulated a situation in which our agents play against individuals within a certain neighbourhood, but compare their payoffs to those of individuals within a neighbourhood that is different from their interaction neighbourhood. We observe that, if the neighbourhood parameter differs from the dispersal parameter by one or more, then cooperation is no longer sustained. Furthermore, the final state is defection, independent of whether the neighbourhood parameter is larger than the dispersal one, or vice versa. It appears as if, when the neighbourhood parameter is smaller than the dispersal parameter, the defectors outside the interaction neighbourhood, but within the learning neighbourhood, manage to ‘‘tempt’’ the cooperators. While in the case when the neighbourhood parameter is larger than the dispersal one, there are simply too many defectors in the interaction neighbourhood, taking advantage of the cooperators. In the economic context, too little or too much information favours defection, and kills the incentive to cooperate.

In the real life, however, there is no rigid separation of neighbourhoods from one-another. Individuals interact not only within a strictly defined neighbourhood, but rather occasionally include other individuals in their sphere of relations. This motivated us to determine what fractional difference between the neighbourhood and dispersal parameters is required for cooperation to be no longer sustained. This can be studied in our model by making the neighbourhood and dispersal parameters "continuous". To do this we constructed a "fractional size" neighbourhood in the following way: suppose the parameter has the form $\langle m.n \rangle$ with m the integer part and $\langle 0.n \rangle$ the fractional part. Then for the $(m+1)$th neighbour we generate a random number with uniform distribution in [0,1]. If the random number is smaller than $\langle 0.n \rangle$, the individual plays against this particular neighbour, otherwise the next event in the queue is generated. If the neighbour is at the corner, the random number is compared to $(0.n)^2$ (i.e. the fractional area of the rectangle). The remaining rules of the game are unchanged.

We find in this situation that cooperation only persists for differences between parameters up to about 0.5, and breaks down when the difference between the neighbourhood and dispersal parameters is 0.5 or larger. We have looked at both the case when the neighbourhood parameter is larger or smaller than the dispersal parameter. The results are the same: as soon as the difference between the two parameters becomes larger than 0.5, cooperation vanishes. Some results with different neighbourhood and dispersal parameters are shown in Fig. 6. Here, we can see that the average investment has already dropped to zero, when the difference between the neighbourhood and dispersal parameters reaches 0.6, and is very small, when that difference is 0.5.

There is no reason why every agent should have the same parameters, so we may treat them as "local", i.e. every individual has her own neighbourhood and dispersal parameters, n_i and d_i, which generally are not integers. When her turn comes, she plays against individuals within a neighbourhood of radius n_i and then compares herself to the individuals within the neighbourhood of radius d_i. However, there are cases when she meets a neighbour j, whose dispersal parameter is smaller than hers (i.e. he does not "see" her, even though she "sees" him). In such cases she could include him into her learning neighbourhood, comparing her payoff to his, and then adopting his investment amount, if he is doing better than her. This would correspond to the economics scenario, when the focal player can learn from players who do not see her. Otherwise she could leave that player who is doing better than her, but cannot see her, out of her learning neighbourhood, even though she sees him. This would correspond to the evolutionary scenario, where a player can only take over a cell he does see. A natural question is: do the two scenarios lead to different results?

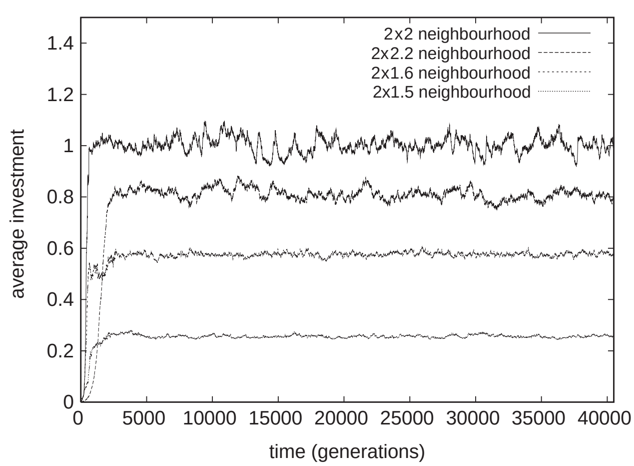

Fig. 6. When both neighbourhood and dispersal parameters are "continuous", the cooperation dies when their difference is about 0.5. All graphs are for neighbourhood parameter equal to 2; the top graph is the control one, corresponding to dispersal parameter equal to 2, then follow from top to bottom the time series for dispersal parameters equal to 2.2 (average investment in steady state is the same as for dispersal parameter equal to 1.8), then dispersal parameters equal to 1.6 and 1.5. When the dispersal parameter is 1.4, the final average investment drops to zero.

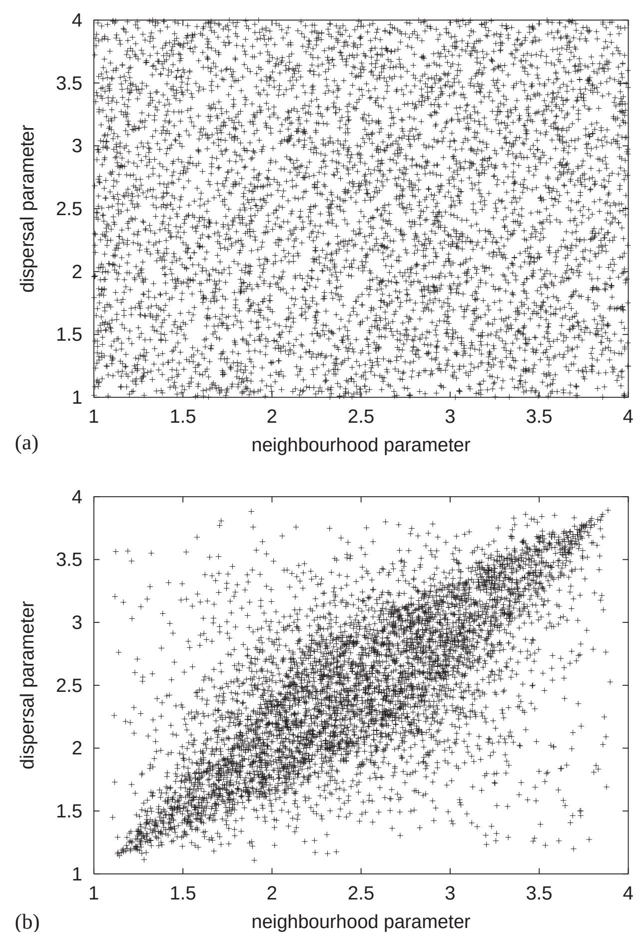

Fig. 7. (a) At the start of the run the neighbourhood and dispersal parameters are uniformly distributed between the values 1 and 4. (b) At the end, they have converged towards one-another. The distribution of points is closer to the diagonal $n_i = d_i$.

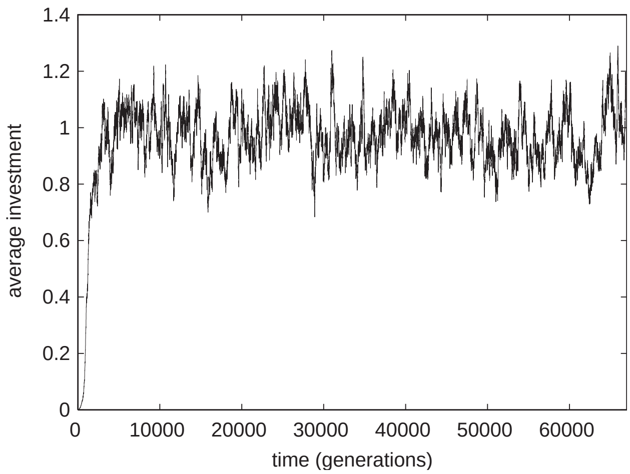

Fig. 8. The evolution of the average investment when both neighbourhood and dispersal parameters mutate, and are passed on from the more successful individual to the less successful one. Cooperation persists and investment remains at considerable levels.

We consider both possibilities: first when she does compare her payoff to that of the neighbour with a smaller dispersal parameter (and, if he is doing better, adopts his strategy, i.e. investment amount), and second when she does not. For that we had both the neighbourhood and dispersal parameters initialized randomly between the values 1 and 4 (which are the interesting values, since for larger parameters there is no sustainable cooperation). The neighbourhood and dispersal parameters are treated as evolutionary phenotypes: the parameters of the neighbour that is doing better are adopted, together with the value of the investment amount. Both parameters, as well as the investment amount, are set to mutate at a rate of 0.01, following a Gaussian curve with a width 10% of its peak.

In both scenarios, something interesting happens with the neighbourhood and dispersal parameters: in Fig. 7(a) we plot their initial values, which are uniformly distributed within a square. At the end of the simulation, we find their values have converged closer to the diagonal $n_i = d_i$ (see Fig. 7(b)). The convergence of the neighbourhood and dispersal parameters toward each-other corresponds to the development of a cooperative state, after which the average investment continues to sustain relatively high values, almost as high as those initially reported by Killingback et al. (1999), but the fluctuations are now larger. A typical time series for the average investment in the evolutionary scenario is shown in Fig. 8.

5. CPD in a Network

Based on the observed dynamics of the spatial CPD on regular lattices, Killingback et al. (1999) formulated the hypothesis that the mechanism that facilitates and maintains cooperation in worlds of this particular topology is their *clustering* properties. It is not easy to study this hypothesis within the regular lattices topology, since, in order to verify or refute it, we would have to obtain results on other topologies, different from the regular lattices. Furthermore, for many systems of interacting individuals, the regular lattices do not provide a fully adequate model for the observed topological properties. These properties include large clustering, and short average path length between any two nodes (individuals, in our context).

Watts and Strogatz first introduced "small world networks" (Watts and Strogatz, 1998; Watts, 1998), which are clustered structures. A spatial structure is called clustered, if the existence of links between nodes A and B, and B and C, makes it very probable that there be a link between A and C (sociologists call this "transitivity"). The regular lattices are highly clustered structures. They also exhibit a long path length, i.e. the number of intermediate nodes between any two nodes A and B is usually large. The random graphs of Erdös and Rényi (Bollobás, 1985), in which a node links to any other with a constant probability, have short path lengths between nodes, but exhibit no clustering, i.e. are very distributed structures. A small world network has the two properties of high clustering and short average path length between two nodes, which increases with the network size N as the logarithm of N (Watts and Strogatz, 1998; Amaral et al., 2000). Social networks (i.e. networks in which humans constitute the nodes, and acquaintances the links) are examples of small world networks (Strogatz, 2001; Albert and Barabási, 2002; Dorogovtsev and Mendes, 2002). A special class of small world networks are the scale-free ones, in which the degree (i.e. the number of the links a node has) distribution obeys a power law (hence it is independent of network size). Many algorithms for generating scale-free networks have been proposed. This kind of topology is also observed in some social networks (Strogatz, 2001; Albert and Barabási, 2002; Dorogovtsev and Mendes, 2002; Newman, 2001; Barabási et al., 2002; Ebel et al., 2002b).

Davidsen et al., 2002; Ebel et al., 2002a introduced an algorithm that produces small world networks which follow closely the characteristics of social and acquaintance networks. Their basic assumption is that the mechanism which generates these networks is that people are introduced to one-another by a common acquaintance, so-called *transitive linking*. At each time step two processes take place: (i) A randomly chosen individual introduces two (randomly picked) acquaintances of hers to one-another. If this individual has less than two acquaintances, she introduces herself to a randomly picked individual. (ii) One randomly chosen individual leaves the network with probability p. All her links are disconnected, and she is replaced by a new individual with one randomly picked acquaintance. This probability p, which is called the death probability, is typically very small. The size of the network N remains constant in the process. The finite lifetime of links brings the network to a steady state, in which the degree distribution is exponential for larger death rates, and becomes power law (with a cutoff) as the death rate decreases.

The hypothesis that clustering in lattices is the key factor that makes possible the establishment and maintenance of cooperation can be verified in networks of different topologies, since some of them exhibit large clustering, and some do not. To do this, we study the evolution of average investment in social networks, and also in random networks, for comparison. The two topologies were chosen, since they represent extremes when clustering properties in networks are considered: the random networks are distributed structures with very little clustering, while the social networks exhibit a high clustering degree. Also, in these two structures we can tune the connectivity (denned as the ratio of the actual number of links in the network to the total number of all possible links): for the random networks it is equal to the probability of linking between two nodes, while for the social networks model it can be varied by varying the death probability.

The game proceeds as follows: "wake-up" times are generated for each node as $-\ln(rn)$, where rn is a random number with uniform distribution in [0,1]. The picked node then plays against the nodes it can "see", i.e. it is linked to. Recall that in a network each node can have different degrees, i.e. number of immediate neighbours. This means that what we previously called neighbourhood parameter differs from node to node, and is equal to the degree of the focal node (player). This focal player then calculates her payoff from playing against her immediate neighbours, according to the rules of the CPD game. These neighbours also play against their immediate neighbours, and calculate their respective payoffs. The picked (focal) node then compares her playoff to that of the neighbour that is doing best, among her immediate neighbours. The neighbours she compares herself with (learns from) are the same ones she played against (interacted with), i.e. albeit different from one node to another, the neighbourhood and dispersal parameters for one node are equal to each-other (and the degree of that node). The focal node then adopts the investment amount of the neighbour that is doing best as her new investment amount, and then the next event is generated. The process is iterated, and the average investment is calculated every few "generations". This process is repeated for different network sizes and averaged over 100 different configurations for each network size.

For any fully connected (saturated) network, with connectivity equal to one, the final state will be of pure defection, since this is a well-mixed system, in which "everybody sees (or connects to) everybody". As the connectivity decreases, for each network size there is a certain threshold value, for which the final state ceases to be that of pure defection, but rather a very small average investment. As the connectivity decreases even further, the steady state average investment increases. The variation of average investment with the connectivity for a social network with $N = 6000$ nodes is shown in Fig. 9. The transition from the cooperative network to the non-cooperative one is what physicists call a critical transition, i.e. the value of the average investment decays slowly, as opposed to exhibiting a sharp drop at the crossover connectivity value.

For a random network of the same size ($N = 6000$), the same transition is present, but the connectivity for which the transition happens is $C_r = 0.003$. This critical connectivity is much smaller than $C_s \simeq 0.025$ we obtained for a social network of the same size. Since the fundamental difference between social and random networks is in their clustering properties, it is natural to check the dependence of the average degree (number of neighbours) per node at the transition point on the network size for both topologies. The results are shown in Fig. 10. For both topologies, the critical average degree remains essentially constant as the network size is varied. It is about 150 for the social network model, and about 20 for the random network. This surprising result is a very strong argument in favour of the hypothesis that clustering is the key mechanism which leads to cooperation being first established and then maintained. Indeed, social networks, with their pronounced tendency to cluster, maintain the cooperative state for a much larger average connectivity (and node degree) than the maximally distributed random networks.

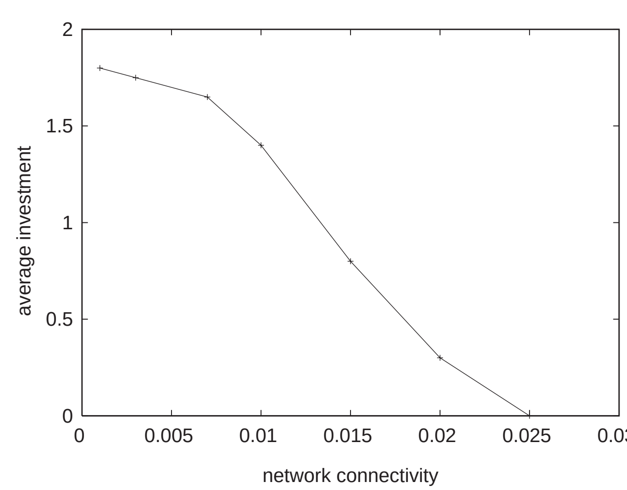

Fig. 9. The variation of average investment in the steady state with the connectivity for a social network of size $N = 6000$.

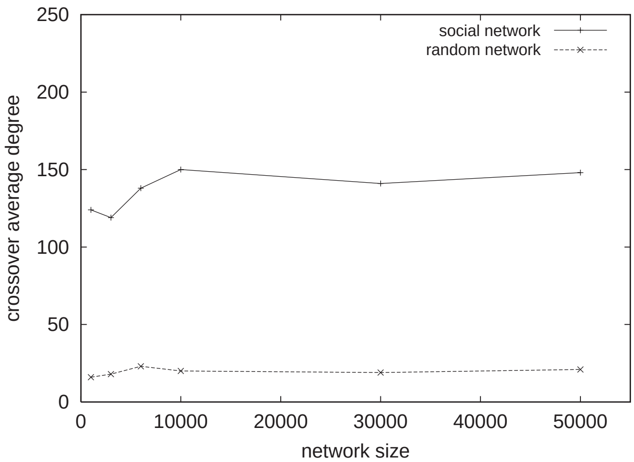

Fig. 10. The average degree at transition vs. network size. The average degree remains practically constant, but for the social networks it is much higher than for the random networks.

6. Conclusions

We have studied the behaviour of the CPD model on different spatial structures, including 2D lattices and networks of different topologies. The CPD is an evolutionary game which is a natural extension of the standard PD. In the CPD each individual makes an investment in favour of herself and the neighbours, and the investment takes on any value, not just two discrete values. In spatial structures like the ones we have considered, and for small neighbourhood sizes/connectivities the investment levels evolve by getting higher and stabilizing around a given value in a steady state.

The cooperation develops and is maintained relatively easy, which leads us to believe that the cooperation is not such a difficult evolutionary paradox. We have tested this in the case of the square lattice, by increasing the neighbourhood sizes, and found that the neighbourhood size for which the steady state is pure defection is about 100 neighbours. As long as the number of the neighbours the individual plays against (which we call the neighbourhood parameter) and that of the neighbours the individual compares herself to (called the dispersal parameter) remains the same, the cooperation is quite robust. The mean-field neighbourhood size limit does not depend on the size of the lattice, as long as the lattice is reasonably large.

Since the interaction neighbourhood and the learning neighbourhood do not have to coincide with one-another, we studied the game when the neighbourhood and dispersal parameters are different. In this case, we found that cooperation only develops for differences between them of about 0.5 or smaller. Too little information favours defection, but apparently so does too much information. Something interesting happens when we allow the neighbourhood and dispersal parameters to mutate, and at the same time, treat them as phenotypes: they are adopted, together with the investment amount of the individual that is doing better. The values of the neighbourhood and dispersal parameters converge toward one-another, i.e. their differences decrease. Cooperation persists, and the average investment fluctuates around relatively high levels in the steady state.

We verified the hypothesis that clustering is the factor that facilitates and maintains high average investment values by considering players in networks of different topologies. In all of them, a transition is observed between the cooperative steady state and the purely defective one, as the connectivity of the network increases. For both social networks and random ones, the average degree at the transition point is practically independent of the network size. However, the average degree at transition for social networks is about 150, while that for random networks is much lower (about 20). The two topologies differ in their degree of clustering. The social networks topology, with its pronounced tendency to cluster, allows the establishment and maintenance of a cooperative state, something the distributed random networks topology do not. However, when the connectivity of the network exceeds a certain value (i.e. too many individuals ‘‘see’’ one-another and communicate), cooperation can not develop or be maintained, and the steady-state strategy is pure defection.

The CPD model deepens our understanding as to how cooperation has evolved gradually from lower to higher levels in many spatially structured systems, where the entities involved can vary from replicating molecules to whole organisms (Wilson, 1980; Michod, 1983; Buss, 1997; Maynard Smith and Szathmáry (1995); Dugatkin, 1997): the clustered topology helps cooperation develop and survive. It is very encouraging that cooperation is quite robust in such systems. On the other hand, in the economic world, globalization brings about an increase in the connectivities of social and economic networks, and cooperation may consequently be less likely to persist.

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References

Albert, R., Barabási, A.-L., 2002. Statistical mechanics of complex networks. Rev. Mod. Phys. 74, 47–97.

Amaral, L.A.N., Scala, A., Barthélémy, M., Stanley, E.H., 2000. Classes of small-world networks. Proc. Natl Acad. Sci. USA. 97, 11149–11152.

Axelrod, R., 1984. The Evolution of Cooperation. Basic Books, New York.

Barabási, A.-L., Jeong, H., Néda, Z., Ravasz, E., Schubert, A., Vicsek, T., 2002. Evolution of the social network of scientific collaborations. Physica A 311, 590–614.

Bollobás, B., 1985. Random Graphs. Academic Press, London.

Buss, L.W., 1997. The Evolution of Individuality. Princeton University Press, Menlo Park, CA.

Davidsen, J., Ebel, H., Bornholdt, S., 2002. Emergence of a small world from local interactions: modeling acquaintance networks. Phys. Rev. Lett. 88, 128701–128704.

Doebeli, M., Knowlton, N., 1998. The evolution of interspecific mutualism. Proc. Natl Acad. Sci. USA 95, 8676–8680.

Dorogovtsev, S.N., Mendes, J.F.F., 2002. Evolution of networks. Adv. Phys. 51, 1079–1187.

Dugatkin, L.A., 1997. Cooperation Among Animals. Oxford University Press, Oxford.

Ebel, H., Davidsen, J., Bornholdt, S., 2002a. Dynamics of social networks. Complexity 8 (2), 24–27.

Ebel, H., Mielsch, L.-I., Bornholdt, S., 2002b. Scale-free topology of e-mail networks. Phys. Rev. E 66, 035103(R)–035106(R).

Eigen, M., Schuster, P., 1979. The Hypercycle: A Principle of Natural Self-Organization. Springer, Berlin.

Epstein, J.M., 1998. Zones of cooperation in demographic prisoner's dilemma. Complexity 4 (2), 36–48.

Gibson, M.A., Bruck, J., 2000. Efficient exact stochastic simulation of chemical systems with many species and many channels. J. Phys. Chem. A 104, 1876–1889.

Guttman, J.M., 1996. Rational actors, tit-for-tat types, and the evolution of cooperation. J. Econ. Behav. Org. 29 (1), 27–56.

Hamilton, W.D., 1964a. The genetical evolution of social behavior I. J. Theor. Biol. 7, 1–16.

Hamilton, W.D., 1964b. The genetical evolution of social behavior II. J. Theor. Biol. 7, 17–52.

Hart, B., Hart, L., 1992. Reciprocal allogrooming in impala. Anim. Behav. 44, 1073–1083.

Irwin, A., Taylor, P., 2001. Evolution of altruism in stepping-stone populations with overlapping generations. Theor. Popul. Biol. 60, 315–325.

Iwasa, Y., Nakamaru, M., Levin, S.A., 1998. Allelopathy of bacteria in a lattice population: competition between colicin-sensitive and colicin-producing strains. Evol. Ecol. 12, 785–802.

Killingback, T., Doebeli, M., 1996. Spatial evolutionary game theory: hawks and doves revisited. Proc. R. Soc. London B 263, 1135–1144.

Killingback, T., Doebeli, M., 2002. Cooperation with variable investment. Am. Nat. 160, 421–438.

Killingback, T., Doebeli, M., Knowlton, N., 1999. Variable investment, the Continuous Prisoner's Dilemma, and the origin of cooperation. Proc. R. Soc. London B 266 (1430), 1723–1728.

Lindgren, K., Nordahl, M.G., 1994. Evolutionary dynamics of spatial games. Physica D 75, 292–309.

Maynard Smith, J., Szathmáry, E., 1995. The Major Transitions in Evolution. W.H. Freeman & Co, Oxford.

Michod, R., 1983. Population biology of the first replicators: the origin of genotype, phenotype, and organism. Am. Zool. 23, 5–14.

Miller, J.H., 1996. The coevolution of automata in repeated prisoner's dilemma. J. Econ. Behav. Org. 29 (1), 87–112.

Nakamaru, M., Matsuda, H., Iwasa, Y., 1997. The evolution of cooperation in a lattice-structured population. J. Theor. Biol. 184, 65–81.

Nakamaru, M., Nogami, H., Iwasa, Y., 1998. Score-dependent fertility model for the evolution of cooperation in a lattice. J. Theor. Biol. 194, 101–124.

Newman, M.E.J., 2001. Scientific collaboration networks II. Shortest paths, weighted networks, and centrality. Phys. Rev. E 64, 016132–016138.

Nowak, M.A., May, R.M., 1992. Evolutionary games and spatial chaos. Nature 359, 826–829.

Roberts, G., Sherratt, T.N., 1998. Development of cooperative relationships through increased investment. Nature 394, 175–179.

Strogatz, S.H., 2001. Exploring complex networks. Nature 410, 268–276.

Szabó, G., Hauert, C., 2002a. Evolutionary PD games with voluntary participation. Phys. Rev. E 66, 062903–062906.

Szabó, G., Hauert, C., 2002b. Phase transitions and volunteering in spatial public goods games. Phys. Rev. Lett. 89, 118101–118104.

Trivers, R., 1971. The evolution of reciprocal altruism. Q. Rev. Biol. 46, 35–57.

Wahl, L.M., Nowak, M.A., 1999a. The continuous prisoner's dilemma I. Linear reactive strategies. J. Theor. Biol. 200 (3), 307–321.

Wahl, L.M., Nowak, M.A., 1999b. The continuous prisoner's dilemma II. Linear reactive strategies. J. Theor. Biol. 200 (3), 323–338.

Watts, D.J., 1998. Small Worlds: The Dynamics of Networks between Order and Randomness. Princeton University Press, Princeton, NJ.

Watts, D.J., Strogatz, S.H., 1998. Collective dynamics of 'small-world' networks. Nature 393, 440–442.

Wilkinson, G.S., 1984. Reciprocal food-sharing in the vampire bat. Nature 308, 181–184.

Wilson, D.S., 1980. The Natural Selection of Populations and Communities. Benjamin Cummings, Menlo Park, CA.