Variable investment, the Continuous Prisoner's Dilemma, and the origin of cooperation

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Cooperation is fundamental to many biological systems. A common metaphor for studying the evolution of cooperation is the Prisoner's Dilemma, a game with two strategies: cooperate or defect. However, cooperation is rarely all or nothing, and its evolution probably involves the gradual extension of initially modest degrees of assistance. The inability of the Prisoner's Dilemma to capture this basic aspect limits its use for understanding the evolutionary origins of cooperation. Here we consider a framework for cooperation based on the concept of investment: an act which is costly, but which benefits other individuals, where the cost and benefit depend on the level of investment made. In the resulting Continuous Prisoner's Dilemma the essential problem of cooperation remains: in the absence of any additional structure non-zero levels of investment cannot evolve. However, if investments are considered in a spatially structured context, selfish individuals who make arbitrarily low investments can be invaded by higher-investing mutants. This results in the mean level of investment evolving to significant levels, where it is maintained indefinitely. This approach provides a natural solution to the fundamental problem of how cooperation gradually increases from a non-cooperative state.

Keywords: evolution of cooperation; Continuous Prisoner's Dilemma; spatial games; cellular automata; stochastic games

1. INTRODUCTION

Obtaining a satisfactory understanding of the evolutionary origin and stability of altruism or cooperation is an enduring problem in evolutionary biology. Cooperation seems to have played a fundamental role in many of the major transitions in evolution (Maynard Smith & Szathmáry 1995), as well as being essential to the functioning of a large number of existing biological systems (Hamilton 1964a,b; Trivers 1971; Dugatkin 1997). In the course of the history of life, cooperation appears to have been crucial at many points. Thus, the earliest replicating molecules may have cooperated to form larger replicating entities capable of encoding more information (Eigen & Schuster 1979; Michod 1983; Maynard Smith & Szathmáry 1995), and the integration of the once free-living prokaryote ancestors of mitochondria and chloroplasts into eukaryotic cells seems to have been a cooperative phenomenon (Maynard Smith & Szathmáry 1995). Also, the ancestors of the cells of multicellular organisms were once free-living single-celled protists, and the transition from single-celled to multicellular organisms appears to have depended on cooperation between ancestral cells (Buss 1987; Maynard Smith & Szathmáry 1995). Finally, cooperation has also been essential for the evolution of many social groups (Maynard Smith & Szathmáry 1995; Dugatkin 1997). Thus cooperation has most probably played a key role in the origin of many

biological systems and it continues to play a key role in ensuring the stability of these systems.

However, the difficulty in explaining the evolutionary origin and stability of cooperation is apparent: selfish individuals always have a higher fitness than cooperators since they receive the benefits of cooperation without bearing the costs. Therefore, in a world of non-cooperators, a cooperative mutant would be eliminated by natural selection, and it is hard to see how cooperation could evolve in the first place. Furthermore, even if cooperation had been established by some means, one would not expect it to be stable—selfish mutants could invade the population and would then increase in frequency until the cooperators had been eliminated. Thus, the essential theoretical problem is to elucidate how cooperative behaviour can originally evolve in a selfish world and how, thereafter, it can be maintained against invasion by selfish individuals.

Most previous theoretical approaches to understanding the evolution of cooperation among non-relatives are based on reciprocal altruism and on the iterated Prisoner's Dilemma (Trivers 1971; Axelrod & Hamilton 1981). This approach assumes that individuals can adopt complex strategies that take into account the past history of their interactions with other individuals (e.g. Nowak & Sigmund 1993, 1998; Roberts & Sherratt 1998). However, many of the most fundamental instances of cooperation, such as those cited above, involve very simple entities for which such assumptions are often implausible. An alternative approach, initiated by Nowak & May (1992), is based on a non-iterated Prisoner's Dilemma played in a

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spatially structured population. In this model every individual either cooperates or defects, and there are no complex strategies involved. The realization that spatial structure allows the maintenance of cooperation in the absence of any strategic complexity represents an important advance in the understanding of cooperation. However, most previous models using either the iterated or the spatial Prisoner's Dilemma considered the invasiveness and stability of fully developed, highly cooperative interactions, despite the fact that the gradual evolution of cooperation from an initially selfish state represents a more plausible evolutionary scenario. Thus, it is more natural to consider a framework in which different degrees of cooperation are possible (Mar & St Denis 1994; Doebeli & Knowlton 1998; Roberts & Sherratt 1998; Wahl & Nowak 1999*a,b*). Once variable levels of cooperation are considered it becomes possible to study the crucial issue of how cooperation can evolve gradually from an initial state consisting of non-cooperative entities. Two recent models attempt to address this problem. Roberts & Sherratt (1998) demonstrated that a 'raise-the-stakes' strategy in the iterated Prisoner's Dilemma both invades and is stable against a number of other strategies. In this model the extent of cooperation can increase during a given iterated interaction between a pair of individuals, and the frequency of this strategy can increase, but the strategy itself is fixed and does not evolve. Doebeli & Knowlton (1998) demonstrated that interspecific mutualism could evolutionarily increase in extent and frequency for iterated interspecific relationships that take place in spatially structured populations. In the latter approach, strategies yielding very low levels of cooperation could evolve gradually to much more cooperative strategies, resulting in a high degree of mutualism between pairs of interacting individuals belonging to different species.

Here we introduce a new model of intraspecific cooperation, formulated in terms of the concept of investment, which develops some of the ideas present in Doebeli & Knowlton (1998). We will refer to the evolutionary game that results from our formulation as the Continuous Prisoner's Dilemma. We show that intraspecific cooperation easily evolves from very low levels in the Continuous Prisoner's Dilemma when the game is played in spatially structured populations.

2. MODEL AND RESULTS

The simplest case for the Continuous Prisoner's Dilemma consists of two individuals, each making an investment. An investment I has the following effects: (i) the fitness of the investor is reduced by $C(I)$, where C is some function of I (the cost of making the investment); and (ii) the fitness of the beneficiary is increased by $B(I)$, where B is another function of I (the benefit resulting from the investment). Therefore, if two interacting individuals X and Y make investments I_1 and I_2, respectively, the pay-off to X is $S(I_1, I_2) = B(I_2) - C(I_1)$ while the pay-off to Y is $S(I_2, I_1) = B(I_1) - C(I_2)$. We assume that the cost and benefit functions are such that for investments between zero and an upper limit I_{max}, $B(I) > C(I)$. Possible functions for $B(I)$ and $C(I)$ are shown in figure 1. This assumption is a necessary condition for cooperation to evolve; otherwise, if every individual invests I, the
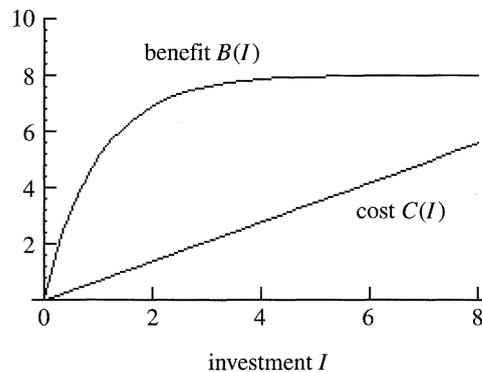

Figure 1. Possible benefit $B(I)$ and cost $C(I)$ functions. In the simulations shown in this paper, we take $B(I)$ $= B_0[1 - \exp(-B_1, I)]$ and $C(I) = C_0\,I$, with $B_0 = 8$, $B_1 = 1$ and $C_0 = 0.7$. For all investments I between 0 and I_{max}, $B(I) > C(I)$. $I_M = (1/B_1)\ln(B_0B_1/C_0)$ is the investment maximizing $B(I) - C(I)$; for the parameters used here $I_M \approx 2.44$.

fitness of every individual is lower if $I > 0$ than if $I = 0$. Moreover, for any positive investments $I_1 < I_2 < I_M$, where I_M is the investment that maximizes $B(I) - C(I)$, we have $S(I_1,I_2) > S(I_2,I_2) > S(I_1,I_1) > S(I_2,I_1)$. Thus, restricting the possible investments to only two values, I_1 (defect) and I_2 (cooperate), results in the standard Prisoner's Dilemma. Therefore, the Continuous Prisoner's Dilemma may be viewed as a generalization of the standard Prisoner's Dilemma in which any level of investment can be made. This aspect of the system mirrors the ability of biological organisms to vary the degree to which they cooperate, with total non-cooperation being one extreme.

The problem of the evolution of cooperation, formulated in terms of investment, is to understand how significant levels of investment can evolve from extremely low initial levels. Since investments are costly, it is intuitively clear, and can be shown formally by considering a suitable adaptive dynamics, that a population consisting of individuals making a positive investment can always be invaded by mutants making a lower investment—a process that results in the level of investment evolving to zero. Thus, in the Continuous Prisoner's Dilemma, an increase in the level of investment cannot evolve without some additional structure. Here we take the additional structure to be spatial extension. This is a natural choice as biological systems are spatially distributed. Moreover, alternative structures, such as individuals adopting complex strategies to deal with repeated interactions between the same individuals, often depend on assumptions of the individuals' cognitive abilities that are inappropriate for simple cooperative entities. We introduce spatial structure following the general approach of spatial evolutionary game theory (Axelrod 1984; Nowak & May 1992; Killingback & Doebeli 1996). Space is represented by a lattice of cells (which, for convenience, we will take here to be a two-dimensional square lattice). Each lattice cell j is occupied by an individual who makes an investment I_j. In each generation, every individual interacts with a defined set of local neighbours (here taken to be the eight immediately surrounding cells) and the fitness of each individual is given by the sum of the pay-offs it receives in its interactions with its neighbours.
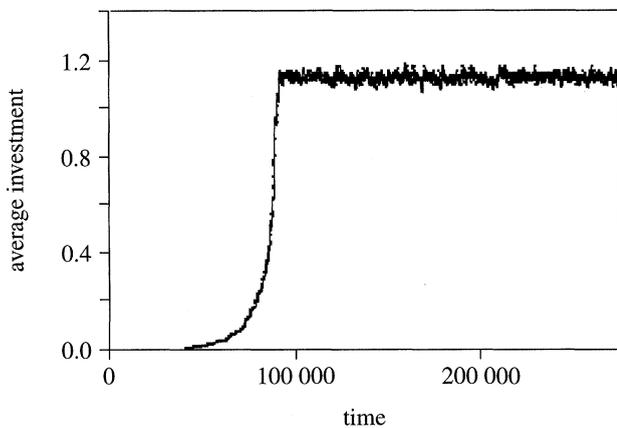
Figure 2. Change in the mean level of investment over time for the cost and benefit functions shown in figure 1. The mean investment per cell at time t, $I(t)$, evolves from very low initial values to levels that are a significant fraction of I_M. The asymptotic value I^* is close to $I_0 = (1/B_1) \ln (B_0 B_1 / 4 C_0)$ $= \ln (8/2.8) \approx 1.05$ (see text). The simulation was performed on a 70×70 square lattice with periodic boundary conditions, starting from an initial configuration with investment values picked uniformly randomly from the range $(0, 0.0001)$. The mutation rate per cell was 0.01, and mutations were picked from a normal distribution with mean equal to the investment of the cell which was mutating and variance equal to 10% of the mean.

At the start of the next generation the individual in each cell adopts the strategy associated with the individual in its local neighbourhood (including the cell itself) that has the highest fitness. This corresponds to an evolutionary scenario in which successful phenotypes replace less successful ones. To study the evolution of cooperation, we start this system from an initial configuration consisting of extremely low levels of investment and allow occasional mutations that change the level of investment associated with a given cell.

The evolutionary dynamics of this system is shown in figure 2 for typical benefit and cost functions. The mean investment per cell increases from an extremely low starting value, representing an initial situation in which all individuals are selfish, to a much higher level, which is a significant fraction of I_M, the investment that maximizes the mean fitness of the population. Once the mean investment per cell reaches this higher level, it is maintained indefinitely close to this value by the dynamics of the spatial system. While it may seem surprising that investments can evolve from arbitrarily low values to significant levels in such a simple system, the mechanisms responsible for this are readily comprehensible.

The first mechanism depends on the fact that I-investors obtain a mutual benefit from clustering. Consider, for example, a cluster of I-investors immersed in a sea of I'-investors, where $I > I'$. Let i and j be two neighbouring cells, occupied by I and I'-investors, respectively. If I has n neighbours who are I-investors and $8-n$ who are I'-investors, and if j has m neighbours who are I-investors and $8-m$ I'-investors, then the necessary condition for i to be able to take over j is that $(n-m)B(I) - 8C(I) > (n-m)B(I') - 8C(I')$. Whether this is also sufficient follows from applying similar arguments to the other neighbours of j. It follows from such
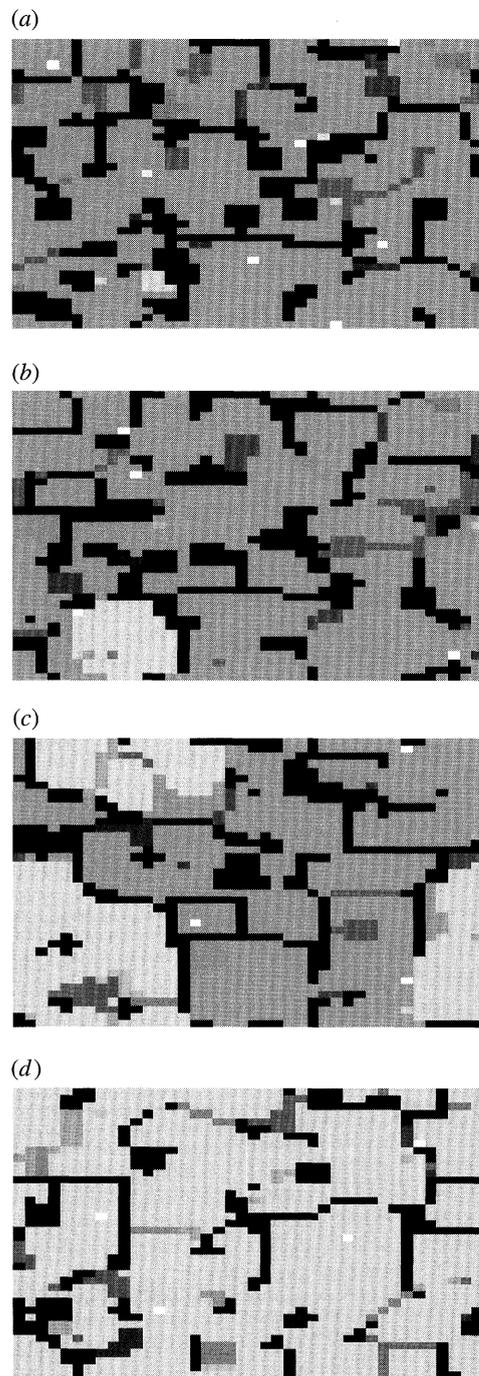
(a)

(b)

(c)

(d)

Figure 3. The ability of higher-investing mutations to invade a world of lower investors is the fundamental process for the evolution of $I(t)$. This process is shown here in a simulation of the spatial theory on a 40×40 square lattice with periodic boundary conditions. Higher investors are represented by lighter shades. (a) The small local cluster (bottom centre-left of the frame) that has been established by a higher-investing mutant (see text). In (b) (nine generations later), and (c) (24 generations later), this cluster grows through the mechanism explained in the text, until it has taken over most cells, as shown in (d) (61 generations later). The repeated functioning of this process results in $I(t)$ evolving from arbitrarily low values to levels that are a significant fraction of I_M.

considerations that in suitable circumstances, a cluster of higher investors can expand in a sea of lower investors. Thus clustering can result in the growth of geometrical structures of higher-investing strategies once basic clusters
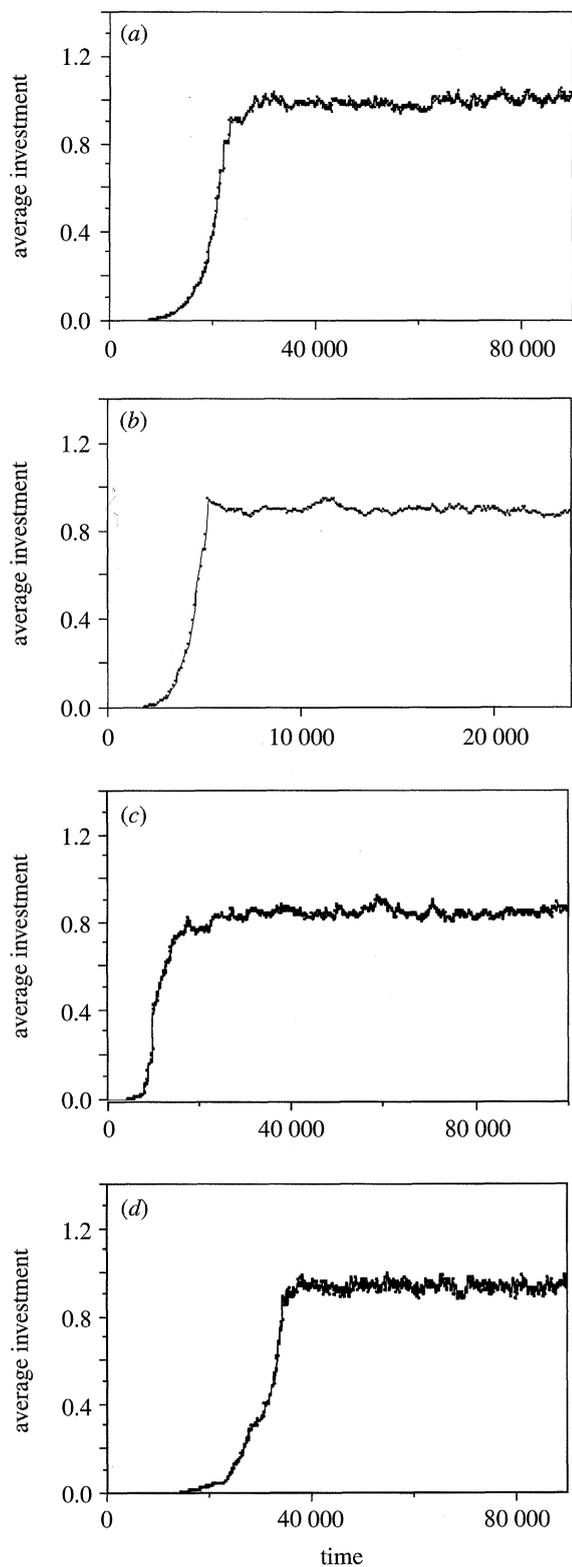
Figure 4. The results of simulations showing the change of $I(t)$ with time for various random effects and spatial irregularities. (a) Stochastic updating in which successful neighbours take over a lattice site only with 80% probability, otherwise the occupant is left unchanged. (b) Asynchronous updating, in which cells are picked randomly and updated independently. (c) Deterministic updating on a random lattice in which each cell can have a different number of neighbours (this is obtained by deleting a randomly picked proportion of cells in a square lattice). (d) Deterministic updating on a regular lattice, but with 10% of the mutations in each generation being in the range (0, 0.0001) of highly selfish

of them have formed. The second mechanism relates to how such basic clusters of more cooperative individuals become established in the first place. Consider a situation in which a given cell j, with associated investment I, has higher fitness than some of its neighbouring cells. In this case, in the next generation, the occupant of j may take over these cells to form a cluster of I-investors. However, if the strategy associated with j undergoes a mutation to a higher-investing strategy I' (where $I' > I$), then if I' is only slightly greater than I it may be that the occupant of j (now with the mutant strategy I') still has a higher fitness than some of its neighbours. In this case, a cluster of I'-investors will be formed. It now follows from the first mechanism that this cluster of higher-investing individuals may be able to expand in the sea of lower investors. For any benefit and cost functions, satisfying the one basic assumption stated above, the repeated operation of these two mechanisms will drive up investments from arbitrarily low values to levels that are a significant fraction of I_M. The process of a higher-investing mutant forming a basic cluster of higher investors, and the subsequent expansion of this cluster in a sea of lower investors, is shown in figure 3.

An analytical estimate for the asymptotic value I^* to which the average investment evolves can be obtained as follows. First, we can give an approximate lower bound I_{min} on I^* by considering the invasion of a 3×3 cluster of slightly higher investors (investing $I + d$, d small and positive) in a sea of I-investors. By considering what happens at the edge of the 3×3 cluster of higher investors, one can show that such a cluster cannot grow further when $I > I_{min} = (1/B_1) \ln (B_0 B_1 / 4C_0)$.

Second, one can obtain an approximate upper bound I_{max} on I^* by considering the invasion of 3×3 clusters of slightly lower investors (investing $I - d$, d small and positive) in a sea of I-investors. By considering what happens at one of the corners of the 3×3 cluster of lower investors, one can show that such a cluster cannot grow further when $I < I_{max}$, where we find I_{max} to be equal to I_{min}. Thus, as the approximate upper and lower bounds on I^* are equal, we deduce the following analytical estimate for I^*: $I_0 = (1/B_1) \ln (B_0 B_1 / 4C_0)$. It appears from our simulations that I_0 is a good approximation to the asymptotic level of investment I^*. (We are grateful to Tom Sherratt for pointing out the possibility of such an argument to us.)

As noted, the mechanisms described above that drive up the mean investment from very low values to much higher levels work for any choice of benefit and cost functions that satisfy the one basic assumption that for a range of investments benefits are higher than costs (and this assumption is a necessary condition for cooperation to evolve in any situation). The form of the cost and

Figure 4 (*Cont.*) investments. In each case the randomness leads to more rapid evolution of $I(t)$ from very low values than in the original case (figure 2), although the asymptotic level I^* is slightly lower with the various random effects. The simulations for (a), (b) and (d) were performed on a 70×70 square lattice with periodic boundary conditions. The simulation for (c) was performed on a random lattice obtained by randomly deleting 20% of the cells in a 78×78 square lattice with periodic boundary conditions.

benefit functions used here was chosen because it has the cost being proportional to investment and the benefit obeying a law of diminishing returns with increasing investment. This type of cost and benefit function is typical of what might realistically be expected in many biological situations, such as, for example, those discussed by Hart & Hart (1992) and Wilkinson (1984).

3. DISCUSSION

Here we have studied the Continuous Prisoner's Dilemma in spatially structured populations. The Continuous Prisoner's Dilemma is an evolutionary game that is a natural extension of the standard Prisoner's Dilemma. It is based on the concept of investment. Investments can take on continuously varying values, and they are costly for the investor but beneficial for the recipient. In spatially structured populations, in which the Continuous Prisoner's Dilemma is played on two-dimensional spatial lattices, investments evolve readily from very low levels to significant levels corresponding to cooperation. This occurs under very general assumptions as long as the spatial lattices are large enough for the interactions between individuals to be local enough compared with the spatial extension of the whole population.

The ease with which cooperation evolves and is maintained in the spatial Continuous Prisoner's Dilemma suggests that cooperation may not be such a difficult evolutionary paradox after all. To support this claim we have tested various aspects of the model for robustness. So far the theory considered has deterministic synchronous updating and is formulated in a completely regular spatial domain. However, the real world abounds with random disturbances and spatial irregularities. Thus any model that seeks to explain the evolution of cooperation must be robust enough to perform well in the presence of these effects. We have investigated the model with stochastic noise in the updating (Mukherji *et al.* 1995), with asynchronous updating (Huberman & Glance 1993; Nowak *et al.* 1994), defined on a random spatial lattice (Nowak *et al.* 1994), and when a significant fraction of the mutations in each generation is to highly selfish individuals. The results are shown in figure 4. Not only does the essential feature of the model remain—in each case the mean investment per cell evolves from very low values to significantly higher levels—but the rate at which the investment evolves to the higher level is considerably faster than that for the deterministic updating–spatially regular model. Although the detailed mechanism operating in each case depends on the specific features of the model, the general effect underlying these results is that, in each case, the various random influences and irregularities allow some higher-investing mutations to form basic clusters when they would be unable to do so in the deterministic updating–spatially regular case. This results in the mean investment per cell evolving more rapidly to high levels.

The present model is much simpler than the approach outlined in our earlier work on mutualism. There we studied a continuous version of the iterated Prisoner's Dilemma in spatially structured host and symbiont populations arranged on dual lattices. Here we consider a single spatially structured species in which individuals

play the Continuous Prisoner's Dilemma without iteration. Remarkably, even in the absence of the possibility of sophisticated iterative strategies, cooperation evolves much more easily in this situation. Moreover, it is maintained at a more stable level, in contrast to the large fluctuations in the degree of investment that we observed in our simulations of the evolution of interspecific mutualisms (Doebeli & Knowlton 1998). The difference probably stems from the fact that mutualists interact with members of the other species but must compete with conspecifics.

In conclusion, a spatially structured theory of investment provides a natural resolution of many of the difficulties associated with the evolutionary origin and maintenance of cooperation in a selfish world. In fact, our results suggest that strict selfishness should be rare in spatially structured and localized intraspecific interactions: any action whose benefits to the receiver exceed the costs to the donor may be favoured if the investments can evolve. This poses a new dilemma, because while the existence of cooperation is widely acknowledged, most interactions are still assumed to be competitive. Some competitive interactions, such as competition between males for mates, are essentially a zero sum game, so that the cost to the cooperator is always comparable with the benefit received by a partner. Competition for other types of resources is more likely to meet the assumptions of our model. In particular, many organisms are spatially distributed and interact much more with neighbouring individuals than with individuals that are far away. Thus, our model may provide a basis for understanding the gradual evolution of cooperative interactions in many spatially structured systems, where the entities involved can range from replicating molecules to whole organisms (Wilson 1980; Michod 1983; Buss 1987; Maynard Smith & Szathmáry 1995; Dugatkin 1997). Since the natural world is invariably noisy and irregular, it is encouraging that our theory is robust against these effects. Future extensions of this model may be relevant for understanding the evolution of both mutualism (Doebeli & Knowlton 1998) and the hypercycle (Eigen & Schuster 1979; Maynard Smith 1979; Boerlijst & Hogeweg 1991).

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