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Ecological Symmetry Breaking can Favour the Evolution of Altruism in an Action-response Game

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The evolution of altruistic behaviour is studied in a simple action-response game with a tuneable degree of conflict of interest. It is shown that for the continuous, mixed-medium approach no stable polymorphism favours altruism. Ecological dynamics are explored with the addition of a spatial dimension and a local energy variable. A continuous spatial model with finite local range does not introduce any substantial difference in the results with respect to the level of altruism. However, the model illustrates how ecological coupling may lead to the formation of stable spatial patterns in the form of discrete and isolated clusters of players as a consequence of inverse density dependence. A discrete, individual-based model is built in which local interactions are also modelled as occurring within a finite neighbourhood of each individual and spatial positions are not restricted as in lattice models. This model shows substantially different results. A high level of altruism is observed for low (but positive) degrees of conflict and this level decreases linearly for higher degrees of conflict. The evolution of altruism is explained by studying the broken symmetries introduced by the spatial clusters themselves, mainly between their central and peripheral regions which, in combination with the discrete and the stochastic nature of the model, result in the stabilization of strategies in which players behave altruistically towards the same type. As a consequence of the activity of the players, energy resources at the centre of an altruistic cluster are very depleted; so much so that, for low conflict, fitter non-altruistic mutants may initially invade only to become locally extinct due to their less efficient use of energy as their numbers increase. In peripheral regions invader may subsist; however, for geometrical reasons long-lasting genealogies tend to originate only at the centre of a cluster.

1. Introduction

A character or behaviour is altruistic if it is costly for its bearer and beneficial to other individuals. Traditional explanatory routes for the evolution of non-reciprocal altruism have concentrated on the different effects of altruism in intra- and inter-group competition (Wade, 1980) and on the effects of limited dispersal ("viscosity") as enhancing the local coefficient of relatedness between interacting individuals (Hamilton, 1964). However, it has been shown that, contrary to the initial intuition, the effect of increased relatedness due to local interactions can be overcome by the effects of increased local competition when the scales of dispersal and the scale of interactions coincide (Taylor, 1992a,b; Wilson *et al.*, 1992). In

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such cases, the quantity that is selectively maximized is individual fitness as in the mixed-medium case. This result does not contradict the theory of kin selection if relatedness is properly calculated (Queller, 1994). However, the cancellation of the effects of higher relatedness and increased local competition is challenged when the scales of dispersal and density regulation do not coincide (Kelly, 1992a,b).

It has also been shown that altruism may evolve in viscous populations if organisms are modelled as discrete entities and the associated stochasticity is taken into account (Goodnight, 1992; van Baalen & Rand, 1998; Krakauer & Pagel, 1995; Nakamaru *et al.*, 1997). Spatial structure in these models usually takes the form of a lattice in which each position can be occupied only by a single organism and interactions or influences occur only with a pre-specified number of neighbouring positions (see Durrett & Levin, 1994b). One rationale behind this choice is that growth is regulated by the exclusion constraint (no two organisms may occupy the same position) and so competition for limited spatial resources ensues. However, the constraints on possible interactions imposed by lattice models need not represent biological situations in a reliable way. Lattice models are used mainly because they facilitate modelling and not because they respond to particular biological considerations. In contrast, treating local interactions as occurring in a local mixed-medium (and so making less assumptions about local structure) leads to models that subdivide space into patches (Chesson, 1981; Durrett & Levin, 1994a,b) with the disadvantage that further spatial relations between patches need to be specified instead of modelling space explicitly and homogeneously as in the lattice case.

In this paper, we present a spatial model of action coordination with conflict of interest in which interactions are local but not structured as in lattice models and the population is not *a priori* sub-divided into patches. Organisms may occupy any position in a common, homogeneous space (including the same position) and they interact only with other organisms chosen at random from a local neighbourhood. Competition for resources and limitation to growth ensues owing to a coupling with local energy sources which are exploited by the organisms and renewed at a fixed rate. The resulting model makes fewer assumptions about the structure of local interactions by modelling them as those of a "non-patchy local mixed medium" which is centred around each organism.

The aim of the paper is to study under what circumstances altruism will evolve and to evaluate the relevance of the broken symmetries introduced by ecological dynamics. These broken symmetries will result as a consequence of a mutual coupling between the evolving population and environmental variables.

In contrast with many other models of the evolution of altruism, the form of altruistic interactions addressed here is better described as "contextual" rather than "intrinsic". This means that whether a behaviour is altruisic or not depends on the current pool of behavioural strategies in the neighbourhood. This form of contextual altruism is more appropriate for describing social behaviours where benefits and costs depend both on the initiating behaviour and on the response by other individuals. For instance, in signalling appropriate perception is crucial; a warning call in the presence of a predator is altruistic not in itself but only in the case in which it elicits an adequate response in others who only then can "claim" the benefits of the caller's action. These circumstances can be modelled quite generally by discrete action-response games (Hurd, 1995).

The model will be studied both for the spatial and non-spatial cases and for organisms modelled both as continuous densities and as discrete entities. It will be shown that altruism is a stable evolutionary outcome for small, but positive degrees of conflict, only for the spatial case in which organisms are discrete, thus strengthening with different modelling techniques, the point made by Goodnight (1992) and van Baalen & Rand (1998) that both space and stochasticity are necessary to favour altruism (see also Durrett & Levin, 1994a; Krakauer & Pagel, 1995; Nakamaru *et al.*, 1997).

We will show that the reason why contextual altruism is able to evolve lies in the coupling between a noisy selective process at the individual level and the stable spatial structures that arise as a consequence of the ecological dynamics. The effects of local reproduction and interaction within a finite neighbourhood around each player are such that the initial spatial homogeneity is broken and players arrange themselves into discrete and stable clusters. These clusters show different densities of players and resources between their central and peripheral regions, thus introducing further broken symmetries in the availability of local resources, in the frequency with which an individual interacts, in the frequency with which an individual plays each role in an interaction, and in the relative length of genealogies that it is likely to initiate depending on its spatial position. It will be shown that altruists can be out-competed by non-altruists but that, for certain parameter values, the latter can find it very hard to survive on the harsher environment set by previous altruistic activity. Local extinction of invaders and altruist re-invasion ensues in these cases.

This rich ecological structure, which is a direct consequence of the assumption that opportunities for interaction are higher in areas of higher density, is an interesting example of how evolutionary processes may be affected by ecological constraints. Many of the features uncovered by a careful study of these constraints can find their natural counterparts in analogous natural structures such as social hierarchies.

2. The Game

We will use a simple action-response (two-role) game (Hurd, 1995) with parameterizable degree of conflict of interest, two possible outcomes (altruistic coordination and non-coordination) and four different strategies.

When two players interact, each one of them performs one move. "Coordination" ensues for certain combinations of moves amounting to 50% of all the possible outcomes. A certain amount of energy E is at stake in each interaction. If the game results in coordination this energy is shared on equal terms and, if not, then the first player gets a proportion c of the energy ($0.5 \leq c \leq 1$) and the second player gets nothing. Higher values of c correspond to higher degrees of conflict.

A natural situation that affords an interpretation using a scheme like this could be the case in which a group of animals can access a source of high-quality food but this access requires the joint effort of two individuals. After accessing the food they may both share it equally or one of them (the initiator) may try to induce the other to do something else thus accessing a higher proportion of food for itself. Notice that the payoff assignment also reflects the fact that the energy contained in the food source may not be totally extinguished by a single individual though it will surely be if two have to share. This is what allows for the degree of conflict to vary as a continuous parameter.

Suppose that there are two classes of moves (e.g. "odd" and "even"), then there are only four possible pure strategies, each one specifying a choice of class for the initial move and a choice for the second move. Without loss of generality, suppose that coordination ensues when the moves played by the players belong to different classes. An individual playing strategy "OE" makes a move of class "odd" when playing the first role and a move of class "even" when playing the second. Notice that strategies "OE" and "EO" will always result in coordination if both individuals play them (therefore, they will be called "self-coordinating"). Figure 1 shows the altruistic relationships between the different

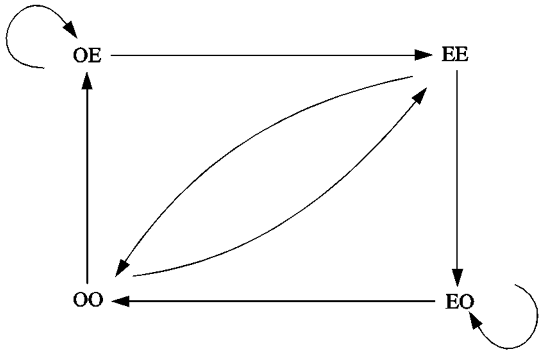

FIG. 1. Altruistic relationships between the four strategies. Each arrow is interpreted as connecting the initiator and responder strategies of those interactions that result in coordination. Thus, a player using strategy "OE" will behave altruistically only towards players using either "OE" or "EE" and this is indicated by the two arrows starting at the "OE" node. An intiator playing "EE", in contrast, will not behave altruistically towards players using "OE" since there is no arrow from "EE" to "OE". Notice the cyclic structure of the resulting graph indicating a Rock-Paper-Scissors type of situation.

strategies for this case. Each arrow is interpreted as connecting the initiator and responder strategies of those interactions that result in coordination. Thus, a player using strategy "OE" will behave altruistically only towards players using either "OE" or "EE" and this is indicated by the two arrows starting at the "OE" node. An initiator playing "EE", in contrast, will not behave altruistically towards players using "OE" since there is no arrow from "EE" to "OE", although it will behave altruisically towards individuals playing "OO" or "EO". Notice the cyclic structure of part of the resulting graph indicating a Rock-Paper-Scissors type of situation which at first sight suggests that no single strategy may become dominant because it will always be invaded by its "neighbour" strategy in the graph.

From the payoff assignment scheme described above and assuming $E = 1$, the payoff matrices for the first and second roles (respectively $M1$ and $M2$) are

$$M1 = \begin{pmatrix} 1/2 & 1/2 & c & c \\ c & c & 1/2 & 1/2 \\ c & c & 1/2 & 1/2 \\ 1/2 & 1/2 & c & c \end{pmatrix},$$

$$M2 = \begin{pmatrix} 1/2 & 0 & 0 & 1/2 \\ 1/2 & 0 & 0 & 1/2 \\ 0 & 1/2 & 1/2 & 0 \\ 0 & 1/2 & 1/2 & 0 \end{pmatrix},$$

where $(M1)_{ij}$ is the payoff obtained by a player of type i when playing the first role against type j and $(M2)_{ij}$ is the payoff obtained by a player of type i when playing the second role against type j. Type 1 corresponds to strategy "EO", 2 to "OO", 3 to "OE" and 4 to "EE".

Players can play either one of the two roles on different occasions. If the frequency for playing one role or the other does not depend on the role or the strategy played and is taken to be equal for each role, then the game can be analysed as symmetric with a payoff matrix M where $(M)_{ij} = (M1 + M2)_{ij}/2$ is the average payoff obtained by a player of type i over a large number of games against players of type j.

Under these circumstances, it can easily be shown that a population constituted by a single strategy can always be invaded. For instance, if the population is constituted by players of strategy "OE" (a self-coordinating strategy) the expected individual payoff per game is $W_o = 1/2$ whereas the payoff for a (non-coordinating) mutant playing strategy "EE" will be $W_i = (1/2 + c)/2$ which is always greater than W_o. If the population is constituted entirely by players of "EE" (non-coordinating) the expected individual payoff per game will be $W_o = c/2$ and for an "OE" (self-coordinating) mutant the payoff will be $W_i = (1/2 + c)/2$ which is again greater than W_o. Analogous conclusion can be drawn for the invadability of the other strategies.

It can be seen that in a randomly constituted large population the proportion of games resulting in coordination will be 50% which is taken as a baseline level.

3. Mixed-medium Approach

A game theoretic analysis for the mixed-medium, infinite population case is performed. Let $p = (p_1, p_2, p_3, p_4)$ be a vector describing the proportion of players of pure types 1, 2, 3, and 4 in a polymorphic population, p belongs to the simplex S:

$$p \in S = \left\{ x = (x_1, x_2, x_3, x_4) \in \mathbf{R}_4 : \sum_j x_j = 1,\ x_i \geq 0,\ \forall i \right\}.$$

An evolutionarily stable strategy (ESS) (Maynard-Smith & Price, 1973), if it exists, is given by a distribution p^* when

$$p^* \cdot Mp^* \geq q \cdot Mp^*, \quad \forall q \neq p^* \qquad (1)$$

and

$$p^* \cdot Mq > q \cdot Mq \quad \text{if } p^* \cdot Mp^* = q \cdot Mp^*, \qquad (2)$$

where M is the payoff matrix.

It is found that for this game no p is an ESS. Maximal payoff is found for a one-dimensional continuous set of points in S given by

$$P = \{p_a = (\tfrac{1}{2} - a, a, \tfrac{1}{2} - a, a);\ 0 \leq a \leq \tfrac{1}{2}\}$$

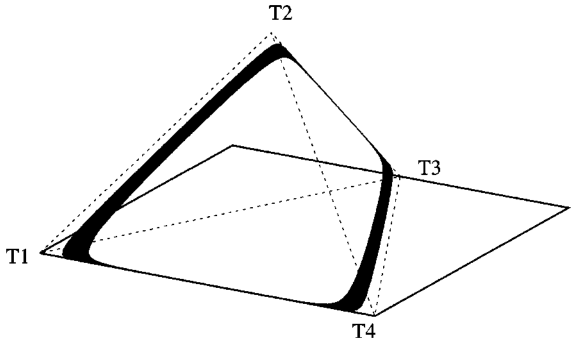

FIG. 2. Typical trajectory in phase space for infinite population dynamics. The vertices indicate monomorphic populations: T1: (1,0,0,0), T2: (0,1,0,0), T3: (0,0,1,0) and T4: (0,0,0,1).

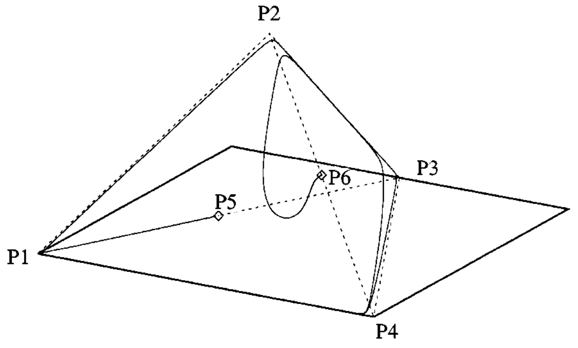

FIG. 3. Typical trajectory in phase space for perturbed finite population dynamics with $N = 100$. The initial condition, labeled P_5, is given by $P_1 = P_3 = N/2$, $P_2 = P_4 = 0$. After a couple of oscillations the population settles on the stable fixed point P_6 given by $P_1 = P_3 = 0$, $P_2 = P_4 = N/2$.

with a payoff of $(c + 1)/2$ for all values of a. This means that the points are at least neutrally unstable and it can be shown that they are strongly unstable for $a < 1/4$ (Di Paolo, 1999).

There is also a periodic attractor (Fig. 2) in which each strategy becomes dominant for a certain period only to be replaced by a competing strategy in the order shown by the straight arrows of Fig. 1. As mentioned above, this is not entirely unexpected given the Rock-Paper-Scissors structure displayed by the relations between the strategies.

More interesting results are obtained for finite populations (Riley, 1979; Vickery, 1987; Schaffer, 1988) in the dynamical case (Taylor & Jonker, 1978; Zeeman, 1979; Hofbauer *et al.*, 1979; Schuster & Sigmund, 1981). Consider a population of N players in which P_i of them play strategy i. Then the evolutionary dynamics can be expressed by

$$\frac{\mathrm{d}P_i}{\mathrm{d}t} = P_i(W_i - \bar{W}), \quad \forall i. \tag{3}$$

where W_i is the average fitness for an individual playing strategy i:

$$W_i = \frac{1}{N-1}\left(\sum_j M_{ij}P_j - M_{ii}\right) \tag{4}$$

and $\bar{W}$ is the average fitness for the whole population:

$$\bar{W} = \frac{1}{N}\sum_k P_k W_k. \tag{5}$$

After a linear stability analysis it is found that $P_1 = P_3 = 0$ and $P_2 = P_4 = N/2$ is the only stable fixed point (although not an ESS; see Zeeman, 1979). This point is not the unique attractor of the dynamics and oscillations are again observed. However, in terms of stability, only the fixed-point attractor is relevant as shown by adding a small noise term to the numerical resolution of the equations (Fig. 3 shows a typical trajectory in phase space in this case).

In consequence, for finite population under noisy conditions, an equal number of strategies "OO" and "EE" is the expected stable outcome. Under these circumstances, the proportion of games resulting in cooperation cannot exceed 50% which is the same as in the random case.

4. Continuous Spatial Model

In the simplified ecological setting assumed so far, the distribution of strategies in a population has no effect on the payoff structure of the game. However, more detailed ecological consideration would require an account of how differently constituted populations exploit the available finite resources. So far, the average energy available as payoff $E(t)$ has been considered constant and equal to 1.

The expression of payoffs in energetic and fitness terms was taken as equivalent in the previous models and it would remain equivalent if there was only a single energy variable accessible to all players. Global optimization would be the expected result. Taking this into consideration, the next logical step is to extend the assumption of ecological coupling to a more realistic setting where resources are locally accessible, which implies the introduction of a spatial dimension.

Cressman & Vickers (1997) have shown how different choices in the way in which a mixed-medium model is extended into a spatial one may dramatically affect the outcome. For the continuous model intended here some considerations will help to constrain this choice.

In general, a deterministic approach to spatial games involves some sort of reaction–diffusion model or similar (see e.g. Murray, 1989). Such models can be formulated simply by adding a diffusion term to the basic dynamics given by eqn (3) in order to account for mobility (Vickers, 1989). Other models may be more complex (Cressman & Vickers, 1997; Durrett & Levin, 1994a). Reaction–diffusion equations are generally intended to model local interaction between infinitesimal components. As a result they typically ignore long-range effects. This is appropriate for contact processes such a chemical reactions but in the present case it would mean that a player's range of interactions would be very small. So an alternative should be found in the form of a spatial model with a finite local scale.

In this model, players are distributed in space in positions that do not change over time (so that dispersal occurs only as a consequence of birth events although, as shown below, a diffusion term may be added to the equations for generality). Each player can only interact with other individuals located within a neighbourhood of finite radius L centred at the player's position x. The neighbourhood is denoted by $Loc(x)$. This model can be seen as an intermediate case between mean-field, non-spatial approaches and contact approaches where interactions occur only at infinitesimally small scales. By varying the parameter L both ends of the spectrum can be reproduced.

A sub-population of players of strategy i is described by its spatial density $p_i(x, t)$. Energy resources are also distributed continuously in space; the amount of available energy at a given position and time is $E(x, t)$. All players play the role of initiator with a frequency which is proportional to the chance of finding within their neighbourhood a partner who will play the second role.

Individual players in this model can only access energy through interaction with other individuals. This is a limiting assumption that will be discussed in the final section, but it may be considered to reflect an environment where subsistence is based mainly on access to the high-quality food source that requires a minimal participation of two individuals, other food sources not being sufficient (i.e. baseline growth rate without interaction is negative). This will accentuate the inverse density dependence (Allee effect; Allee, 1931; Stephens & Sutherland, 1999; Courchamp *et al*., 1999) for very low densities that already exists on the assumption that interaction gives access to resources of more quality.

It is supposed that energy is extracted from the location of the initiator. The rate of change in the number of individuals of a given strategy will be proportional to the net energy accumulated by those individuals. This net energy is calculated by summing the contributions of the energy an individual gains when playing the first role $E_i^1(x, t)$ and the energy it gains when playing the second role $E_i^2(x, t)$ which depend on the strategy played (i) minus its net individual energy cost for self-maintenance which is assumed to be constant for all players. Both $E_i^1(x, t)$ and $E_i^2(x, t)$ will involve integral expressions over the $Loc(x)$ (see Appendix A).

Changes in the energy variable $E(x, t)$ will be due to a constant renewal rate, a time constant of saturation and the effect of the consumption by the players $E_C(x, t)$ which is also given in Appendix A.

Dropping the dependence with (x, t), the system is defined by

$$\frac{\partial p_i}{\partial t} = Bp_i(E_i^1 + E_i^2 - Lo) + D\nabla^2 p_i,$$

$$\frac{\partial E}{\partial t} = R - \gamma_e E - E_C. \tag{6}$$

A diffusive term has been added to the first equation to account for possible mobility effects. The constant B gives the number of newborn players per unit of space for each unit of energy gained and Lo indicates the energy losses per unit of time due to self-maintenance for a density value of one. R represents the rate of energy renewal per unit of time per unit of spatial dimension and γ_e the energy saturation constant.

It can be shown by testing the stability of homogeneous solutions to eqn (6) that the model is capable of pattern formation in space even in the absence of a diffusion term (Di Paolo, 1999; Murray, 1989). This is mainly due to the coupling between local densities of players within distances shorter than L. Clearly, the frequency of interactions for an individual will depend on the number of potential co-participants in the neighbourhood. If these are scarce, the density of players in the area will tend to diminish and vice versa (Allee effect).

The model is studied by solving eqn (6) numerically in a finite one-dimensional domain. The results presented here are for the case without diffusion ($D = 0$). Periodic boundary conditions are used as well as random uniform distribution for the initial conditions of the population densities and uniform initial value for the energy (see Appendix B for parameter values).

Figure 4 shows the time variation of the total number of players of each strategy where strong oscillations can be observed. In contrast with the non-spatial cases, oscillatory solutions are stable under noisy conditions while non-oscillatory solutions have only been observed in the total absence of noise. The spatial constitution of the population at four different times can be observed in Fig. 5 (corresponding to the same run as in Fig. 4). The neighbourhood size is equal to 2 and the total size of the spatial domain is equal to 20. A clearly defined cluster of players has formed out of a uniformly random initial condition. The figure shows the presence of different oscillatory spatial modes. In general, more than one cluster may be simultaneously present.

While the introduction of space to the continuous model is interesting from the point of view of the formation of localized clusters, it does not add much to the previous results regarding the evolution of altruism. According to observations the global level of interactions resulting in coordination always remains close to 50% for all the values of c tested in the range [0.5, 1].

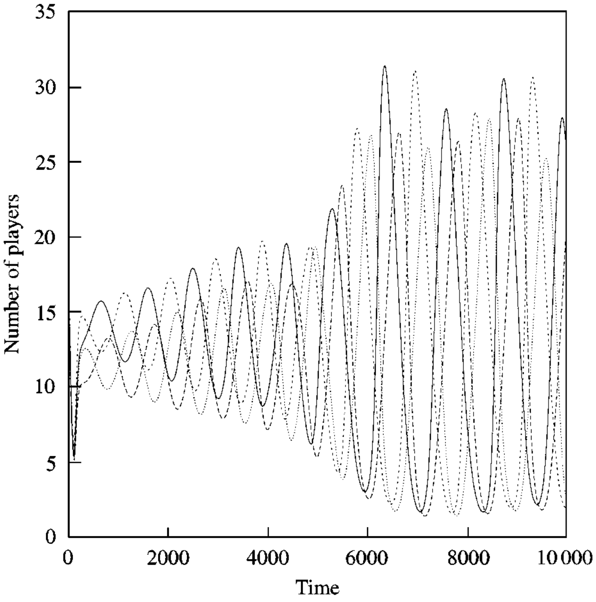

FIG. 4. Number of players corresponding to each strategy as a function of time for a typical numerical resolution of eqn (6) with $c = 0.6$ (see text): (——) EO; (– – –) OO; (- - -) OE; (-----) EE.

5. Individual-based Model

Evolutionary models in which individuals are not treated as discrete entities can be problematic, especially if infinitesimally small densities are allowed (Goodnight, 1992; van Baalen & Rand, 1998; Kepler & Perelson, 1995; Abramson & Zanette, 1998). If the minimal volume of interest is V, any value of density less than V^{-1} is meaningless unless it is zero. By taking this fact seriously one can introduce interesting differences for instance in Lotka–Volterra dynamics (Abramson & Zanette, 1998). As a consequence of discreteness, in certain stochastic models (Tsimring *et al.*, 1996; Gandhi *et al.*, 1999) as well as in experimental observations (de la Torre & Holland, 1990), the condition of invadability does not rest entirely upon the higher fitness of the invader relative to the mean population but it may also depend on the achievement of a minimal threshold number above which the mutant is able to invade.

5.1. THE MODEL

An individual-based stochastic model of the scenario presented in the previous section has

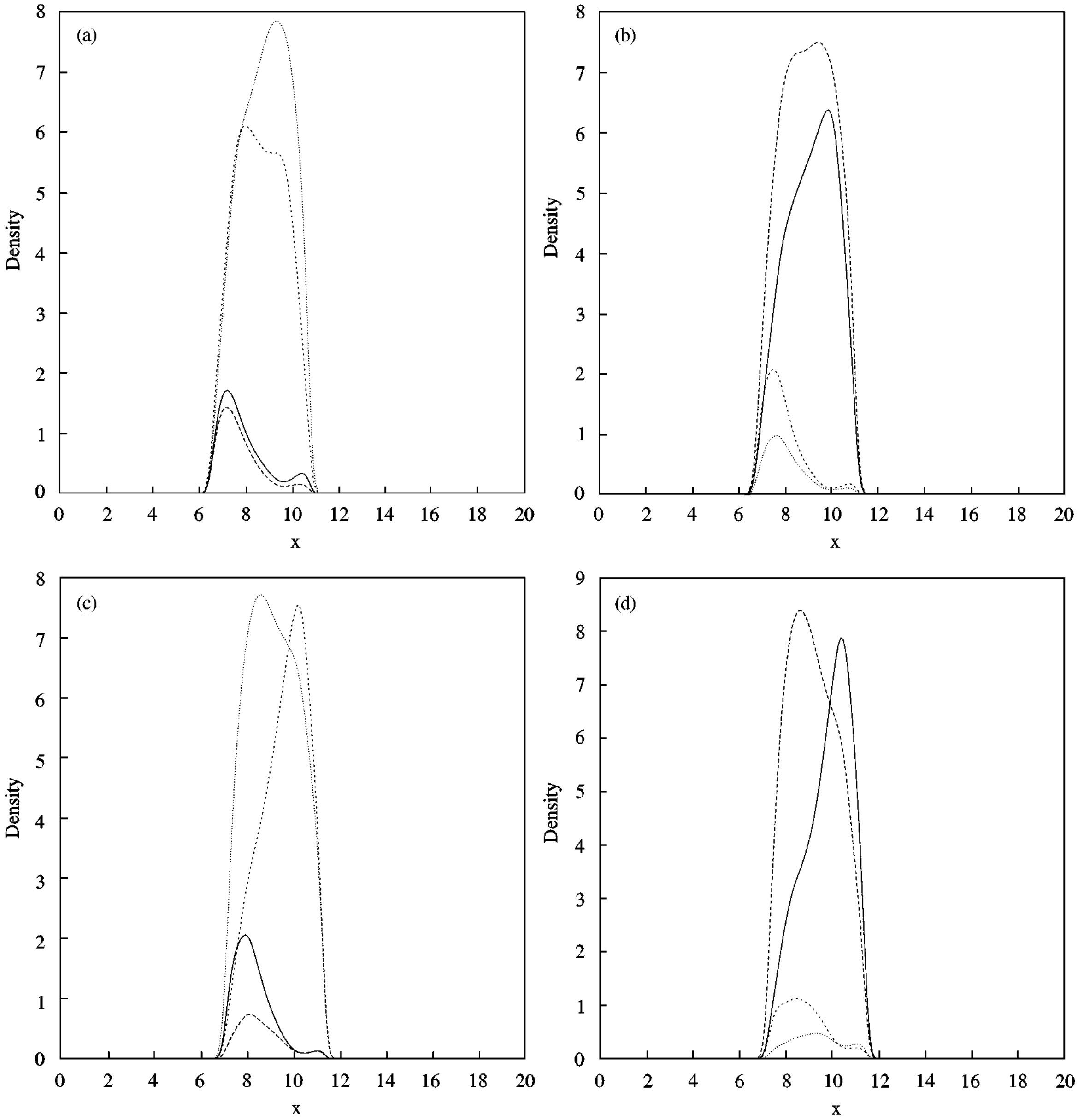

FIG. 5. Spatial composition of the population for the run depicted in Fig. 4: (a) $t = 6000$, (b) $t = 6600$, (c) $t = 7200$, (d) $t = 7800$: (——) EO; (– – –) OO; (- - -) OE; (-----) EE.

been developed to address the issue of discreteness. The spatial domain is two-dimensional. Players subsist on energy which they gain by interacting and reproduce with a rate which is proportional to their capacity for accumulating extra energy.

Population size is variable and generations overlap. At each time step N players are asynchronously selected to act, where N is the current population size. A selected player will try to find a partner within its neighbourhood to interact with. The probability of finding a partner is, as before, proportional to the local density. If after $N_a = 10$ trials a partner is not found the player loses its turn. If a partner is found, a local food source is selected and the first player plays the role of initiator and the second player the role of responder.

Strategies are encoded in a haploid binary genotype. If a player's level of energy surpasses

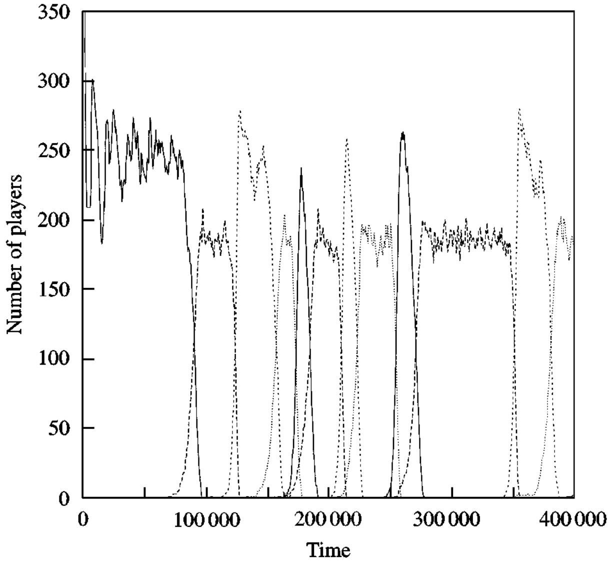

FIG. 6. Number of players for each strategy in the non-spatial case in a typical run. Initial condition: all players with strategy "EO": (——) EO; (– – –) OO; (- - -) OE; (-----) EE.

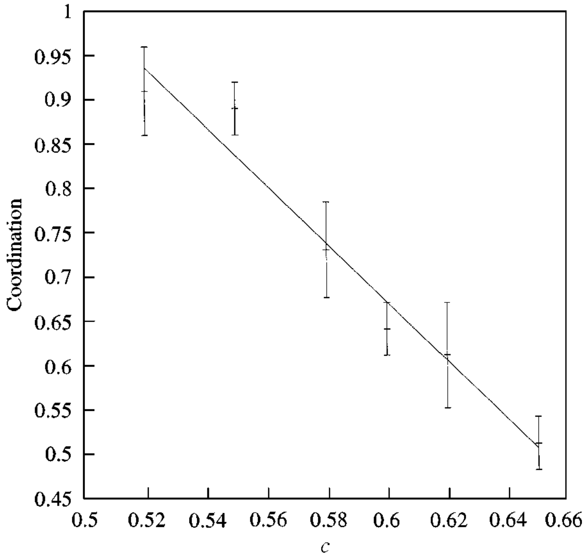

FIG. 7. Average value for the level of altruistic coordination for different values of c. Each point is the average of five simulation runs. The line represents a linear regression (linear correlation coefficient: -0.982). Errors indicate standard deviation.

a certain threshold the player will reproduce, and for this a mate must be found within the neighbourhood. Offspring receive their genetic material from their parents after recombination and a small probability of point mutations (chosen so that the probability of a genotype to remain unchanged is about 0.95). After being born, they are allocated within the neighbourhood of their parents receiving their initial energy values from them. A player who cannot afford its own energy costs (paid each time the player is selected to act) will eventually die. The population is initialized at random.

The non-spatial situation can be simulated in this model by making the size of the local neighbourhood as big as the whole spatial environment. In this case it has been observed that the oscillatory solution is recovered (Fig. 6).

In the spatial case, neighbourhoods have been modelled either as circles or as squares. The position of a player could be either an integer or a real-valued coordinate. The choice between these two neighbourhood shapes (conserving the same area) does not seem to play any major role in the final outcome, nor does the type of coordinates used which shows that the use of a finite range of interaction is robust to these implementation details.

The results for a square neighbourhood of side 10 in a toroidal unstructured spatial environment of size 100 × 100 can be observed in Fig. 7 where the average (population-based) proportion of interactions that result in altruistic coordination is plotted as a function of the degree of conflict c. The results are time-averaged over the steady state and over five simulation runs for each point. Error bars indicate standard deviations. It is apparent that for an important range of values of conflict (approximately up to 65%), cooperative coordination lies above the baseline level of 50% predicted by the continuous models. It is also clear that as c increases, this global level decreases in a linear fashion (slope: -3.32, linear correlation: -0.982) showing that altruism is no longer favoured for higher degrees of conflict.

5.2. SPATIAL PATTERNS

The initial spatial distribution of players is uniformly random. After a short transient stable clusters form and remain more or less distinct (Fig. 8). As a consequence of the inverse density dependence, players in densely packed areas tend

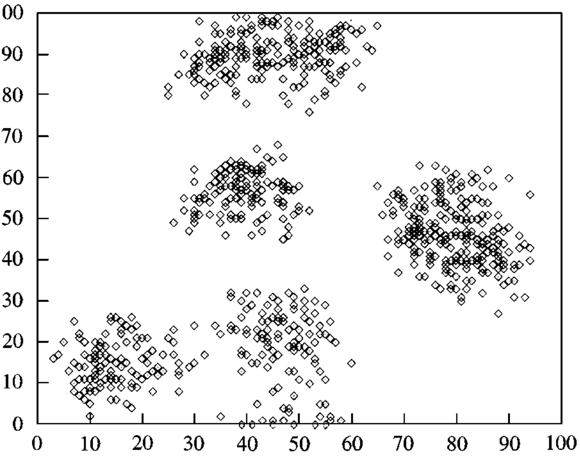

FIG. 8. Example of the spatial distribution of the population.

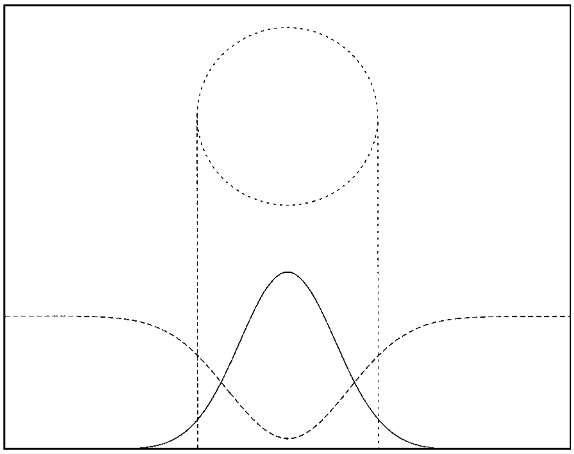

FIG. 9. Qualitative energy and population distribution inside and around a cluster (circle) in one spatial dimension: (——) Density; (- - - -) Energy.

to benefit from a high frequency of games per unit of time in comparison with relatively isolated players who eventually die. The continued stability of clusters may be explained in similar terms. Figure 9 shows qualitatively the average spatial distribution of players and resources inside a cluster. At the periphery games are for higher stakes. So clusters would seem to have a tendency towards expansion. In contrast, at the centre of a cluster the high density of players implies a higher frequency of games than at the periphery, so that clusters would also have an opposing tendency to contract. The equilibrium between these tendencies determines the size of a cluster and its stability as a discrete ecological entity.

Cluster formation and stability have been observed independently of the shape of the local neighbourhood but (as expected) not independently of its size as larger neighbourhoods approach the mixed-medium case and very small neighbourhoods do not suffice to break the spatial symmetry of the uniform initial condition (Di Paolo, 1999). Clusters were always observed when the neighbourhood characteristic length was about one order of magnitude smaller than the characteristic length of the spatial domain.

5.3. BROKEN SYMMETRIES

Clusters are constituted as a result of a dynamical equilibrium in the energy consumption per unit of space. This equilibrium would seem to establish a degree of spatial “neutrality” in the sense that spatial position does not matter for the rates of energy intake and offspring production. Players at the centre interact more often than those at the periphery but they do so for poorer resources. If the rates of net energy intake were different, the cluster would not be at equilibrium. Such a homogeneous rate of energy consumption (and reproduction) is indeed what is observed in the simulations. However, it is *not* true that spatial position is neutral in evolutionary terms.

If a player is born from a parent near the periphery of the cluster there is a high chance that it will be placed “outside” the cluster in the sense that it will have a very small number of neighbours. Those players will tend to die before they reproduce. In fact, the chances of originating a lasting genealogy of players diminish as the originating position moves from the centre to the border of a cluster. This is a geometrical consequence of the stochastic and local character of the process of offspring allocation. In different terms, given the current cluster population, the position of its ancestors will tend to be concentrated near the centre of the cluster as we travel backwards in time and this is what is observed (Fig. 10). It is reasonable to conclude that a player’s position within a cluster plays a role with bearing on its fitness but which is not under genetic control.

The above phenomenon is a case of symmetry breaking of the spatial homogeneity. Other

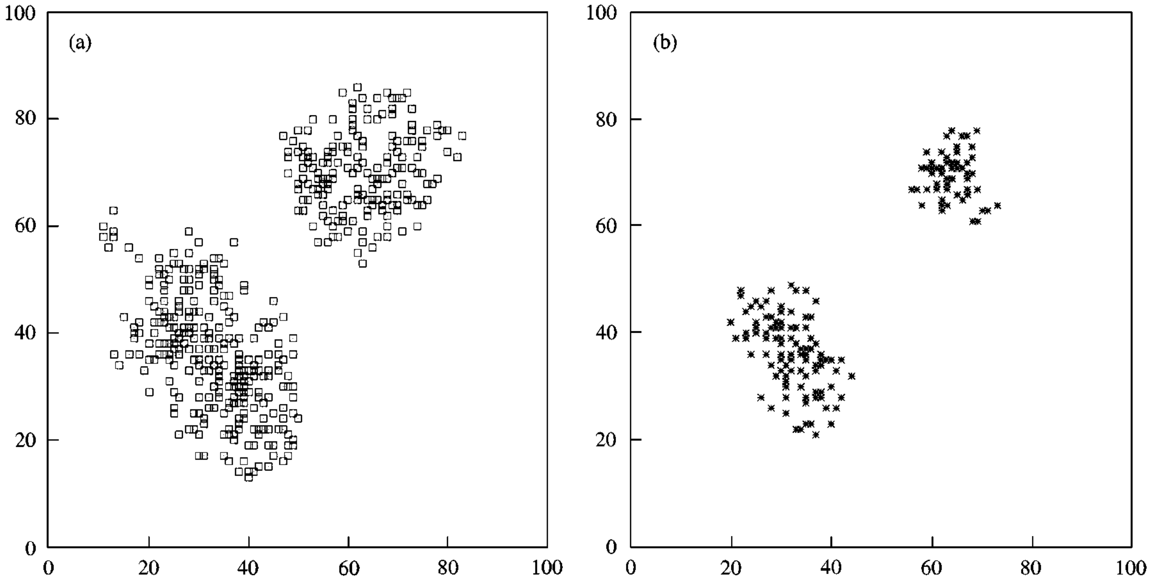

FIG. 10. Spatial distribution of ancestors; (a) current position of players, (b) position of ancestors 10 generations ago.

symmetries are also broken by the centre/periphery structure. Consider the frequencies with which individuals play each role in the interactions. In the non-spatial situation all players play both roles with the same frequency. However, players at the centre of a cluster tend to play the role of responder more often than that of initiator (Fig. 11). This is another geometrical consequence of the distribution of players in a cluster. Central players are more numerous and are neighbours to a greater number of individuals than peripheral players. The latter may be called to act as responders mainly by those neighbours that lie in the direction of the centre while central players are called to act as responders from all directions.

We can conclude that the rupture of spatial homogeneity provokes a series of broken symmetries between the central and peripheral regions: in the density distributions of players and energy, in the lengths of genealogies, in the frequency of interaction and in the frequency of role assignment. In view of these broken symmetries let us analyse the evolutionary stability of a population constituted by a single strategy within a cluster.

A group of altruists consumes more energy locally and per unit of time than a group of non-altruists so that, at a constant rate of renewal, the average value of available energy per game will be lower in the first case than in the second. This is indeed observed in simulations where only one strategy is permitted to evolve (i.e. non-random initialization and mutation rate set to zero). In altruistic clusters, the available

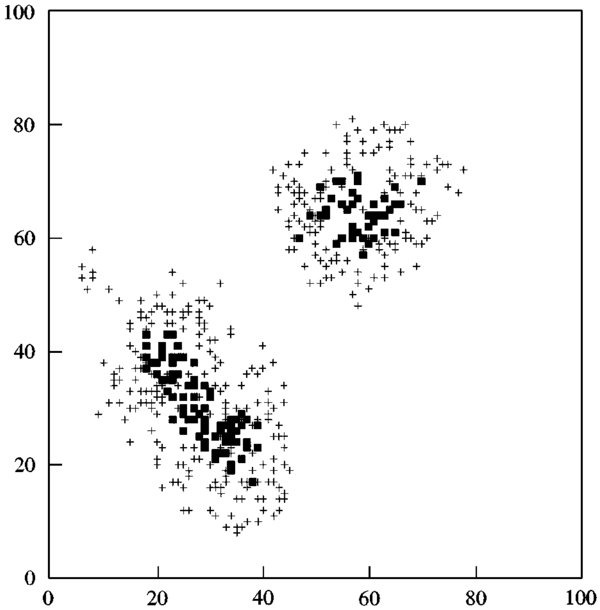

FIG. 11. Distribution of players according to the most frequently played role. Those who play the role of responders more often (■) are located at the centre of each clusters.

TABLE 1

Average energy within a players neighbourhood for different values of c and for altruistic (E_a) and non-altruistic (E_{na}) clusters. Errors correspond to standard deviations

c	E_a	E_{na}
0.52	0.87 ± 0.14	1.9 ± 0.3
0.55	0.9 ± 0.2	1.8 ± 0.4
0.60	0.95 ± 0.16	1.8 ± 0.3
0.65	0.89 ± 0.13	1.8 ± 0.4

energy per unit of time is roughly twice as much as in the case of non-altruistic clusters (Table 1). In fact, for the same set of parameters we observe that non-altruistic clusters tend to be more disperse while altruistic clusters tend to be compact. This suggests that conditions at the centre of a cluster are rather disadvantageous for purely non-altruistic strategies given the poorer resources available in this region. In contrast, this harsh region presents no major problem for the altruists. It can easily be shown that an altruistic mutant capable of invading a non-altruistic cluster will not be restricted since the energetic environment is roughly twice as favourable as in a purely altruistic cluster. However, non-altruistic invaders in an altruistic cluster may find that the energetic balance becomes locally unfavourable before fixation is achieved.

To show this, consider a purely altruistic cluster into which a non-altruist capable of invasion is introduced at the centre. Let p_o indicate the local central density of altruists and p_i the same quantity for the invaders. The corresponding average payoffs are

$$W_o = p_o E_a/2 + p_i(1-f)E_a/2 - L_{oa},$$

$$W_i = p_o[f/2 + (1-f)c]E_a + p_i(1-f)E_a - L_{oa},$$

where f is the frequency for playing the role of responder (which is higher at the centre of the cluster with typical average values of 0.53), L_{oa} are the individual losses per unit of time within an altruistic cluster (i.e. a combination of energy losses and losses due to density-dependent effects) and E_a is the available energy for an altruistic cluster. It can be shown that $W_i > W_o$ always. However, it may happen that $W_i < 0$. This would be the case in which a local accumulation of non-altruists would be unable to subsist on the low resources of the central region.

It is possible to estimate the value of p_i above which the invader cannot subsist. For this we make the following approximations. First, we consider that the values of local resources and losses change slowly in comparison with the rate of invasion. This assumption will be good if the limit for p_i found is small which would mean that a very low density of invaders is enough for the local environment to become disadvantageous. Second, we use an estimation for L_{oa} by considering that initially the altruistic cluster is in a stable condition (i.e. no growth). This will give us an approximate value for the losses in terms of energy intake both of them averaged over the whole cluster (expressed respectively as $\langle L_{oa} \rangle$ and $\langle E_a \rangle$). The approximation will be that local values are not very different from this average value, so that the local payoff in an altruisic cluster ($p_i = 0$) will be

$$W_0 = E_a/2 - L_{oa} \cong 1/2\langle E_a \rangle - \langle L_{oa} \rangle = 0$$

This approximation will give us a rough idea of when the invaders of an altruistic cluster will start to lose their ability to subsist due to their local increase in density. Considering that $p_o + p_i = 1$ we ask for which values of p_i the invader's payoff W_i remains above zero; this yields

$$p_i < 1 + \frac{2c(1-f) - 1}{f}.$$

This gives us an estimation of the maximum local density achievable by non-altruistic invaders in an altruistic environment.

This restricting effect for the number of invaders will be harsher near the centre of the cluster where the local energy is below the average. We can see that for $c = 0.5$ (no conflict) the maximum density of invaders is zero. For values of c near 0.5 a very small increase in the local density of invaders renders them unviable in the central region (and this justifies, in this case, the assumption made above about the rate of change in the local energy being slow in comparison).

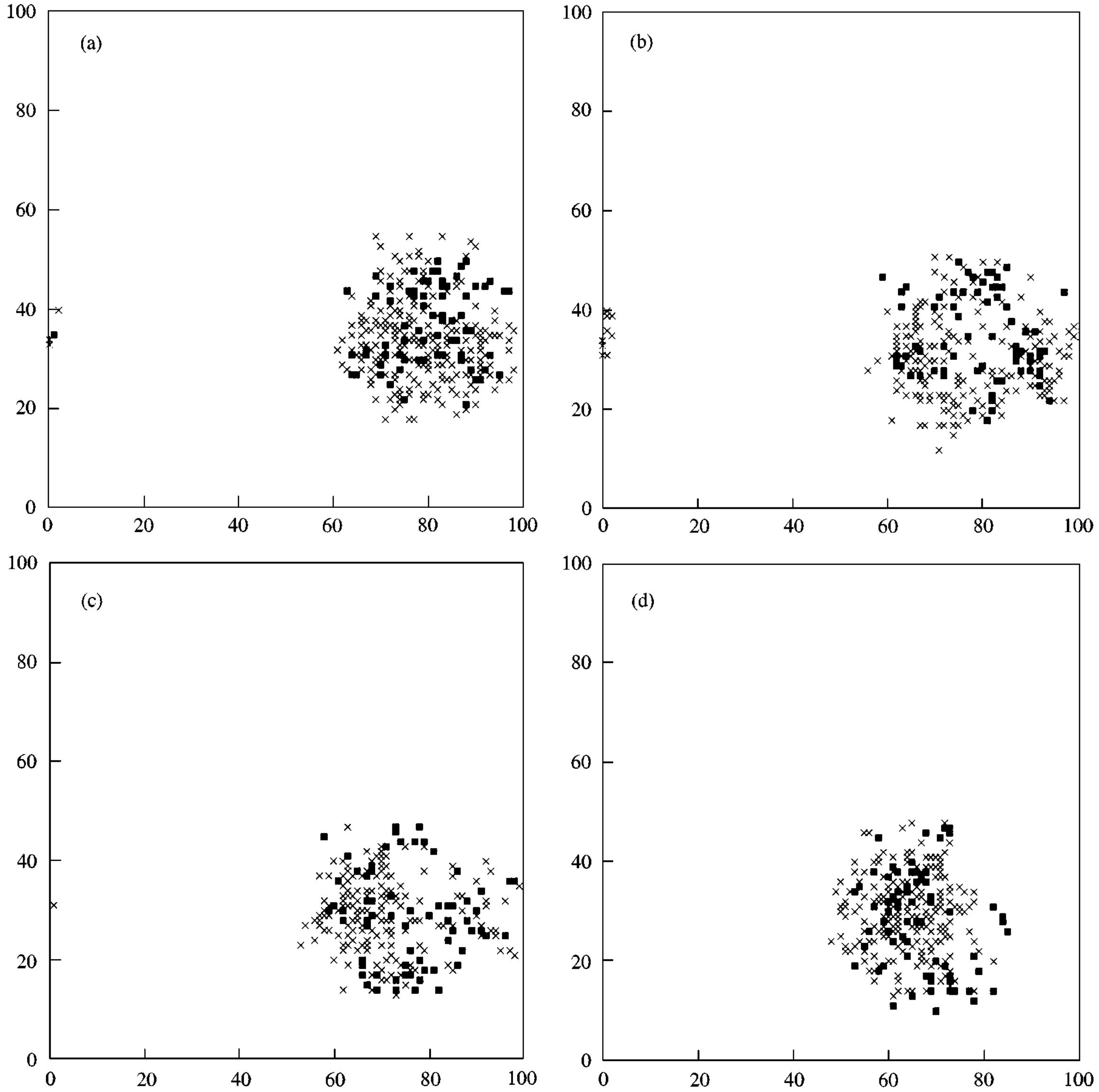

FIG. 12. Example of invasion dynamics of a predominantly altruistic cluster. Each frame shows the cluster constitution at intervals of 3000 time steps (about half an average individual lifetime); $c = 0.55$. Altruists are marked with × 's and invaders with squares. The first frame (top-left) shows a high concentration of invaders in the central region. The following frame shows a density gap in the same central region due to the local disappearance of invaders. The bottom-left frame shows an expanded gap leading to a separation into two clusters, and only one of these survives in this case as shown in the last frame.

Invasions will occur locally but will be followed by the local disappearance of the invaders, leaving a gap at the centre of the cluster which the altruists can re-invade or which may cause the cluster to break off into two smaller ones (see Fig. 12).

For several reasons, near the periphery of a cluster the above analysis will break down. After all, the conditions in the peripheral region are the opposite in terms of role frequencies and energy values. But, as discussed above, the length of genealogies initiated in the peripheral region tends to be short. At any given moment, the whole population of the cluster can be traced back to a group of ancestors in the *central* region, so that whatever happens at the centre of the cluster, although it does not completely determine what happens in the cluster as a whole, it strongly influences its final composition.

We may expect that, at any given time, a proportion of invaders will inhabit the peripheral region anyway as descendants of invasions

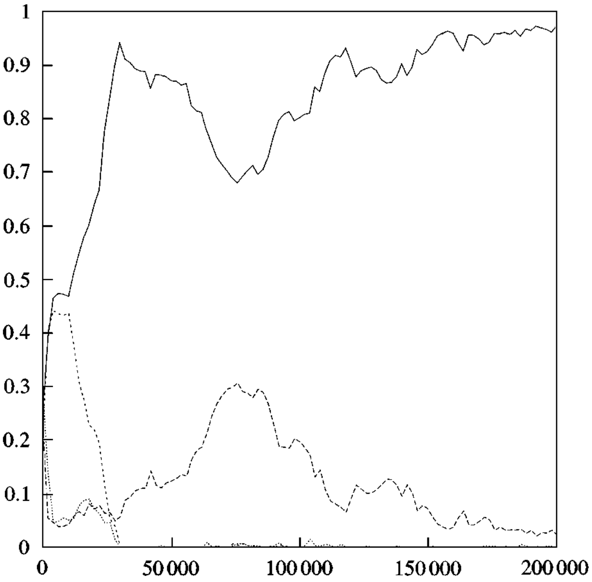

FIG. 13. Population constitution for a simulation run with $c = 0.52$. (——) EO; (– – –) OO; (- - -) OE; (-----) EE.

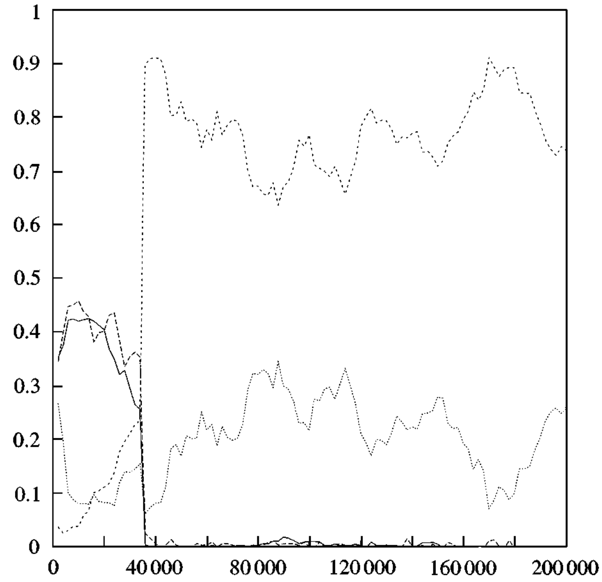

FIG. 14. Population constitution for a simulation run with $c = 0.55$. (——) EO; (– – –) OO; (- - -) OE; (-----) EE.

initiated at the centre and in a proportion which presents a similar variation with c as the maximum value of p_i before local extinction. Notice that this is a linear dependence with c suggesting an explanation of Fig. 7 although some care must be exerted here since the approximations made above will remain valid only for low values of p_i (i.e. low values of c). In fact, this dependence with c overestimates the actual level of altruism observed. We then would see that, for small values of conflict, a cluster would be composed by a self-coordinating strategy and a low proportion of non-altruists near the periphery. Figures 13 and 14 show examples of the time evolution of the population composition for $c = 0.52$ and 0.55; for larger values of c, occasional oscillations are observed.

6. Conclusions

Using basic ecological assumptions such as local noisy interactions, finite neighbourhood size, energy conservation, discreteness of players and asynchrony, the individual-based model has shown that altruistic behaviour can be evolutionarily stable under certain circumstances owing to a combination of selective and ecological factors. Thus, this model contributes to the growing recognition of the relevance of combining spatial and stochastic dynamics by using less-restrictive assumptions about the structure of spatial interactions.

We have shown the methodological value of using a comparative approach to modelling. In particular, one of the issues highlighted by the comparison of discrete and continuous models deals with the differences introduced by treating individuals as discrete entities (Goodnight, 1992; Durrett & Levin, 1994a; van Baalen & Rand, 1998; Gandhi *et al.*, 1999). Similar differences have been observed in alternate models of spatially distributed hypercycles. While a cellular automata approach shows that spatial patterns can induce resistance to parasitic invasions (Boerlijst & Hogeweg, 1991; Boerlijst *et al.*, 1993; Savill *et al.*, 1997), an approach based on partial differential equations (even with the additions of minimum cutoff values for spatial densities) does not replicate the same result (Cronhjort & Blomberg, 1994). It is interesting to notice that, important differences notwithstanding, a similar discrepancy is observed between the continuous and discrete spatial models presented here.

It is important to point out that altruism is favoured by a combination of discreteness and ecological organization. Neither of these factors is sufficient on its own, as shown by the results of the continuous spatial model and the non-spatial individual-based model. The rupture of spatial homogeneity is essential for altruism to be favoured in the case of low conflict. But some of the ensuing broken symmetries occur only as a consequence of the discreteness of the players as in the case of the dependence of the genealogy length on spatial position within a cluster. Discreteness also plays a role in the local extinction that may occur when non-altruistic players start invading the centre of an altruistic cluster. If sufficiently fine-grained density values were permitted this would not occur since there would always remain a small residue of invaders which could change slowly enough for the local environment to become more favourable.

Even though there is no significant interaction between clusters, and, consequently, interpretations of these results in terms of group selection are not possible at this level, there is a sense in which such an interpretation could be reasonable for units of selection *within* a cluster (van Baalen & Rand, 1998). The local invasions of altruisic players, followed by local extinction, can indeed be interpreted in terms of the viability of two different groups in a specific local environment that one of them sets and the other cannot change fast enough. On the flip-side of this interpretation, and also following van Baalen & Rand (1998), we could equally say that an appropriately defined coefficient of relatedness, taking into consideration density-dependent effects, would bring this result within the domain of Hamilton's rule. This is also a viable interpretation of the results. Even though a simple estimation of purely genetic coefficients of relatedness (following Queller & Goodnight, 1989; Queller, 1994) was inconclusive in this respect (Di Paolo, 1999), such a coefficient may not be directly applicable to this case. Finally, it would also be possible to construe these results as a consequence of reciprocal altruism (Trivers, 1971) although there would be little or no difference between this and the kin-selective interpretation since there is no segregation into different species in this model. However, a constant fact in all these possible interpretations remains the two-way coupling between selection and ecological dynamics and the resulting broken ecological symmetries due to the activity of the players.

The formation of clusters relies on the competing effects of expansion towards regions where local density is below the local carrying capacity, and of the increased fitness which is associated with more frequent social interaction in the central region. At first sight, this latter factor might be considered to be an artifact of the way the spatial models are implemented (higher density implies more frequent interactions) and the Allee effect introduced as a consequence. However, it reflects the benefits encountered by many species in social interaction even if, in an apparent paradox, interactions are antagonistic, thus reflecting the fact that games are played for high stakes. It is recognized, however, that a more realistic model would also allow for a minimum rate of growth due to individual, non-social activity. The relative payoff between this activity and the energy gained in interaction would be the parameter of interest in a more general class of models. It can easily be seen that if fitness due to non-social activity is much greater than fitness due to interaction, then there may be little to be gained by interacting. This paper has explored the other end of this spectrum: the case when social interaction is necessary for survival.

It is also recognized that the spatial individual-based model does not represent natural situations in a direct manner, but it is rather a tool for exploring some of the consequences of embedding a selective process in a dynamical ecological setting. Once the relevant mechanisms have been identified, similar factors may be looked for in natural cases. For instance, the asymmetries introduced by clusters may have natural counterparts in structured groups, whether spatially or hierarchically, which present analogous centre/periphery differentiation. The formation and stability of these structures seem to follow patterns similar to the clusters in the above model. "Position" within the group may also be assigned a similar non-genetic fitness component as the one assigned to the spatial position within a cluster (e.g. Krause, 1994). This suggests that the dynamics of formation and maintenance of group structures may be a natural locus for understanding eco-evolutionary processes of the kind described above.

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APPENDIX A

Some of the terms in eqn (6) are hereby described in more detail.

Each player per unit of space "intends" to play the first role with a fixed uniform frequency

F_0 making N_a attempts at finding a partner. If the probability of succeeding in locating a partner is $P_S(x, t)$ then the frequency for playing the first role will be given by

$$F_1(x, t) = F_0\{1 - [1 - P_S(x, t)]^{N_a}\},$$

where the factor in curly brackets indicates the probability of having located a partner after N_a trials.

The probability of a successful trial, $P_S(x, t)$, is taken to be proportional to the total number of players $P^L(x, t)$ in $Loc(x)$, the neighbourhood centred at x:

$$P_S(x, t) = \frac{P^L(x, t)}{\int_\Omega p_T(u, t)\,\mathrm{d}u},$$

where a normalization has been made by dividing by the total number of players in the whole space Ω and $p_T(x, t) = \sum_i p_i(x, t)$. The number of players in $Loc(x)$ is the sum of the total number for each sub-population, $P^L(x, t) = \sum_i P_i^L(x, t)$, and each term in the sum is calculated as

$$P_i^L(x, t) = \int_{Loc(x)} p_i(u, t)\,\mathrm{d}u.$$

The energy received by an individual of type i situated at x as a result of its participation in interactions as an initiator is given by

$$E_i^1(x, t) = F_1(x, t)E(x, t)\sum_j M1_{ij}\frac{P_j^L(x, t)}{P^L(x, t)},$$

where $M1_{ij}$, the ijth element of the payoff matrix for the first role, is used to denote $(M1)_{ij}$, as defined in Section 2. The factor $P_j^L(x, t)/P^L(x, t)$ represents the local average density of players of strategy j within the neighbourhood $Loc(x)$. Given that energy is extracted from the location of the initiator, $E_i^1(x, t)$ must be proportional to the available energy in that position and to the frequency with which an individual plays the first role; hence the first two factors in the above equation. The remaining factor is the average payoff that a player of strategy i will receive given the number of players of each strategy present in the neighbourhood.

The energy received by the same individual of type i due to its involvement in games as a responder depends on the number of contests in which other players in the neighbourhood have selected this individual as a partner and on the strategies played by those neighbours. The probability that the partner found by an individual located in position u be located in position x is the inverse of the total number of players in $Loc(u)$, that is $[P^L(u, t)]^{-1}$. Integrating over all the positions u in $Loc(x)$, the total energy received by a player of strategy i located at x for playing the second role is

$$E_i^2(x, t) = \int_{Loc(x)} F_1(u, t)[P^L(u, t)]^{-1}\,E(u, t) \times \sum_j [p_j(u, t)M2_{ji}]\,\mathrm{d}u.$$

The integrand is readily interpretable as the proportion of all interactions originating at u which find a partner located at x times the average energy payoff received by that partner if it is of type i for the participation as a responder.

The term $E_C(x, t)$ in the energy equation indicates how much energy is being consumed at (x, t). This is the local energy value $E(x, t)$ times the frequency of interactions initiated at (x, t) times the sum of average first- and second-role payoffs for each interaction. Dropping the dependency on (x, t) we obtain

$$E_C = F_1E\sum_{i,j} p_i(M1_{ij} + M2_{ji})P_j^L/P^L.$$

APPENDIX B

In order to reduce the number of parameters in the continuous spatial model, eqn (6) can be non-dimensionalized:

$$\frac{\partial p_i}{\partial t} = p_i[A_1(E_i^1 + E_i^2) - A_2] + D'\nabla^2 p_i, \quad \text{(A.1)}$$

$$\frac{\partial E}{\partial t} = 1 - E - E_C,$$

where all variables are non-dimensional and

$$A_1 = \frac{BF_0R}{\gamma_e^2}, \quad A_2 = \frac{BL_0}{\gamma_e}, \quad D' = \frac{D}{\gamma_e L^2}.$$

The non-dimensional parameter A_1 gives an idea of the strength in the coupling between energy and density of players, it can be interpreted as a comparison between the energy needed to "produce" a typical number of players per unit of space $[(BF_0/\gamma_e)^{-1}]$ and the maximum value for the environmental energy (R/γ_e). A_2 can be interpreted as a comparison between the characteristic saturation times for the energy (γ_e^{-1}) and the density of players $[(BL_0)^{-1}]$.

Not all values of A_1 and A_2 guarantee pattern formation and this depends on the scaling relation between neighbourhood size and the whole spatial domain. If the spatial domain is between 10 and 100 times the neighbourhood size, a good choice is $A_2 = 0.05$ and $A_1 = 0.25$.

The number of attempts at finding a partner made by each player is $N_a = 2$.