

The spatial spread of altruism versus the evolutionary response of egoists

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Several recent models have shown that altruism can spread in viscous populations, i.e. in spatially structured populations within which individuals interact only with their immediate neighbours and disperse only over short distances. I first confirm this result with an individual-based model of a viscous population, where an individual can vary its level of investment into a behaviour that is beneficial to its neighbours but costly to itself. Two distinct classes of individuals emerge: egoists with no or very little investment into altruism, and altruists with a high level of investment; intermediate levels of altruism are not maintained. I then extend the model to investigate the consequences of letting interaction and dispersal distances evolve along with altruism. Altruists maintain short distances, while the egoists respond to the spread of altruism by increasing their interaction and dispersal distances. This allows the egoistic individuals to be maintained in the population at a high frequency. Furthermore, the coevolution of investment into altruism and interaction distance can lead to a stable spatial pattern, where stripes of altruists (with local interactions) alternate with stripes of egoists (with far-reaching interactions). Perhaps most importantly, this approach shows that the ease with which altruism spreads in viscous populations is maintained despite countermeasures evolved by egoists.

Keywords: altruism; cooperation; spatial games; dispersal distance; cellular automata

1. INTRODUCTION

The spread and stability of altruistic behaviour remain unresolved puzzles in evolutionary ecology. Why should an individual increase another individual's fitness at the expense of its own? Indeed, selfish individuals should always have higher fitness than cooperators, since they receive the benefits of cooperation without having to pay the cost. One would therefore predict that any cooperative strategy would soon be eliminated by natural selection.

Nevertheless, cooperation appears to be widespread among animals (Dugatkin 1997) and is thought to have been a driving force in several of the major transitions in evolution, e.g. the evolution of multicellularity from unicellular ancestors (Buss 1987; Maynard Smith & Szathmáry 1995).

One of the first propositions to solve this dilemma was based on kin selection (Hamilton 1963): a gene promoting altruism may increase its frequency if the beneficiary also happens to carry it. This is likely to be the case if the beneficiary is a close relative of the altruist. In many cases of cooperative behaviour, however, interacting individuals do not appear to be related. Thus, mechanisms that do not require kin selection are needed.

One of these mechanisms relies on the assumptions that individuals repeatedly interact with the same partner and that each partner's strategy can take into account the past history of their interactions. These assumptions often lead to the spread of altruistic strategies (Nowak & Sigmund 1993; Roberts & Sherratt 1998), the best known being tit-for-tat (Axelrod & Hamilton 1981): cooperate in the first interaction and copy your partner's move for all subsequent interactions.

A second mechanism is based on group selection rather than on repeated interactions between pairs of individuals.

If subpopulations with altruistic individuals fare better than subpopulations dominated by egoists, the proportion of altruists in the population as a whole may increase despite the altruists having lower fitness than egoists in direct competition between the two (Haldane 1932; Maynard Smith 1964; Wilson 1977). Recently, the approach involving discrete subpopulations, where local population growth alternates with dispersal connecting subpopulations, has been modified to study the evolution of altruism in viscous populations (i.e. populations without discrete subpopulations, but nevertheless with limited dispersal because offspring tend to remain close to their parents). One of the motivations for this approach is that it moves the level of selection from the group to the individual. In the models so far published, each individual interacts with its immediate neighbours and its reproductive success is evaluated by the number of cooperators and defectors in its neighbourhood. Though earlier attempts at models that allow altruism to spread in viscous populations have failed (Taylor 1992*a,b*; Wilson *et al.* 1992), a more recent model has shown elegantly the possibility of invasion of altruism using pair approximations of the dynamics (Van Baalen & Rand 1998). These results are corroborated by approaches based on spatial lattices of cellular automata (Killingback *et al.* 1999; Nowak & May 1992); these differ from the viscous populations in that individuals do not reproduce or disperse but rather are replaced by individuals with the highest success within the neighbourhood. In all of these models, altruistic behaviour can spread under very general assumptions, including in situations where individuals from two species show altruistic behaviour, i.e. mutualisms (Doebeli & Knowlton 1998).

Thus, the recent models based on spatial systems suggest that altruism may not be such a difficult evolutionary dilemma after all. However, the models also

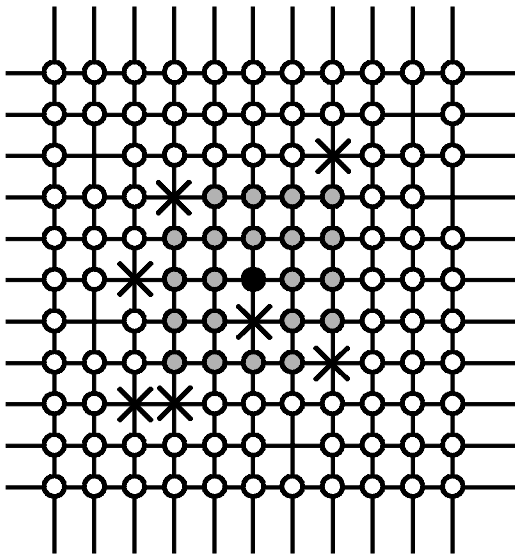


Figure 1. Example of a spatial lattice. Occupied spaces are shown by circles. A focal individual is shown in black. It interacts with its neighbours (shown in grey) up to the interaction distance of 2; its offspring can potentially disperse to the empty sites (marked by crosses) up to the dispersal distance of 3. Note that the local environment of a focal individual (for interaction and dispersal) is assumed to form a square.

suggest that altruists can invade only if their dispersal distance and the distance over which they interact with neighbours is limited. Thus, it is reasonable to expect that evolutionary pressure will cause egoists to evolve further dispersal and interaction distances in response to the spread of altruism, so that they are more efficient at invading altruistic clusters (Van Baalen & Rand 1998). But what are the consequences of such an evolutionary response by the egoists, and in particular, will it lead to exclusion of altruism? The two possibilities are that altruistic strategies are eliminated from the population by the evolutionary response of the egoists or, alternatively, that two classes of individuals are formed: altruists with very local interactions and egoists with far-reaching dispersal and interactions.

I investigate these questions by modelling a viscous population of cellular automata. Following several recent models, I allow investment into altruism to vary as a continuous trait (Killingback *et al.* 1999; Sherratt & Roberts 1998; Van Baalen 1998; Wahl & Nowak 1999). Additionally, and in contrast to these models, I allow the simultaneous evolution of the dispersal distance of offspring and the distance over which individuals interact with their neighbours. In doing so, I have two goals: first, to confirm the results reached with a pair approximation of the viscous population (Van Baalen & Rand 1998) and, second, to investigate the destabilizing consequences of the simultaneous evolution of investment into altruism, dispersal distance and interaction distance.

2. GENERAL MODEL

In all of the models presented here, individuals interact with one another on a spatial lattice (figure 1). The lattice

has the shape of a torus, i.e. individuals on the edges interact with individuals on opposite edges, eliminating edge effects. Every site on the lattice can be either empty or occupied by an individual investing level I into altruistic behaviour. Investment into altruism takes values between 0 and 0.99, with random mutations changing the investment in steps of ± 0.01 . Individuals interact with their neighbours up to a distance that is called the interaction distance.

The state of the lattice changes at each time-step as a consequence of random birth and death events. The probability of death is constant and identical for each individual (i.e. independent of the chosen strategy). An individual's probability of reproducing, however, is determined by its own strategy and by its neighbourhood. Specifically, investment into altruism incurs a cost, c , which is assumed to be proportional to the investment (i.e. $c = \gamma I$), and reproduction increases with the average level of the neighbours' investment into altruism according to the function $\beta(1 - e^{-k\bar{I}})$. Thus, the birth rate of an individual can be defined as

$$b(I) = b_0 + \beta(1 - e^{-k\bar{I}}) - \gamma I, \quad (1)$$

where b_0 is the probability of reproduction without any interactions and the benefit due to the N neighbours' investment is calculated as the mean level of investment of individuals within the focal individual's interaction distance, i.e. $\bar{I} = \sum I_i / N$. Alternative benefit functions, e.g. a function where an individual's reproduction increased proportionally to its neighbours' investment, gave similar results.

The offspring are successful only if they find an empty site within dispersal distance of their parent. Each empty site is occupied by the offspring of the parent with locally (i.e. within dispersal distance) the highest probability of reproduction. (Alternatively, offspring could be chosen randomly with probability proportional to the birth rate of the parents within dispersal distance of the site; this gave similar results, though evolution was slower due to increased drift.)

Finally, mutations modify the genetic basis of the individuals' behaviour. They are assumed to occur randomly with a low probability (in all simulations shown, the probability was set to 0.001) and to have a small effect, i.e. they can change the investment into altruism by only one step in either direction.

(a) Results of the general model

In all of the simulations, the size of the lattice is set to 50×50 individuals and the individuals are initialized with no investment into altruism.

The typical results of simulations confirm previously established results: investment into altruism spreads readily in a population when dispersal distance is low (figure 2a). The system eventually reaches a dynamic equilibrium, where the mean level of investment in the population remains more or less constant (figure 2a). At this equilibrium, the population is divided into a group of individuals with almost no level of investment into altruism (egoists) and a distinct group with considerable investment into altruism (altruists); no individuals have intermediate levels of investment (figure 2b). As dispersal

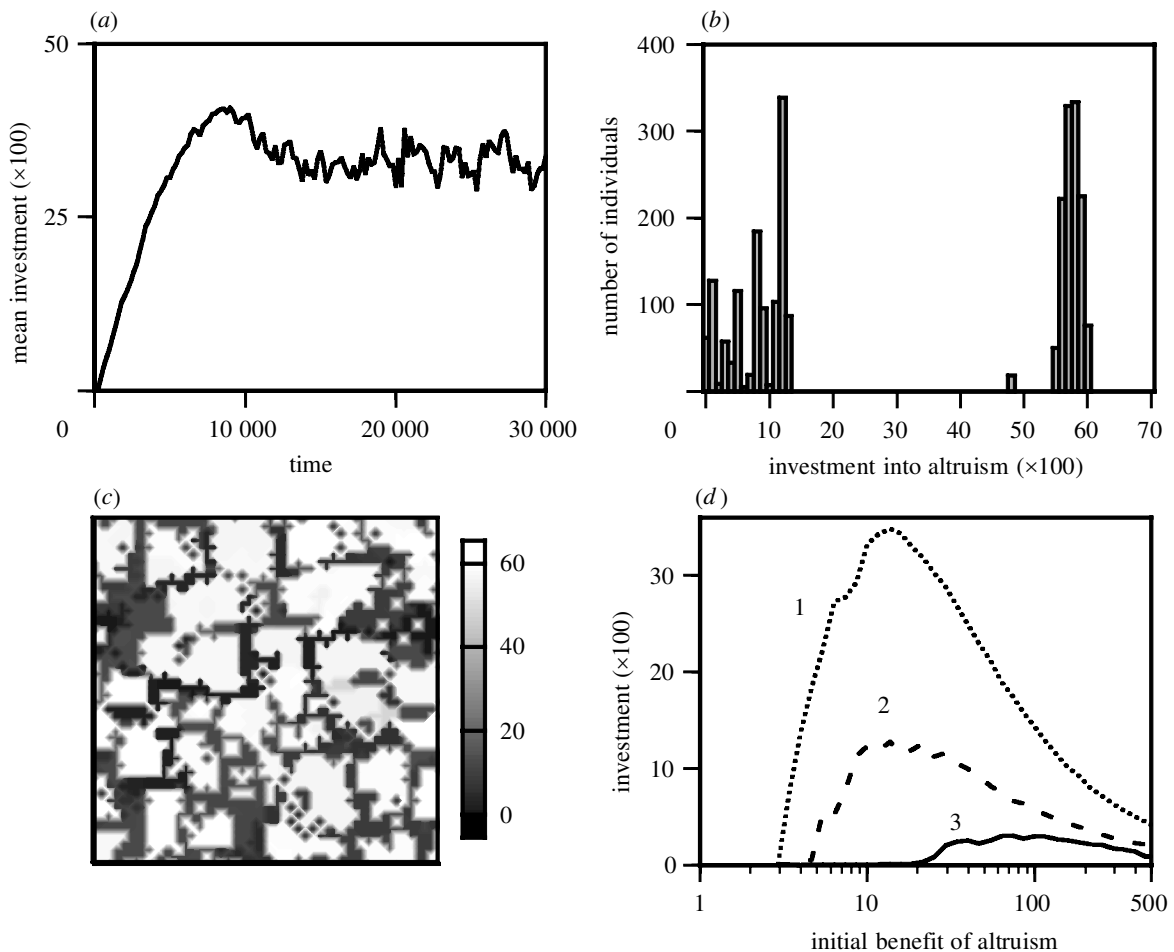


Figure 2. Typical results of simulations using the basic model where only investment into altruistic behaviour is allowed to evolve. (a) Evolution of the average investment into altruism. (b) Distribution of investment reached after 30 000 generations. (c) Spatial distribution of investment reached after 30 000 generations. The square represents the 50×50 grid. As indicated in the legend, dark patches represent egoistic individuals and light patches represent altruistic individuals. (d) Average investment into altruism reached after 100 000 generations for various slopes of the benefit function (product of k and β in equation (1)) and dispersal distances 1 (dotted line), 2 (dashed line) and 3 (solid line). As investment fluctuates because of the randomness of the processes, the mean of the last 50 000 generations is shown. The parameters in the simulations are size of arena, 50×50 ; fecundity in the absence of any interactions, b , 1; maximal benefit of altruism, β , 5; slope of cost of altruism, γ , 1; death rate, 0.1; interaction distance, 1; and mutation rate, 0.001. In (a–c) the slope of the benefit of altruism at zero investment ($k\beta$) is 5 and the dispersal distance is 1. Note that in (d) the parameter β is maintained at 5 while k is allowed to vary.

distance increases altruism can spread if the benefit gained by altruistic neighbours is sufficiently high (figure 2d). The mean level of investment into altruism within the population reaches its maximum at an intermediate value of ‘initial benefit’ (figure 2d). Note that the term ‘initial benefit’ in figure 2d refers to the slope of the benefit function when all neighbours are egoistic, i.e. βk in equation (1). Therefore, as initial benefit (the slope of the function) in equation (1) increases, a birth rate close to the maximal value is reached with lower levels of altruism.

Furthermore, the altruists form clusters of individuals that profit from their altruistic behaviour while remaining resistant to invasion by the egoists they are surrounded by (figure 2c), again confirming previous results (Killingback *et al.* 1999; Van Baalen & Rand 1998). The mechanisms leading to the spread of altruistic clusters have been described earlier (Killingback *et al.* 1999; Van Baalen & Rand 1998) and will not be discussed here; rather, I will in §§ 3 and 4 concentrate on the effect of coevolution with dispersal and interaction distance, respectively.

3. COEVOLUTION OF DISPERSAL DISTANCE

In a first modification of the basic model described above, the maximal dispersal distance of offspring is allowed to evolve with random mutations changing dispersal distance by ± 1 (while the interaction distance is maintained at a constant value of one spatial unit). As dispersal in models with no selection pressure is likely to drift into the population (and thus to prevent the spread of altruistic behaviour), a small cost of dispersal is subtracted from the equation defining the number of offspring. Thus, the birth function becomes

$$b(I) = b_0 + \beta(1 - e^{-kI}) - \gamma I - \delta d, \quad (2)$$

where d is the dispersal distance and δ is the cost of dispersal (which is assumed to be 0.01 in all simulations).

As in the previous model, the population is initialized with egoistic individuals that invest nothing into altruism.

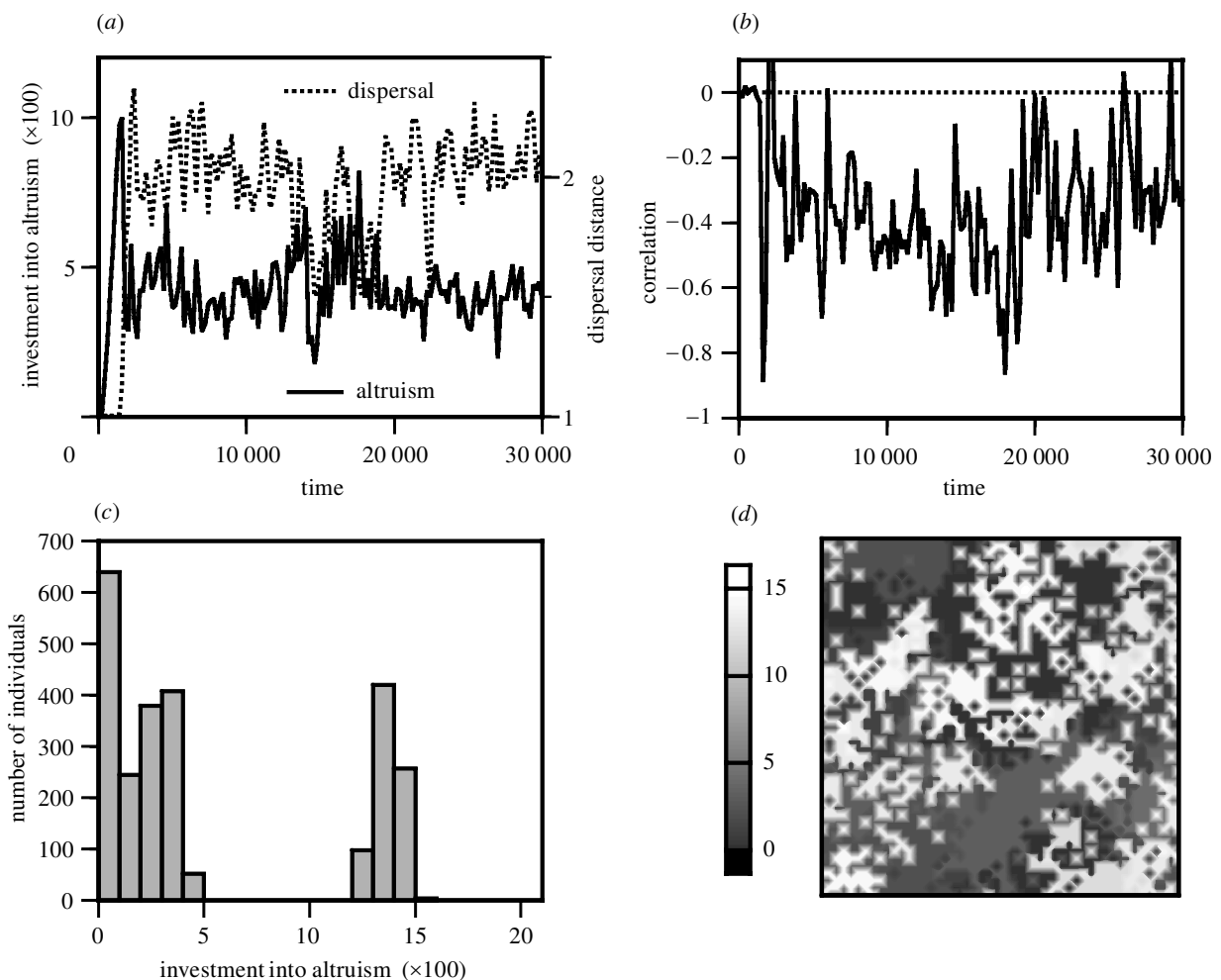


Figure 3. Typical results of simulations using the model where dispersal distance can evolve as well as investment into altruistic behaviour. (a) Evolution of the average investment into altruism (solid line) and average dispersal distance (dotted line). (b) Evolution of the correlation between dispersal distance and investment into altruism. (c) Distribution of investment reached after 30 000 generations. (d) Spatial distribution of investment reached after 30 000 generations. The square represents the 50×50 grid. As indicated in the legend, dark patches represent egoistic individuals and light patches represent altruistic individuals. The parameters in the simulations are as in figure 2, except that dispersal distance is not held constant and the cost of dispersal (δ) is 0.01.

Additionally, the dispersal distance is set to 1 (the lowest possible value) in the initial generation.

When the benefit of altruism is sufficiently high, investment into altruism can again increase (figure 3a). However, the egoistic individuals (maintaining low levels of investment into altruism) respond to the spread of altruism by increasing their dispersal distance. This allows them to invade altruistic clusters more effectively and keeps the altruistic individuals from evolving high levels of investment. As altruistic individuals disperse only short distances to maintain the integrity of their local clusters, the evolutionary response of the egoists to increasing levels of altruism generates a negative correlation between dispersal distance and investment into altruism (figure 3b). Thus, the discrete distributions of investment formed for egoistic and altruistic individuals (figure 3c) are reflected in their dispersal distances. At the end of the simulations shown in figure 3, about 41% of the altruistic individuals spread their offspring by only one spatial unit, while 97% of the egoistic individuals had a dispersal distance greater than one unit. Additionally, none of the altruists spread their offspring more than

two units, while almost a quarter of the egoistic individuals spread their offspring over three or four units. The increased dispersal changes the spatial pattern: while the clustered pattern of altruists and egoists remains apparent, the clusters tend to become larger than for the basic model (figure 3d).

4. COEVOLUTION OF INTERACTION DISTANCE

In a second modification of the basic model, the dispersal distance is held constant (one unit in all simulations) but instead the interaction distance of individuals is allowed to evolve with random mutations changing it by ± 1 (see figure 1). There is no direct cost of interacting, so that the birth function (equation (1)) is used.

The population is initialized with egoistic individuals that interact only with their immediate neighbours. As in the basic model, the mean level of investment increases rapidly to an equilibrium level that is maintained by the dynamics of the spatial system (figure 4a) and two discrete groups of individuals are formed with either very low or quite high levels of investment into altruism

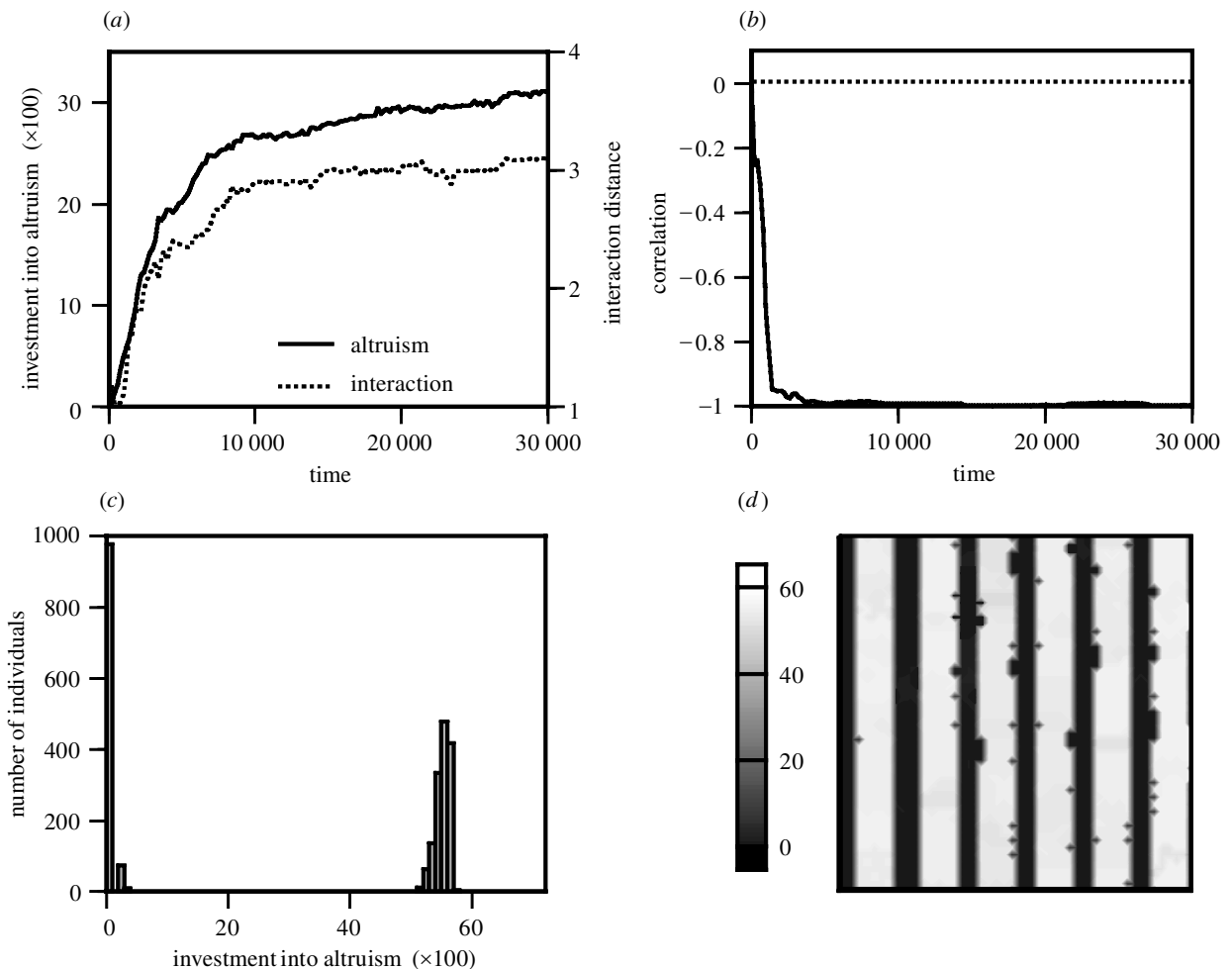


Figure 4. Typical results of simulations using the model where interaction distance can evolve as well as investment into altruistic behaviour. (a) Evolution of the average investment into altruism (solid line) and average interaction distance (dotted line). (b) Evolution of the correlation between interaction distance and investment into altruism. (c) Distribution of investment reached after 30 000 generations. (d) Spatial distribution of investment reached after 30 000 generations. The square represents the 50×50 grid. As indicated in the legend, dark patches represent egoistic individuals and light patches represent altruistic individuals. The parameters in the simulations are as in figure 2, except that interaction distance is not held constant.

(figure 4c). A strong negative correlation between investment into altruism and interaction distance shows that while altruistic individuals evolve to interact only with their immediate neighbours, the egoists evolve a greatly increased interaction distance (figure 4b). Finally, and in contrast to the previous models, the coevolution of interaction distance and investment into altruism leads to a stable spatial pattern with alternating stripes of egoists and altruists (figure 4d). The direction of the stripes (horizontal or vertical) depends on the initial conditions. Simulations where the arena does not have periodic boundary conditions (i.e. where individuals on an edge cannot interact with or disperse to the opposite edges) reveal the same pattern (results not shown).

5. DISCUSSION

The main results of the described models are: first, that investment into altruism can evolve to a high level under rather general conditions; second, that egoists cannot be eliminated from the population, but rather respond to the spread of altruism by increasing their dispersal distance

and the distance over which they interact with their neighbours; and third, that the combined evolution of investment into altruism and the interaction distance can lead to stable spatial patterns.

When investment into altruism can evolve, but dispersal and interaction distances remain constant, the results of the model confirm previous attempts at describing the spread of altruism in spatially structured populations (Killingback *et al.* 1999; Nowak & May 1992; Van Baalen & Rand 1998). Altruism can spread if the benefit to the recipient of the altruistic behaviour is sufficiently high to compensate for the cost of behaving altruistically. As described in detail previously (Killingback *et al.* 1999; Van Baalen & Rand 1998), the success of altruistic behaviour can be explained with group-selection arguments. In viscous populations such as the ones described in this paper, individuals sharing an ancestor (and thus with similar traits) form clusters because of limited dispersal. As cooperation within groups of individuals interacting only among themselves benefits all individuals in the group, a cluster of altruistic individuals has a higher rate of spread than a cluster of egoistic individuals, which leads to

the spread of altruism in the population as a whole. However, altruism can spread only when interactions are local, i.e. when the distance over which individuals interact with their neighbours and the distance their offspring disperse are small. Furthermore, egoistic cheaters can generally invade clusters of altruists because of the reduced cost of their behaviour, so that the population as a whole is held in a dynamic equilibrium at an intermediate investment into altruism. What has received less attention in earlier literature is that the level of investment into altruism is bimodal: while some individuals invest very little into altruism, others invest very high levels; intermediate levels of investment are not maintained.

When, in addition to investment into altruism, dispersal distance or distance over which individuals interact with their neighbours can respond to natural selection rather than being fixed, egoistic individuals can respond to the spread of altruists and thus limit the level and prevalence of altruism.

One of the responses of egoists to the spread of altruism is to increase their dispersal distance. This enables them to penetrate the interiors of altruistic clusters and thereby to increase their likelihood of reproducing and spreading. At the population level, the increased dispersal distance increases the mixing of the population, which makes it more difficult for altruistic clusters to form and thus for altruism to spread. Furthermore, the simultaneous evolution of dispersal distance and investment into altruism leads to the coexistence of two types of individuals, rapidly moving egoists and sedentary altruists, as predicted in earlier studies (Van Baalen & Rand 1998). However, the separation between altruists and egoists is not as clear as when altruism alone evolves, as the increased dispersal distance of the egoistic individuals maintains a low level of investment by the altruists.

Egoists can also respond to the spread of altruism by increasing the distance over which they interact with their neighbours, as egoists with far-reaching interactions may benefit from many altruistic interactions while not having to pay the cost of altruism. In contrast, altruists maintain close interactions within their local clusters, so that they run less risk of interacting with egoists outside their cluster. This result is reminiscent of the simultaneous evolution of altruism with choosiness (Sherratt & Roberts 1998): if individuals can choose with whom to interact, altruism is more likely to evolve. In the model described in this paper, altruists are choosy in the sense that they interact only with their immediate neighbours, while egoists interact with a larger (and thus more diverse) sample of neighbours. This choosiness leads to two clearly distinct classes of individuals: egoistic individuals with far-reaching interactions and altruists with local interactions. This, in turn, leads to a stable spatial pattern of altruism. Indeed, the interactions between egoistic and altruistic individuals are similar to the frequency-dependent interactions between two discrete species, which lead to similar spatial patterns (Molofsky *et al.* 1999). More generally, the patterns found here and in earlier studies (Molofsky *et al.* 1999), which describe interactions that are governed by random processes, reflect the spatial patterns that can be found in deterministic systems of interacting populations (Hassell *et al.* 1994; Molofsky 1994; Okubo 1980).

Overall, the model presented here, together with previous models of the spread of cooperation in spatially structured populations (Killingback *et al.* 1999; Nowak & May 1992; Van Baalen & Rand 1998), provides a basis for the understanding of cooperative and altruistic behaviour. Together, these models show that high levels of investment in altruistic behaviour can evolve with relative ease from a population of egoists, and that the evolutionary process will generally lead to a mixture of highly altruistic and highly egoistic individuals with very few intermediate behaviours.

Naturally (though this has not previously been considered), the egoists will evolve additional strategies to exploit altruists and thus to check their spread; in the model presented here they respond by increasing their dispersal or interaction distance. Despite this evolutionary response, altruistic behaviour is maintained in the population; in fact, though either evolutionary response decreases the prevalence of altruism, evolution of interaction distance tends to enhance the difference in investment levels between altruists and egoists and to stabilize the spatial pattern.

Thus, modelling the coevolution of investment into altruistic behaviour and the response by the egoists may help to understand more thoroughly not only the invasion but also the stability of cooperative behaviour observed at all levels of biological organization, from the cooperation between replicating molecules (Eigen & Schuster 1979; Maynard Smith & Szathmary 1995) to the social organization of organisms (Dugatkin 1997).

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