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The evolution of altruism by costly punishment in lattice-structured populations: score-dependent viability versus score-dependent fertility

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ABSTRACT

Question: What part might punishment play in maintaining cooperation in animal and human societies?

Mathematical method: Evolutionary game theory. The game's score modifies either viability or fertility.

Key assumptions: The population is spatially structured. After a player dies, a copy of one of its nearest neighbours fills the vacancy. Altruists may punish selfish individuals by forcing them to pay a 'fine', but the punisher itself must pay to impose the fine.

Conclusions: Punishment can make altruism an evolutionarily stable strategy. In a well-mixed population, if the score affects fertility, then an altruist-punisher cannot invade a selfish population. But it can invade if the score affects viability and the fine is large. In a spatially structured population, an altruist-punisher can invade a selfish population whether the score affects viability or fertility. In the viability model, large fines promote altruism. But in the fertility model, either a large fine or a high benefit of cooperation promotes altruism.

Keywords: altruism, lattice, punishment, score-dependent fertility, score-dependent viability.

INTRODUCTION

Altruism improves the fitness of the recipient but reduces the fitness of the actor. The evolution of altruism by natural selection is a focus of behavioural ecology. It has been explained by kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971) and group selection (e.g. Cohen and Eshel, 1976; Sober and Wilson, 1998). More recently, indirect reciprocity has attracted attention, in which an altruist can receive help from a third person who knows his good deed. Indirect reciprocity can be performed by help based on reputation (e.g. Nowak and Sigmund, 1998; Brandt and Sigmund, 2004; Nakamaru and Kawata, 2004; Ohtsuki and Iwasa, 2004), in which non-altruistic individuals with bad reputations are discriminated against and receive less cooperation than altruistic players.

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The punishment of selfish individuals has also been considered. Punishment is an action that reduces the fitness of selfish individuals in the population, but a punisher has to pay a cost to perform it. In experiments using humans, Fehr and Gachter (2002) showed that the opportunity for punishment, or a sanction, is able to maintain a high level of cooperation among players. A physiological study of brain activity indicates that people obtain emotional reward by punishing defectors or norm violators (de Quervain *et al.*, 2004). Non-human animals use punishment to maintain the cooperation of group members (Clutton-Brock and Parker, 1995), and even soybeans impose sanctions on rhizobium when they do not fix N_2 effectively (Klers *et al.*, 2003).

Whether costly punishment can be maintained and successfully promote the evolution of altruism has been the focus of recent theoretical studies. Sigmund *et al.* (2001) analysed a replicator dynamics and showed that punishment and reputation can make an altruist-punisher an evolutionarily stable strategy (ESS). The effect of spatial structure on the evolution of altruism by punishment has been studied in metapopulation models (Boyd *et al.*, 2003; Bowles and Gintis, 2004) and in a hexagonal lattice model (Brandt *et al.*, 2003). In general, the spatial structure of the population has a strong effect on the propensity for the evolution of altruism or cooperation. Whether it is formulated as a lattice model, a meta-population model or a reaction-diffusion model, spatial structure tends to allow assortment of the same strategies. Then the same strategies interact more frequently than a random sample from the whole population, which causes a kin selection (or group selection) effect favouring the evolution of cooperation. On the other hand, players of the same strategies tend to compete with each other locally for vacant sites, which discourages the evolution of cooperation. The net effect of spatial structure is determined by the balance of these two tendencies (Matsuda *et al.*, 1987, 1992; Nowak and May, 1992; Taylor, 1992; Wilson *et al.*, 1992; Nakamaru *et al.*, 1997, 1998; Mitteldorf and Wilson, 2000; Le Galliard *et al.*, 2003; Hauert and Doebeli, 2004).

Punishment is a form of spite, because a punisher pays a cost to reduce the fitness of other players. In studying the evolutionary dynamics of toxin-producing, slow-growing bacteria and toxin-sensitive, fast-growing bacteria, Iwasa *et al.* (1998) showed that the spatially structured population facilitates the evolution of a spiteful behaviour (i.e. toxin production). The rare spite (toxin-producing) strain can invade the population occupied by the non-spite (toxin-sensitive) strain in the lattice model, which is not possible in a completely mixed population. In analysing the repeated prisoner's dilemma game in a lattice-structured population, Nakamaru *et al.* (1997, 1998) also showed that the spatial structure does not always help altruism to evolve, but sometimes promotes the evolution of spite.

In these lattice models, each player engages in a repeated prisoner's dilemma game with its nearest neighbours and obtains a game score. The empty site produced after the death of a player is filled by a copy of one of its nearest neighbours. Mortality or fertility may depend on the game's score. Nakamaru *et al.* (1997) studied the case in which the probability of death depends on the game's score, but fertility is independent of the score. This is called the score-dependent viability model, or 'viability model'. In contrast, in the score-dependent fertility model ('fertility model'), an individual dies randomly and one of its nearest neighbours colonizes its empty site according to the probability determined by the game's score (Nakamaru *et al.*, 1998). In both models, a reciprocal altruistic strategy ('tit-for-tat') can invade the selfish population, which is not possible in a population without spatial structure (the completely mixed model). However, the two models differ greatly in their propensity to favour the evolution of cooperation. The condition for the cooperative strategy to be an ESS is broader in the fertility model than in the completely mixed model, which is in turn

broader than in the viability model. In the viability model, the score affects survivorship, and hence players who reduce their neighbours' score enjoy a greater opportunity to reproduce because reproduction can occur only when one of the neighbours dies. Therefore, the lattice structure favours the evolution of spite. The situation is quite different in the fertility model, in which the score affects the birth rate but not survivorship. Competitors for a vacant site do not interact with each other directly. Since having a neighbour with a high score does not harm the opportunity of the focal player, the propensity to favour spite does not exist in the fertility model (Nakamaru *et al.*, 1998). Cooperation is selected for in the fertility model more than in the corresponding viability model, which Irwin and Taylor (2001) also showed for the metapopulation model.

In this paper, we consider a game in a lattice model between altruistic and selfish players when altruists also engage in costly punishment. The two strategies are altruist-punisher and pure-selfishness among four strategies studied by Sigmund *et al.* (2001). Here we focus on the difference between when the game's score affects viability and when it affects fertility in the lattice model. We also examine the effect of the spatial structure by comparing a completely mixed model, a pure lattice model and models intermediate between the two.

MODEL

We consider the evolutionary dynamics of altruists and selfish players arranged on a regular square lattice, in which each site has four neighbours (Neumann neighbourhood). Players engage in a game with others, and the game's pay-off modifies the fitness. An altruist increases the fitness of its opponent by a benefit b, but decreases its own fitness by a cost c. We assume $b \geq c > 0$. When two altruists interact, both increase their fitness by $b - c$. In contrast, a selfish player does not improve the fitness of its opponent, but it pays no cost. When two selfish players interact, their fitness remains unchanged, which is smaller than when both are altruists ($b - c$). However, if a selfish player engages in the game with an altruistic player, the selfish player improves its fitness by b and the altruist reduces its fitness by c. This makes it difficult for altruists to be maintained in the face of selfish invaders.

To overcome this difficulty, we consider punishment (Sigmund *et al.*, 2001). In the presence of a punisher, a selfish individual has to pay a 'fine', which reduces the benefit of being selfish, promoting the spread of altruists. However, a punisher also has to pay a cost. If a punisher interacts with a selfish player, the selfish player suffers the cost of being punished ($-p$) and the punisher also suffers the cost of imposing punishment ($-q$). We here consider the situation in which altruists also act as punishers. Table 1 illustrates the pay-offs of two strategies: altruist-punisher and selfish-non-punisher (left column).

Each player interacts with four opponents, and obtains its score, which is the sum of pay-offs given in Table 1. For example, if an altruist-punisher interacts with three other altruists and one selfish player, the score of the focal altruistic player is $3(b - c) + (-c - q)$.

The choice of four opponents for each player is controlled by parameter θ. With probability θ, a player chooses its opponent randomly from the whole lattice, and with probability $1 - \theta$, a focal individual chooses one of its nearest neighbours as the opponent. Hence θ is the fraction of a long-range interaction. When $\theta = 0$, a focal player interacts only with its four nearest neighbours, and the model is a straightforward lattice model with a Neumann neighbourhood. In contrast, when $\theta = 1$, the model corresponds to a completely mixed population without spatial structure. When a focal player dies and a site becomes empty, one of these four partners colonizes that site.

Table 1. The pay-off matrix of a focal player interacting with its opponent (we assume that $b \geq c > 0$, $q > 0$ and $p > 0$)

		Opponent	
		Altruist-punisher AP	Selfish-non-punisher SN
Actor	Altruist-punisher AP	$b - c$	$-c - q$
	Selfish-non-punisher SN	$b - p$	0

We study two cases differing in the life-history parameter that depends on the game's score. In the score-dependent viability model (Nakamaru *et al.*, 1997), the mortality of each individual decreases with its score. After the death of an individual, the site becomes empty and one of the four opponents in the game, chosen at random, colonizes it immediately. In contrast, in the score-dependent fertility model (Nakamaru *et al.*, 1998), after an individual dies randomly regardless of its score, the vacant site created is subsequently filled by an offspring of a player that is chosen from among the four opponents in the game with the probability proportional to its score. Hence, the opponents in the game are also the potential parents of a newborn that fills the gap created by the death of the focal player.

In a Monte Carlo simulation, in one unit of time, each lattice site is chosen once on average for examining the possibility of transition – though the actual transition occurs at the probability determined by the score-dependent rate. In one unit of time, all the N sites are examined for their possibility of transition. Here a 50×50 lattice is used ($N = 2500$). To remove the effect of the edge of the lattice, we assumed the periodic boundary condition.

For the completely mixed model (the lattice model with $\theta = 1$), the result of Monte Carlo simulations was compared with the ordinary differential equation for the fraction of altruist-punishers (Appendix 1). In the regular lattice population ($\theta = 0$), we compared the Monte Carlo simulation with the prediction by the pair-edge approximation in a one-dimensional lattice (Appendix 3).

VIABILITY IS SCORE-DEPENDENT

The completely mixed model ($\theta = 1$)

If each player interacts with its four opponents chosen randomly from the whole lattice, and if the vacancy created by the death of a player is filled by a copy of a randomly chosen player in the lattice, the population develops no spatial structure. Then, we can calculate the densities of two strategies using ordinary differential equations. The analysis in Appendix 1 indicates that, as the population consists of two strategies, altruist-punisher (AP) and selfish-non-punisher (SN), AP always beats SN when the fine or punishment (p) is very large compared with the benefit (b). Let $T_1 = p - 4q - 4c$, and $T_2 = 4p - q - 4c$. Then, AP always beats SN when $b < T_1$; SN always beats AP when $b > T_2$. In between these two ($T_1 < b < T_2$), whichever initially dominates the population would rebuff the invasion of the other – the system is bistable (see Appendix 1).

Figure 1 illustrates the condition in which an altruist-punisher is an ESS and an altruist-punisher can invade the population occupied by selfish-non-punishers. The vertical axis represents the fine or punishment p and the horizontal axis represents the benefit b. Each circle indicates the outcome of the Monte Carlo simulations of the viability model when $\theta = 1.0$. The dark grey portion of each circle indicates the fraction of runs in which the selfish-non-punisher won (among 100 simulation runs); the light grey portion indicates the fraction of runs in which the altruist-punisher won. The lines in Fig. 1A and 1B indicate the equations $b = T_1$ and $b = T_2$, respectively. Figure 1A shows that an altruist-punisher (AP) can invade the population occupied by a selfish-non-punisher (SN) when $b < T_1$, otherwise a selfish-non-punisher can be an ESS. Figure 1B shows that an altruist-punisher is an ESS when $b < T_2$, otherwise the selfish-non-punisher can invade the population dominated by the altruist-punisher. The Monte Carlo simulations were concordant with the predictions of the differential equation for the density of altruist-punishers in Appendix 1.

The regular lattice model ($\theta = 0$)

In the two-dimensional lattice structured population with two strategies, AP and SN, starting from an initial random spatial pattern, clusters of the players of the same strategy are formed quickly, and then they grow or shrink (Fig. 2A and 2B). The fine or punishment (p) determines the evolution of altruist-punisher (AP) (Fig. 2C and 2D) when both c and q are fixed. When p is larger than a threshold ($2 \sim 3$ in $c = q = 1$), AP beats SN, irrespective of the initial frequency. On the other hand, AP cannot invade the SN population in the completely mixed model (Fig. 1A) with the same parameters as in Fig. 2D. Figure 2E also shows the evolution of AP depends not on b, but on q, a cost of punishing a defector, when both c and p are fixed. In the completely mixed model with the same parameters as Fig. 2E, AP cannot invade the SN population. Hence, the lattice structure promotes the invasion of

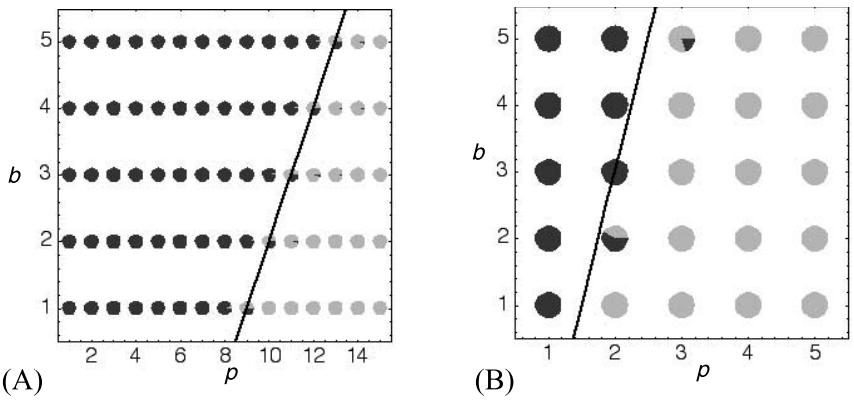
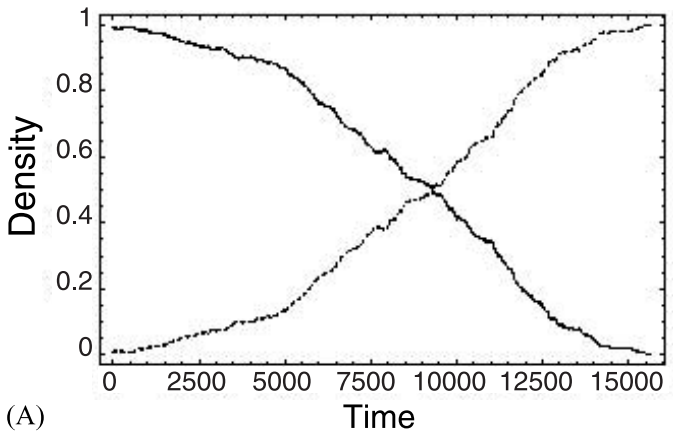


Fig. 1. The parameter region in which altruist-punisher (AP) is an ESS in the viability model of the completely mixed population. The population includes AP and SN. The parameters are: $c = q = 1$. Each circle indicates the outcome of Monte Carlo simulations of the fertility model when $\theta = 1.0$. The dark grey portion of each circle is the fraction of runs in which SN won (among 100 simulations); the light grey portion is the fraction of runs in which AP won. (A) The initial density of AP is 0.01 and that of SN is 0.99. The line is the equation $b = T_1$. (B) The initial density of AP is 0.9 and that of SN is 0.1. The line is the equation $b = T_2$.


Density
Time
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0
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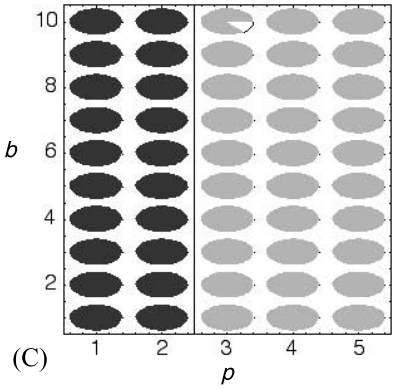
5000
7500
10000
12500
15000

(A)

(B)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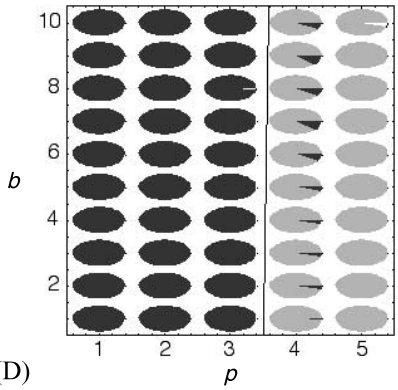
(C)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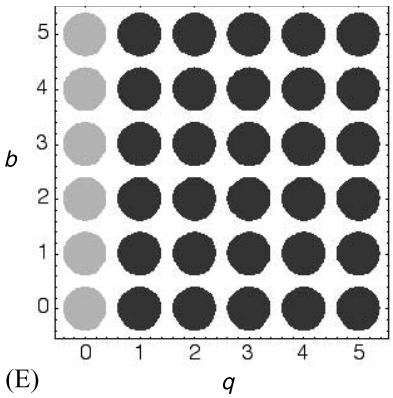
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(E)

AP. Solid lines in Fig. 2C and 2D indicate the boundary lines separating the regions in which AP and SN win, respectively. They are calculated by the method explained in Appendix 2.

Pair-approximation is a method used to analyse the population and evolutionary dynamics of lattice models, as explained by Iwasa (2000). By focusing on the nearest neighbour correlation of states, pair-approximation can handle the propensity of clumping or the extent of spatial mixing between different states. It is based on the assumption that the pair correlations are homogeneous. However, some lattice models show clear regions within which the states are rather homogeneous, but between which state composition and pair correlation differ greatly. In such cases, another method, called 'pair-edge approximation', is a very powerful tool (Ellner *et al.*, 1998). It focuses on the movement of the boundary between two regions – one dominated by the altruist-punisher and another dominated by the selfish-non-punisher. This method is based on the observation of the development of spatial pattern in the lattice population. After a brief initial period of forming clusters of the same strategy, the boundary between clusters moves and the direction of movement of the boundary determines the outcome of the game (Ellner *et al.*, 1998). To discuss the propensity of the movement of a boundary between two regions, we explain the pair-edge approximation for the case of a one-dimensional lattice in Appendix 3. The analysis concludes:

$$\text{AP beats SN, if } p > 2c + q \tag{1a}$$

$$\text{SN beats AP, if } p < 2c + q \tag{1b}$$

It predicts that altruist-punisher (AP) beats selfish-non-punisher (SN) in the viability model when the fine or punishment (p) is larger than a threshold in the viability population. Note that the criterion for equation (1) is independent of b, which is consistent with Fig. 2C, 2D and 2E. This criterion derived from a one-dimensional lattice can provide a fairly accurate prediction of the behaviour of two-dimensional lattice models.

Mixture of long-distance and nearest-neighbour interaction ($0 < \theta < 1$)

When the fraction of long-distance interaction θ increased, the dynamics of the lattice model changed suddenly at an intermediate value. For example, altruists can beat the selfish strategy when θ is less than 0.05, and altruists cannot win when θ is more than 0.1 when $b = 4$ (Fig. 3). When b is large ($b = 10$), the threshold of θ becomes larger.

Fig. 2. The results of the viability model of the regular lattice structured population ($\theta = 0$). (A) The dynamics of two strategies, AP (dashed line) and SN (solid line). (B) The spatial pattern of a lattice population when $t = 10{,}000$. The white area is for AP and the black area is for SN. (C) and (D) show the outcomes of the Monte Carlo simulation when $c = q = 1$. The dark grey portion of each circle indicates the fraction of runs in which SN won; the light grey portion indicates the fraction of runs in which AP won; the white portion represents the fraction of runs in which the dynamic did not converge (among 100 simulations). (C) The initial density of AP is 0.9 and that of SN is 0.1. (D) The initial density of AP is 0.1 and that of SN is 0.9. The solid lines in Fig. 2C and 2D are estimated by the method explained in Appendix 2. (E) $c = 1$, $p = 3$, and the initial density of AP is 0.1 and that of SN is 0.9.

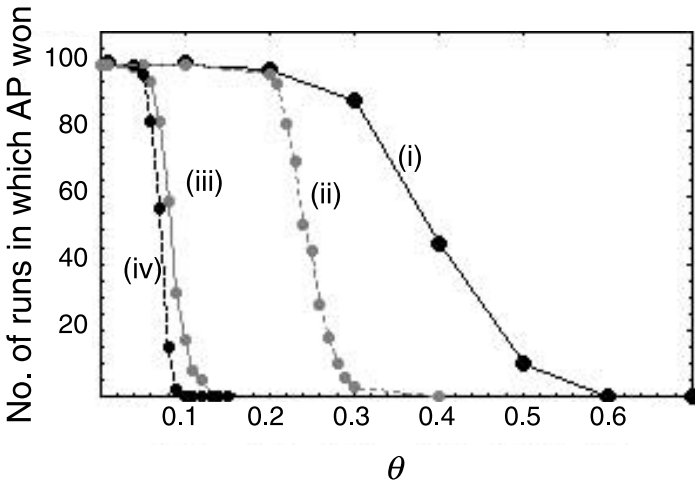


Fig. 3. The effect of the fraction of long-distance interaction (θ) on the evolution of AP in the lattice-structured population. The black lines [(i) and (iv)] are for the viability model; the grey lines [(ii) and (iii)] are for the fertility model. The horizontal axis is for θ; the vertical axis is for the number of runs in which AP won over 100 simulations. (i) $b = 4$, $p = 10$, the initial density of AP is 0.01; (ii) $b = 10$, $p = 5$, the initial density of AP is 0.1; (iii) and (iv) $b = 4$, $p = 5$, the initial density of AP is 0.1. The other parameters are: $c = q = 1$.

FERTILITY IS SCORE-DEPENDENT

The completely mixed model ($\theta = 1$)

We derive the differential equations for the two strategies in a completely mixed population in Appendix 1. If $p > c$, altruist-punisher beats selfish-non-punisher when the density of AP is higher than a threshold; otherwise, SN wins. If $p \leq c$, SN always beats AP. Hence, AP is an ESS when $p > c$ (Fig. 4), while SN is always an ESS.

We conclude that AP cannot invade an SN population in the fertility model. This is in sharp contrast to the viability model, in which AP can invade an SN population when the fine or punishment is large.

The regular lattice model ($\theta = 0$)

The Monte Carlo simulations of the lattice model starting from a random spatial pattern show that, after a relatively short transient, clusters of the same strategy are formed. The outcome of the competition of AP and SN is determined by the movement of the boundaries between two regions, one dominated by AP and another dominated by SN, as is the case in the viability model (e.g. Fig. 2). When the two-dimensional lattice structured population with $\theta = 0$ has two strategies (AP and SN), the benefit from altruism b determines the evolution of altruist-punisher (Fig. 5). When b is small, high p can encourage AP to beat SN, and when b is large AP always beats SN for any value of p. Interestingly, AP beats SN when there is no fine or punishment ($p = 0$). This result holds regardless of the initial frequency. Figure 5C also shows that a high b as well as a low q enables AP to invade the SN population, and Fig. 5 indicates that the lattice-structured population promotes

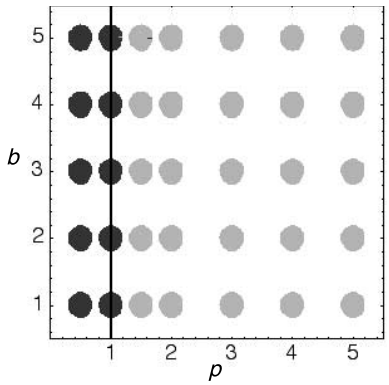
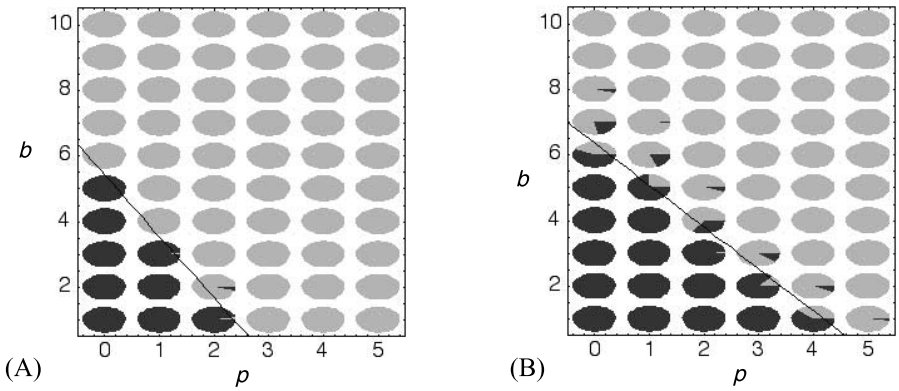


Fig. 4. The condition in which an altruist is an ESS in the fertility model without spatial structure ($\theta = 1.0$). Parameters are: $c = q = 1$. The line indicates $p = c$; an altruist can be an ESS when $p > c$. See caption to Fig. 1 for further information.



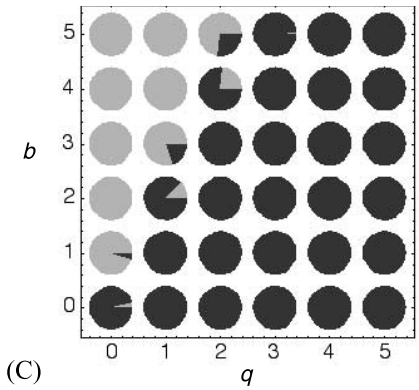


Fig. 5. (A)–(C) show the outcomes of the Monte Carlo simulation in the fertility model of the lattice-structured population ($\theta = 0$). Parameters are: $c = q = 1$. (A) The initial fraction of altruists is 0.9. (B) The initial fraction of altruists is 0.1. See Fig. 2C and 2D for further information. (C) The horizontal axis is for q, and the vertical axis is for b. Parameters are: $c = 1, p = 3$, and the initial fraction of altruists is 0.1. See Fig. 2E for further information.

the invasion of AP. Solid lines are for the boundaries between two regions, calculated from the results of computer simulation by the method explained in Appendix 2.

An altruist-punisher beats a selfish-non-punisher in the viability model when the fine (p) is larger than a threshold in the viability population. In contrast, in the fertility model, AP wins when either the benefit from cooperation (b) or the fine (p) is high.

In Appendix 3, the pair-edge approximation of the one-dimensional lattice population indicates:

$$\text{AP beats SN, if } 2(b - 2c - q)(b - c) > w_0(-2b + 4c - p + q) \tag{2a}$$

$$\text{SN beats AP, if } 2(b - 2c - q)(b - c) < w_0(-2b + 4c - p + q) \tag{2b}$$

Equation (2) includes both the cooperation benefit b and the fine or punishment p. This contrasts with equation (1) for the corresponding inequality for the viability model, the latter being independent of b. This result, based on the one-dimensional model, is again consistent with the direct computer simulation of the two-dimensional model. Hence we can conclude that the magnitude of the benefit of cooperation (b) also plays an important role in the fertility model.

Mixture of long-distance and nearest-neighbour interaction ($0 < \theta < 1$)

Parameter θ (fraction of long-distance interaction) has a similar effect in the fertility model as in the viability model (Fig. 3). If $p = 5$, the evolutionary dynamics change when θ is between 0.05 and 0.1. When p is large ($p = 10$), the threshold of θ moves to a high value.

DISCUSSION

The main results of our analysis are summarized in Fig. 6. The two axes are the fine or punishment p and the benefit of cooperation b. The graphs illustrate the three parameter regions for different outcomes of invasion when one rare type invades the population dominated by the other. They are: (1) SN beats AP irrespective of the initial frequency in the black region, (2) AP beats SN irrespective of the initial frequency in the grey region, and (3) bistability in the white region – whichever is abundant in the initial population has an advantage and rebuffs the invasion of the other. The boundary lines separating these in Fig. 6B and 6D are based on the results of the direct computer simulation, calculated by the method explained in Appendix 2. The boundaries in Fig. 6A and 6C are based on the method in Appendix 1. Figures 6A and 6B are for the score-dependent viability model. Figures 6A and 6B are the results for the completely mixed model and the lattice model, respectively.

In the completely mixed model (Fig. 6A) there is a large region of bistability, whereas in the lattice model (Fig. 6B) this region is rather narrow. This is related to the general result that the dependence of the competitive outcome on the initial condition disappears in an infinitely large lattice (Liggett, 1978; Durrett and Levin, 1994; Iwasa *et al.*, 1998).

In the completely mixed model (Fig. 6A), boundary lines between regions have positive slopes, indicating that a greater benefit of cooperation favours the selfish strategy (i.e. a large b discourages cooperation). This does not hold for the lattice model (Fig. 6B), in which parameter b has no effect and the condition for which the altruist wins is determined only by

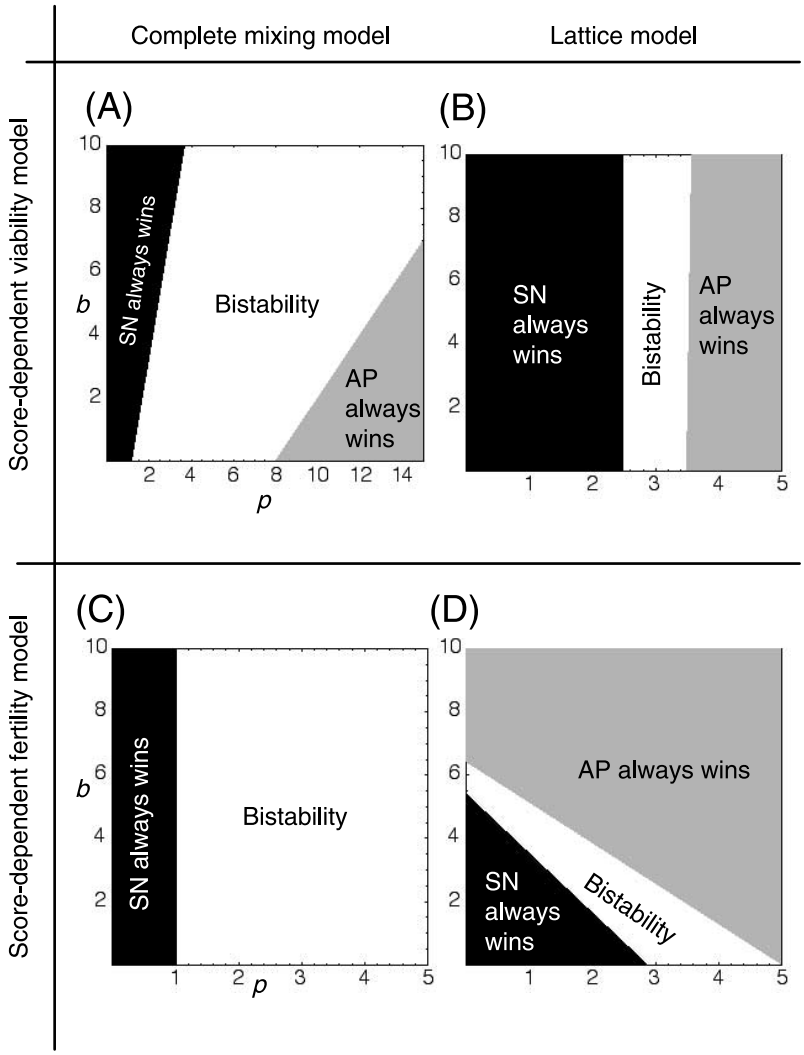


Fig. 6. A comparison of four cases. The horizontal axis represents a fine or punishment p, and the vertical axis represents the benefit from cooperation b. Three regions indicate that SN always beats AP in the black region, AP always beats SN in the grey region, and bistability exists in the white region. Boundaries of the regions in Fig. 6B and 6D are determined from 100 replicates of the computer simulations by the method explained in Appendix 2. The initial condition treats one type as abundant (0.9) and the other as rare (0.1). The lattice size was 2500 (50×50). Boundaries in Fig. 6A and 6C are calculated by the method explained in Appendix 1. Other parameters are $q = c = 1$.

the effectiveness of punishment (a fine or punishment, p), as suggested by the boundaries between the three regions being vertical.

When we compare the three regions between the completely mixed model and the lattice model, the region for AP to win becomes much broader in the lattice model than in the completely mixed model for a relatively large b. However, for small b, there is a region in which SN wins irrespective of the initial condition in the lattice model, while SN cannot

invade the AP population in the completely mixed case. Hence we cannot conclude in general that the lattice structure favours cooperation by punishment.

Figures 6C and 6D show the results of the models with score-dependent fertility. For the completely mixed model (Fig. 6C), there is a broad range of parameters for bistability, and there is no region for AP to win. In contrast, the bistability region becomes narrower for the lattice model, as shown in Fig. 6D.

In the completely mixed model (Fig. 6C), the outcome of competition is independent of b and is determined by a fine (p). In contrast in the lattice model (Fig. 6D), higher b strongly favours the altruist. This dependency on b in fertility models is very different from the corresponding viability models.

Evolutionary advantage of spite

We observed that evolutionary dynamics depend strongly on whether the game's score affects viability or fertility. In the lattice models, if viability depends on the score, the evolution of altruist-punisher is promoted by a large fine or punishment p (Fig. 2C, 2D, 6B); however, if fertility depends on the score, altruism is promoted strongly by a large benefit from cooperation b as well as a large fine p (Fig. 5A, 5B, 6D). Previous studies of repeated prisoner's dilemma games on a lattice-structured population demonstrated a clear difference in the propensity for cooperation to evolve between the score-dependent fertility model and the score-dependent viability model, and the difference was explained by the opportunity for spite to evolve in a different setting (Nakamaru *et al.*, 1997, 1998).

In light of this argument, we can interpret the observed difference between the two models in the presence of costly punishment as follows (Fig. 7). In the lattice-structured model, the successful reproduction of a player is achieved only when a vacancy is created due to the death of its neighbour(s). In the viability model, lowering the score of the neighbours can enhance the availability of vacant neighbouring sites by enhancing the mortality of the game's opponents. If a focal player punishes a selfish neighbour, the score of the selfish neighbour is lowered, which improves the availability of neighbouring empty sites in which to reproduce. In contrast, a high benefit of cooperation b would increase the score of both AP and SN, which would have no effect on the movement of the boundaries between two clusters, as illustrated in Fig. 7A (see also Appendix 3).

In the fertility model, an improvement in a neighbour's score will not harm the availability of empty neighbouring sites because the viability is independent of the score. Hence the propensity to favour spite is weak. Figure 7B shows that AP receives more benefits from cooperation than SN when they compete for an empty site that is located next to the boundary between the AP cluster and the SN cluster. In addition, if an AP player can reduce its neighbouring SN's score, it can also increase its opportunity to reproduce. Therefore, both a high benefit from cooperation (b) and a large fine or punishment (p) contribute to the evolution of the altruist-punisher.

Many theoretical studies on the evolution of cooperation in the lattice model assumed that fertility depends on the game's score, but that mortality is independent of the score (Nowak and May, 1992; Wilson *et al.*, 1992; Mitteldorf and Wilson, 2000; Brandt *et al.*, 2003; Le Galliard *et al.*, 2003; Hauert and Doebeli, 2004). In contrast, Matsuda *et al.* (1987, 1992) and Nakamaru *et al.* (1997) studied lattice models with score-dependent viability. Nakamaru *et al.* (1998) examined the lattice model with score-dependent fertility, but they assumed the order of choosing the player to die and choosing the player to reproduce to be different from many other studies: Nakamaru *et al.*

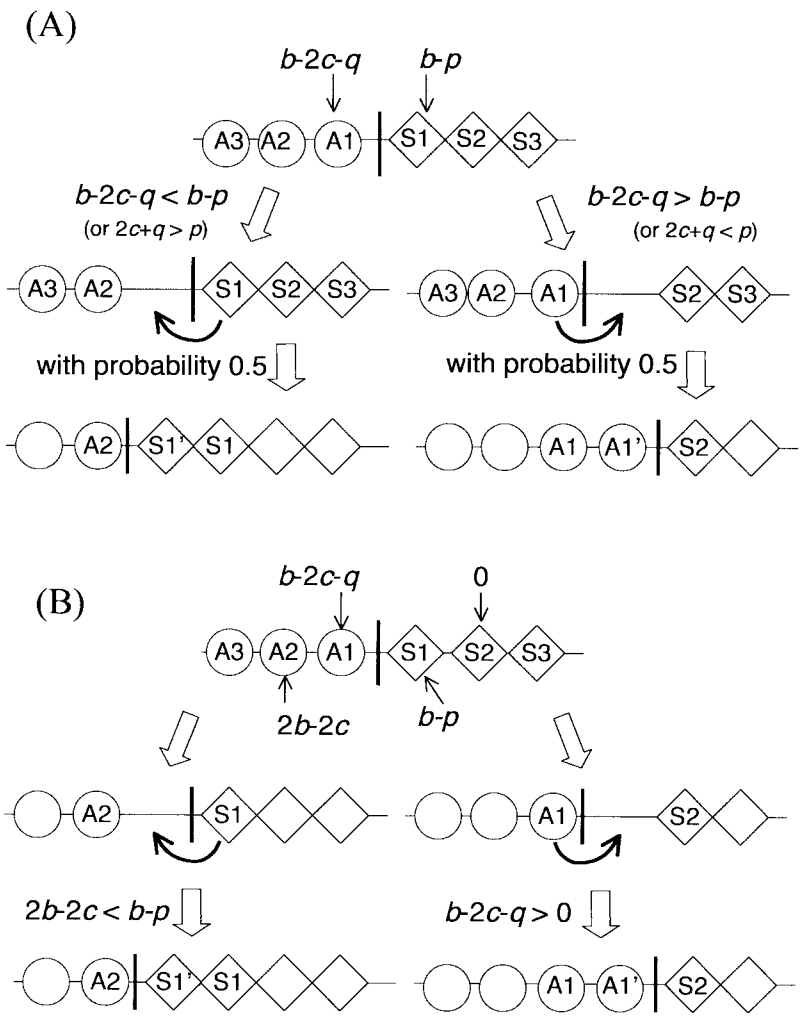


Fig. 7. Evolution in a one-dimensional lattice-structured population. We assume that the same strategies form clusters, and then the movement of the boundary between an AP-cluster and an SN-cluster determines the evolutionary dynamics. For simplicity, we use the one-dimensional lattice here. (A) The score-dependent viability model. There are three APs (A1, A2, A3) and three SNs (S1, S2, S3) in the one-dimensional lattice, and the boundary of the clusters is between A1 and S1. Since a focal player interacts with its two nearest neighbours, the score of A1 is $b - 2c - q$, and that of S1 is $b - p$. If $b - 2c - q < b - p$, the probability of A1 dying is higher than that of B1, and thus the probability that the site occupied by A1 becomes empty is high in comparison with that of B1. If S1 colonizes an empty site with probability 0.5, the boundary moves to the left. If $b - 2c - q > b - p$, the probability of B1 dying is higher than that of A1. If A1 colonizes an empty site with probability 0.5, the boundary moves to the right. We can see b does not affect the dynamics. The scores of the game partners (A1 and S1 here) are crucial for the dynamics. (B) The score-dependent fertility model. When A1 is chosen randomly and dies, the boundary moves to the left if the score of S1 ($b - p$) is higher than that of A2 ($2b - 2c$). When S1 is chosen randomly and dies, the boundary moves to the right if the score of A1 ($b - 2c - q$) is higher than that of S2 (0). Two competitors for a vacant site (A2 and S1; A1 and S2) are not the nearest neighbours and hence they do not play the game directly.

first chose the player who died randomly, and then filled the vacancy by neighbours with a probability depending on their score. In contrast, in many other models with score-dependent fertility, a player was chosen to reproduce first and then they killed and replaced one of their neighbours (Nowak and May, 1992; Wilson *et al.*, 1992; Mitteldorf and Wilson, 2000; Brandt *et al.*, 2003; Hauert and Doebeli, 2004). In these papers, spite has an advantage – players can improve their longevity by reducing their opponent's score.

Lattice-structured models differ considerably in the extent of favouring spite, as pointed out by Nakamaru *et al.* (1998). Two factors control the outcome: the first is whether the viability or the fertility depends on the game's score; the second is the order of choice – whether we first choose the player who dies and then determine the parent who fills the vacancy (Matsuda *et al.*, 1987, 1992; Nakamaru *et al.*, 1997, 1998; Le Galliard *et al.*, 2003), or we first choose the player who reproduces and then determine the neighbour who should be replaced by the newborn offspring. Recently, Hisashi Ohtsuki and his colleagues noted the importance of this difference when they examined the 'fixation probability' in a game played on a graph with a finite size (H. Ohtsuki, E. Liebermann and M.A. Nowak, unpublished).

Long-range versus short-range interactions

The evolutionary dynamics changed sharply between when the fraction of long-distance interaction θ exceeded a threshold and the threshold level depended on the pay-off matrix (Fig. 3). For parameters that promote the evolution of an altruist-punisher, the threshold of θ is moved to a higher value. The effect of θ on the one-dimensional lattice has been studied widely in the context of the small-world network (Watts and Strogatz, 1998), but our results go beyond the small-world network as Nakamaru and Levin (2004) indicated. To know the effect of θ on the two-dimensional lattice structure, further investigations are required. In line with this change, the parameter region for the evolution of altruism is very different in a well-mixed population than in a lattice-structured population (Fig. 3) (Boots and Sasaki, 1999; Iwasa, 2000).

In our models, the candidate individuals who filled a newly created vacant site by their offspring were the opponents of the focal player who inhabited the site originally. Hence even in the completely mixed case with $\theta = 1$, reducing the viability of the game's opponent provides an enhanced opportunity to the player, which favours spite. However, the opponent of the game's player is changed every generation, and hence this propensity to favour spite is much weaker than in the lattice model in which neighbouring players engage in the game over many generations. Hence the result of direct computer simulation of the lattice model when $\theta = 1$ is close to the prediction given by the ordinary differential equations, the latter assuming perfect independence (Appendix 1) (see Figs. 1 and 4).

Future study of punishment

In this paper, we focused on a game in which altruists also act as punishers, and selfish players do not punish others. Sigmund *et al.* (2001) considered a game that included two more strategies: altruist-non-punisher and selfish-punisher. Altruist-non-punishers are exploited by selfish individuals, but altruist-punishers can prevent them from being exploited. In this sense, the altruist-non-punisher (pure altruism) acts as a 'free rider', as it can avoid paying the cost of a punishment. The selfish-punisher is similar to spite (Iwasa *et al.*, 1998; Nakamaru and Iwasa, 2000). It is a paradoxical strategy because it punishes other players of the same strategy.

It may encourage the evolution of cooperation because it reduces the fitness of selfish-non-punisher (or pure selfishness). Elsewhere, we explore the cases including four strategies and show the evolution of altruist-punisher in both viability and fertility models (M. Nakamaru and Y. Iwasa, unpublished).

Recent experimental studies have demonstrated that people tend to punish a defector regardless of a cost (e.g. Price *et al.*, 2002; de Quervain *et al.*, 2004). This result can be explained by the good reputation of punishers helping them to obtain reward from observers, which compensates for the cost. Fehr and Rockenbach (2003) showed that a punisher who is regarded as performing a moral sanction can impress observers more than a punisher who is regarded as a performer of personal retaliation. In the meanwhile, analysis of our study showed that the score-dependent viability model enables an altruist-punisher to evolve in the lattice-structured population regardless of a benefit from cooperation (b). People are willing to punish a defector regardless of a benefit from cooperation (b) possibly because the human mind has evolved in the social environment in which being spiteful is advantageous, such as in the viability model.

In this paper, we assume that punishment is meted out to the opponent who defects. An alternative form of punishment is called 'third-party punishment', which is performed by an observer of the defection who is not the opponent of the game. Fehr and Fischbacher (2004) show that third-party punishment enforces the social norm, and Shinada *et al.* (2004) suggest that players punish in-group members more than out-group members in the case of third-party punishment, while it is known that a player cooperates with in-group members more than out-group members (Tajfel and Turner, 1979). Third-party punishment towards in-group members and its relationship with the social norm would be an important theme of a future theoretical study.

In this paper, we consider the cost of punishing a defector (q). Rumour and gossip are important themes for theoretical studies, as they may act as costless punishment, and they may be responsible for the relationship between altruism and language in human (Nakamaru and Kawata, 2004; Ohtsuki and Iwasa, 2004).

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APPENDIX 1

Ordinary differential equations of the density of AP for the completely mixed model ($\theta = 1$)

In a completely mixed model ($\theta = 1$), the spatial structure is not formed. We can construct the differential equations for the density of AP in the viability model.

Viability model

Let ρ_1 and ρ_2 be the density of AP and SN in the population, respectively. When the game's score affects the viability, we have

$$\frac{d\rho_1}{dt} = \sum_{i=1}^{z} d_2(i)\binom{z}{i}\rho_2{\rho_1}^i{\rho_2}^{z-i}\frac{i}{z} - \sum_{i=0}^{z-1} d_1(i)\binom{z}{i}\rho_1{\rho_1}^i{\rho_2}^{z-i}\frac{z-i}{z} \tag{A1}$$

where $d_1(i)$ or $d_2(i)$ is the death rate of AP or SN, which has i APs and $(z-i)$ SNs next to it; $d_i(i) = a\exp(-\beta \times e_i(i))$ ($i = 1$, 2 and $a = 0.1$ and $\beta = 0.1$); and $e_1(i)$ or $e_2(i)$ is the score for AP or SN, which has i APs and $(z-i)$ SNs. $e_1(i) = i \times (b-c) + (z-i)(-q-c) + w_0$, $e_2(i) = i \times (b-p) + w_0$. w_0 is the basic fitness. The first term of the middle of equation (A1) indicates AP colonizes the empty site randomly, produced after SN dies by probability $d_2(.)$, and the second term indicates that SN colonizes the empty site randomly, produced after AP dies by probability $d_1(.)$. When $\rho_1 \approx 1$, $d\rho_1/dt > 0$ if $d_2(4) - d_1(3) > 0$ and $d\rho_1/dt < 0$ if $d_2(4) - d_1(3) < 0$. Here $z = 4$.

Fertility model

The differential equation for the density of AP in the fertility model is:

$$\frac{d\rho_1}{dt} = \rho_2\sum_{i=1}^{z} A \times \frac{iE_1}{iE_1 + (z-i)E_2} - \rho_1\sum_{i=0}^{z-1} A \times \frac{(z-i)E_2}{iE_1 + (z-i)E_2} \tag{A2}$$

where $A = {\rho_1}^i{\rho_2}^{z-i}z!/(i!(z-i)!)$, and E_1 and E_2 are the expected score for AP and SN respectively, when each individual interacts with z other ones chosen randomly from the whole population, defined as: $E_x = \sum_{i=0}^{z} e_x(i){\rho_1}^i{\rho_2}^{z-i}z!/(i!(z-i)!)$ ($x = 1$, 2). The first term in equation (A2) indicates the rate at which SN

dies randomly and AP colonizes its empty site based on the probability proportional to its score, and the second term is the one in which AP dies randomly and then SN colonizes its empty site based on the probability relative to their scores. Since we assume that each individual interacts with four other individuals randomly, the expected score of each strategy (E_1 and E_2) can be used as the probability of colonization.

APPENDIX 2

Lines separating the parameter regions for different evolutionary outcomes from the outcome of direct computer simulations

For most parameters, the final population is composed only of SN or only of AP, but there are some cases in which neither occupies the whole population. For each parameter set and the initial condition, we ran 100 replicates of simulations, and calculated the fraction of runs with fixation of SN, from the number of runs in which SN becomes fixed and the number of runs in which AP becomes fixed. We neglected the intermediate frequency at the end of the simulation. To indicate the parameter regions in which the fixation of SN occurred more frequently than the fixation of AP, we first pick up all the neighbouring pairs of points on the (p,b)-plane, one of which has a fixation fraction higher than 0.5 and the other has one lower than 0.5. We calculate an intermediate point that corresponds to the fraction of 0.5, by linear interpolation. Then we calculate the best fit line by the least square method among these candidate points.

We performed this using two different initial conditions – one in which AP is abundant and the other in which AP is rare. $p = 2.5$ in Fig. 2C, $b = 115p - 402$ in Fig. 2D, $b = -1.87p + 5.41$ in Fig. 5A, and $b = -1.28p + 6.39$ in Fig. 5B. Combining these, we produced Fig. 6B and 6D.

APPENDIX 3

Pair-edge approximation for lattice models ($\theta = 0$)

The pair-edge approximation developed by Ellner *et al.* (1998) is a very convenient tool with which to analyse the one-dimensional lattice model (e.g. Nakamaru *et al.*, 1998). In this model, the lattice population has two clusters: an AP-cluster and an SN-cluster. The pair-edge approximation calculates the speed (v) of the boundary between two clusters, the sign of the speed and the direction to which the boundary moves (see Fig. 7). Here $z = 2$.

In the viability model, the speed of AP's spread is

$$v = \Delta t \times d_2(1) \times 1/2 - \Delta t \times d_1(1) \times 1/2$$

where the first term shows SN next to the boundary is replaced with AP with probability $d_2(1)/2$ and then the boundary pushes into the SN cluster during Δt. $v > 0$ means the cluster size of AP grows, and therefore AP can beat SN when $p > 2c + q$.

In the fertility model, the speed of AP's spread is

$$v = \Delta t \times \frac{1}{N} \times \frac{e_1(1)}{e_1(1) + e_2(0)} - \Delta t \times \frac{1}{N} \times \frac{e_2(1)}{e_1(2) + e_2(1)}$$

where the first term shows SN next to the boundary is replaced with AP with probability $1/N$. This is because SN is chosen from the whole population and dies randomly and N is the population size. This is multiplied by the probability which depends on the relative score during Δt. This analysis indicates that AP can beat SN when $2(b - 2c - q)(b - c) > w_0(-2b + 4c - p + q)$. As an example, suppose $c = q = 1$. If $b > -0.5p + 2.5$, the right-hand side is negative, and AP can beat SN when $b > 3$.