

The evolution of cooperation on fragmented landscapes: the spatial Hamilton rule

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ABSTRACT

Question: How does habitat destruction affect the evolution of cooperation?

Methods: Differential equations of the probabilities for different states in pairwise sites based on the Prisoner's Dilemma game in a regular network.

Key assumptions: Individuals play the Prisoner's Dilemma game with other individuals on directly connected (adjacent) sites. Individuals' average payoff affects the birth rate. The population undergoes a birth–death process. Habitat loss and fragmentation in the network affect the population dynamics and the invasion and persistence of cooperation.

Predictions: (1) The evolution of cooperation is made possible through non-random encounters in a spatially local process. (2) Derive a spatial Hamilton rule whereby the proportion of cooperators among the neighbouring individuals of a cooperator serves the same role of relatedness as in kin selection, which is consistent with other forms of Hamilton rules. (3) The evolution of cooperation becomes easier in harsh environments. (4) The co-existence of multiple strategies in a species can maintain population size at a constant level.

Keywords: evolutionary game, habitat loss, invasion analysis, pair approximation, Prisoner's Dilemma.

INTRODUCTION

The evolution of cooperation and altruism remains a conundrum in biology and social science (Doebeli and Hauert, 2005). Cooperative individuals benefit others at personal cost and are easily exploited by other, selfish individuals (defectors). Therefore, cooperative behaviour is not an evolutionarily stable strategy (ESS) and fosters incompatibility with Darwinian natural selection. Nonetheless, examples of cooperation abound in nature, both between

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and within species, ranging from microbial interactions to the behaviour of complex organisms (Wilkinson, 1984; Sella, 1985; Pierce *et al.*, 1987; Hemelrijk, 1990, 1991; Lombardo, 1990; Noe, 1990; Hauser, 1992). This contrast between theoretical prediction and empirical evidence begets the paradox of cooperation. Specifically, this paradox centres on two questions: (1) how altruism emerges in a selfish population through natural selection, and (2) how the cooperators, once successfully invaded, can withstand the deceitful individuals in the population.

Three theories, namely group selection, kinship, and (direct-, indirect-, and network-) reciprocity, have been proposed for the evolution of cooperation (for a review, see Nowak, 2006). The mathematical essence of reciprocal cooperation can be incorporated into a Prisoner's Dilemma game, which has been considered as a paradigm for tackling the evolution of altruism (e.g. Trivers, 1971; Axelrod and Hamilton, 1981). A Prisoner's Dilemma game describes a pairwise interaction between players with different behavioural strategies (either to cooperate or to defect). According to the game theory of Nash equilibrium and replicator equations (Hofbauer and Sigmund, 1998), it is better to defect in a Prisoner's Dilemma game irrespective of the opponent's decision. A cooperative society is therefore impossible even though mutual cooperators receive a higher payoff than mutual defectors, posing a social dilemma (Axelrod, 1984).

A key factor that leads to this paradox of cooperation is the mean-field assumption – that is, the game is played in a well-mixed population without individual identity. As a result, any mechanisms that can break this mean-field assumption will inevitably lead to the invasion and persistence of the altruistic behaviour. Theories such as group selection (Wilson, 1975), kin selection (Hamilton, 1963, 1964a, 1964b), reciprocal altruism (Trivers, 1971), and spatial game theory (Nowak and May, 1992) can break this mean-field assumption and create non-random encounters [known as assortment in game theory (Eshel and Cavalli-Sforza, 1982)]. Specifically, in a spatial game, an individual is restricted to interact only with its direct neighbours, indicating that the spatial structure of the playground (i.e. the habitat structure of species) can have a potential effect on the evolution of cooperation (Nowak and May, 1992; Sigmund, 1992; Huberman and Glance, 1993; Szabo and Toke, 1998; Nowak and Sigmund, 2000). An important process in creating spatial changes in the playground is habitat destruction (loss and fragmentation). Habitat destruction is the principal threat to the long-term survival of species, both locally and globally (Tilman *et al.*, 1994; Wilcove *et al.*, 1998). Therefore, it is not only of intrinsic value but also of applied significance to examine how habitat destruction affects (1) the dynamics of Prisoner's Dilemma games and (2) the condition for cooperators to invade a selfish population successfully.

In a canonical spatial Prisoner's Dilemma game, spatial saturation (i.e. no empty sites) is assumed (Nowak and May, 1992; Szabo and Toke, 1998; but see Alizon and Taylor, 2008). To examine the effect of habitat destruction on the invasion and persistence of cooperation in a Prisoner's Dilemma game, we extended the canonical spatial Prisoner's Dilemma game in two ways: (i) empty sites due to demographic stochasticity and (ii) spatially non-random (clustered) unsuitable sites due to habitat destruction. This extended game was then expressed using differential equations and analysed by pair approximation (Iwasa, 2000) and numerical simulations. The invasion condition of cooperative behaviour in a selfish population and the population dynamics, under different spatial structures of habitat destruction, were examined. A general spatial Hamilton rule was developed.

MODEL

Spatial Prisoner's Dilemma game

In a regular network where each site connects to a number of sites n (defined as its neighbourhood), each site can be categorized as either suitable or unsuitable. The existence of unsuitable sites represents habitat destruction. The global density of unsuitable sites (p_E) indicates the probability that a randomly chosen site is unsuitable, and the local density of unsuitable sites ($q_{E|E}$) indicates the probability that a randomly chosen neighbour of an unsuitable site is also unsuitable. These two probabilities measure the level of habitat loss and fragmentation. A random habitat destruction can be described by $p_E = q_{E|E}$, a spatially clustered habitat destruction by $p_E < q_{E|E}$, and a spatially segregated habitat destruction by $p_E > q_{E|E}$ (Hui *et al.*, 2006, in press). An inequality $q_{E|E} \geq 2 - 1/p_E$ defines the feasible region of these two probabilities (Hiebeler, 2000). Overall, there are four states for each site: C (occupied by a cooperator), D (occupied by a defector), H (suitable but empty), and E (unsuitable).

In a Prisoner's Dilemma game, the two players simultaneously decide whether to cooperate or to defect during an encounter. A cooperator yields a benefit b to its opponent at a cost to itself c ($b > c$); a defector yields no benefit but suffers no cost. This leads to the following payoff matrix (Taylor *et al.*, 2007):

$$\begin{array}{cc} & \begin{array}{cc} C & D \end{array} \\ \begin{array}{c} C \\ D \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix}. \end{array} \quad (1)$$

Let μ_Ω and δ_Ω denote the birth and death rate respectively, where Ω is either C or D . We assumed that only the birth rate is affected by the payoff in a Prisoner's Dilemma game, whereas the death rate is the same for both strategies ($\delta_C = \delta_D = \delta$). The offspring is located in an empty but suitable neighbouring site around its haploid parent. As a result, the birth rate equals the intrinsic birth rate (μ_0) plus the average payoffs of the individual (Le Galliard *et al.*, 2003):

$$\begin{aligned} \mu_C &= \mu_0 + (1 - \varphi)((b - c)q_{C|C} - c \cdot q_{D|C}), \\ \mu_D &= \mu_0 + (1 - \varphi)b \cdot q_{C|D}, \end{aligned} \quad (2)$$

where $\varphi = 1/n$ and $q_{\Omega|\Omega'}$ represents the conditional probability that a randomly chosen neighbour of a Ω' -site is in state Ω . Consequently, we have the following equations for the Prisoner's Dilemma game:

$$\begin{aligned} \frac{dp_{\Omega\Omega}}{dt} &= 2\beta_\Omega \cdot p_{H\Omega} - 2\delta \cdot p_{\Omega\Omega} \\ \frac{dp_{\Omega E}}{dt} &= \alpha_\Omega \cdot q_{\Omega|HE} p_{HE} - \delta \cdot p_{\Omega E} \\ \frac{dp_{CD}}{dt} &= \alpha_C q_{C|HD} p_{HD} + \alpha_D q_{D|HC} p_{HC} - 2\delta p_{CD} \\ \frac{dp_{H\Omega}}{dt} &= \alpha_\Omega \cdot q_{\Omega|HH} p_{HH} + \delta(p_{CD} + p_{\Omega\Omega}) - (\beta_\Omega + \alpha_\Omega q_{\Omega|H\Omega} + \delta) p_{H\Omega} \end{aligned} \quad (3)$$

where $p_{\Omega\Omega'}$ is the probability that a randomly chosen pairwise site is in state $\Omega\Omega'$; $q_{\Omega|\Omega\Omega'}$ is the conditional probability that a randomly chosen neighbour of the Ω' -site in a $\Omega'\Omega''$ pair is a Ω -site; and Ω' in the last part of equation (3) is the opponent strategy to Ω (i.e. if $\Omega = C$, then $\Omega' = D$). Parameters α_Ω and β_Ω are $\alpha_\Omega = (1 - \varphi)\mu_\Omega$ and $\beta_\Omega = \varphi\mu_\Omega + (1 - \varphi)\mu_\Omega q_{\Omega|\Omega\Omega}$, respectively. According to pair approximation (Iwasa, 2000), we let $q_{\Omega|\Omega\Omega'} = q_{\Omega|\Omega}$, indicating that the probability of finding a Ω -site next to a Ω' -site does not depend on the state of its other neighbour (Ω''). Thus all conditional probabilities in the above equations can be calculated according to the probability theory, $p_{\Omega\Omega'} = p_\Omega q_{\Omega|\Omega'}$.

Spatial Hamilton rule

To examine the effect of habitat destruction on the invasion condition of the cooperative strategy in a selfish population, we calculated the spatial invasion fitness of cooperation, i.e. the rate of per capita increase for the initial rare cooperators in a selfish population at equilibrium. When a selfish population is at equilibrium, probabilities $p_{\Omega\Omega'}$ and $q_{\Omega|\Omega'}$ ($\Omega, \Omega' = D, H, E$) are constant. The conditional probabilities $q_{C|D}$ and $q_{C|H}$ equal zero. Therefore, the invasion dynamics of cooperation is controlled by four equations regarding the pairwise probabilities p_{CC} , p_{CD} , p_{CH} , and p_{CE} (see equation 3). We can then rewrite equation (3) in matrix form, $dP_C/dt = M(Q_C)P_C$, where P_C is a vector $P_C = (p_{CC}, p_{CD}, p_{CH}, p_{CE})^T$, and $M(Q_C)$ is a 4×4 matrix:

$$\begin{pmatrix} -2\delta & 0 & 2\beta_C & 0 \\ 0 & -2\delta & (\alpha_C + \alpha_D)q_{D|H} & 0 \\ \delta & \delta & \alpha_C q_{H|H} - (\beta_C + \alpha_D q_{D|H} + \delta) & 0 \\ 0 & 0 & \alpha_C q_{E|H} & -\delta \end{pmatrix}.$$

This matrix depends on the local-density vector $Q_C = (q_{C|C}, q_{D|C}, q_{H|C}, q_{E|C})^T$. When cooperative individuals invade a selfish population, the local-density vector Q_C rapidly reaches a pseudo-equilibrium, while the global density of the population and defectors remain unchanged (Ferriere and Le Galliard, 2001). In general, the pseudo-equilibrium of the local-density vector Q_C can be calculated by solving $M(Q_C)Q_C = \lambda \cdot Q_C$, where λ is the dominant eigenvalue of matrix $M(Q_C)$ and is a measure of spatial invasion fitness (van Baalen and Rand, 1998; Ferriere and Le Galliard, 2001). The cooperative individuals can invade a selfish population if λ is positive. The condition $\lambda = 0$ defines an invasion boundary. Therefore, we have the following condition for the invasion of cooperation:

$$\frac{q_{C|C}}{q_{C|C} + q_{D|C}} \cdot b > c. \quad (4)$$

This condition is a spatial form of the Hamilton rule in the context of a spatial Prisoner's Dilemma game. The proportion of cooperators among the neighbouring individuals of a cooperator, $q_{C|C}/(q_{C|C} + q_{D|C})$, is analogous to: the genetic relatedness between individuals in kinship selection (Hamilton, 1964a, 1964b; Maynard Smith, 1964); the probability of having another round of the game, as in direct reciprocity (Axelrod and Hamilton, 1981); the probability of knowing the social score of the opponent, as in indirect reciprocity (Nowak and Sigmund 1998); and the average degree of nodes, as in graph selection (Ohtsuki *et al.*, 2006; for a review, see Nowak, 2006).

Equation (4) demonstrates an invasion condition that depends on the spatial correlation (or local density) of cooperative individuals ($q_{C|C}$) and the spatial attraction of cooperators to defectors ($q_{D|C}$) at their pseudo-equilibrium. Therefore, the local spatial structure of different strategies at the pseudo-equilibrium (Q_C) determines the dynamics of cooperation invasion.

To demonstrate the above analysis of the spatial Hamilton rule and the effect of the Prisoner's Dilemma game on the population dynamics when facing habitat destruction (loss and fragmentation), we provide two numerical solutions. First, because the pseudo-equilibrium of the local-density vector Q_C is difficult to calculate due to the non-linearity of the above system, we present a numerical solution for the threshold of altruistic cost (c) under different levels of habitat loss and fragmentation when the altruistic benefit is fixed ($b = 1$). Second, the above invasion analysis and the spatial Hamilton rule (equation 4) only provide a condition for cooperation to invade a selfish population. The analysis does not indicate the dynamics of cooperators and populations after the invasion, especially when facing habitat destruction. Therefore, by solving equation (3) numerically, we can reveal the long-term dynamics of the population.

RESULTS

The spatial structure of the habitat (or the playground) affected the threshold for the invasion of cooperation (Fig. 1). First, with an increase in the proportion of unsuitable sites in the habitat (p_E), the threshold of the altruistic cost (c) for cooperation invasion increased, indicating a wider window of possibility for cooperation invasion (Fig. 1). Second, with a decrease in clustering of habitat destruction (i.e. increasing habitat fragmentation, measured by $q_{E|E}$), the threshold for cooperation invasion increased (Fig. 1). This effect of habitat fragmentation on widening the window of possibility for cooperation invasion became more conspicuous when the habitat loss was high (Fig. 1). Therefore, habitat destruction, in general, can facilitate the successful invasion of cooperation in a spatial Prisoner's Dilemma game.

A further examination of the population size (at equilibrium) under different levels of habitat loss and fragmentation revealed interesting results (Fig. 2). First, the habitat connectivity, as described by the number of neighbouring sites of a focal site (n), had a negative impact on the persistence of both cooperators and the population (compare Fig. 2a and 2b). The parameter zones for cooperation–defection co-existence and pure cooperation, as projected on the $p_E - q_{E|E}$ plane at the bottom of the figure, shrank when connectivity was enhanced (from $n = 4$ in Fig. 2a to $n = 8$ in Fig. 2b). Interestingly, there was a parameter zone for pure cooperation, implying that it is possible for cooperators to expel defectors completely just before the population goes extinct (Fig. 2). In addition, the decline in population size due to habitat destruction was almost halted and even reversed for some parameters in the parameter zone of co-existence, in contrast to the fast decline in population size with pure strategies (i.e. all individuals are either cooperators or defectors). This result suggests that multiple behavioural strategies within a population could be an efficient way to deal with habitat destruction.

In contrast to the above result that population size was more sensitive to changes in habitat structure in the pure-strategy parameter zone, the effect of the cost (c) and benefit (b) in the Prisoner's Dilemma game on population size provided a different picture (Fig. 3a). Population size became highly sensitive in the parameter zone of co-existence,

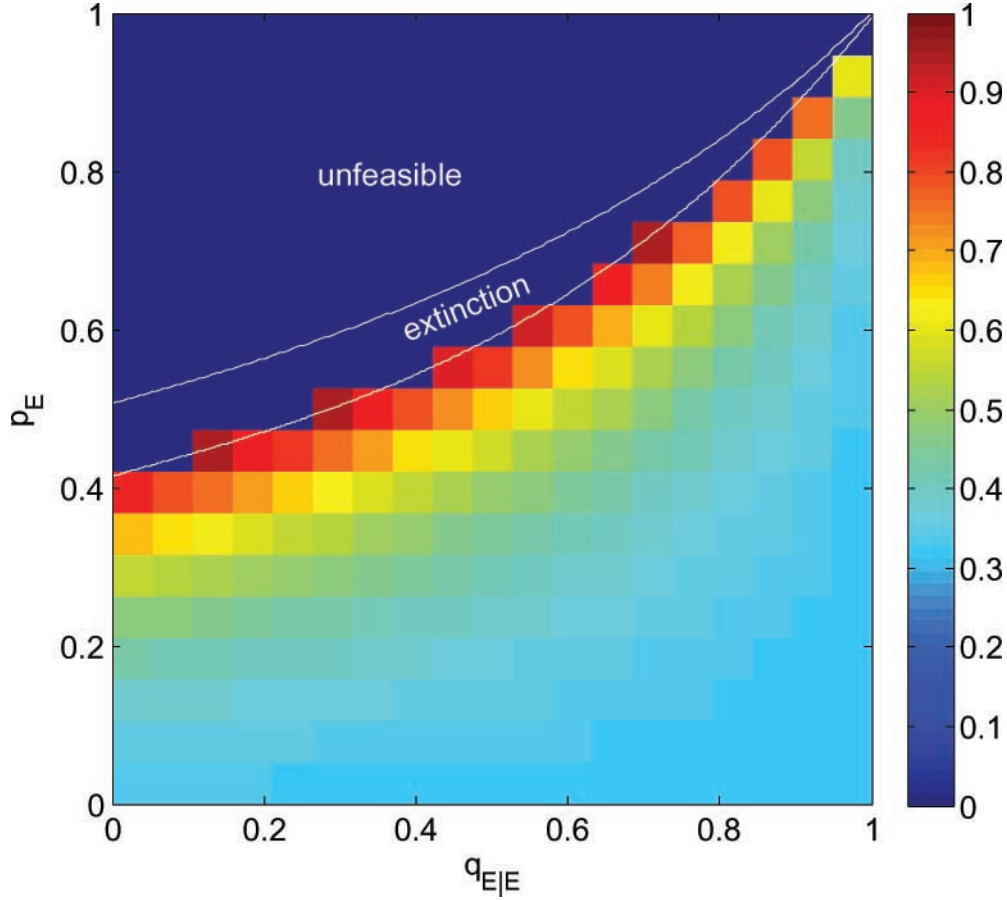


Fig. 1. Cost threshold for successful cooperation invasion in a selfish population under different levels of habitat loss (p_E) and fragmentation ($q_{E|E}$). Parameter zones separated by lines indicate, from the upper right-hand corner on the $p_E - q_{E|E}$ plane, unfeasible, extinction, and persistence. Parameters are $\mu_0 = 1$, $n = 4$, $b = 1$, and $\delta = 0.2$.

whereas it remained constant when all individuals were defectors. The effect of the birth rate (μ_0) and death rate (δ) on population size (Fig. 3b) produced relatively similar results to the effect of habitat destruction (Fig. 2). Population size remained constant in the parameter zone of co-existence regardless of the birth and death rates, whereas it fell sharply in the pure-strategy parameter zone with the increase/decrease of the death/birth rate (Fig. 3b).

DISCUSSION

Four propositions arise from the results of this study: (1) the evolution of cooperation is made possible in the spatial Prisoner's Dilemma game by assortment in spatially local processes; (2) the spatial Hamilton rule (equation 4) derived is consistent with other forms of Hamilton rules; (3) the invasion and persistence of cooperation become easier in a harsh

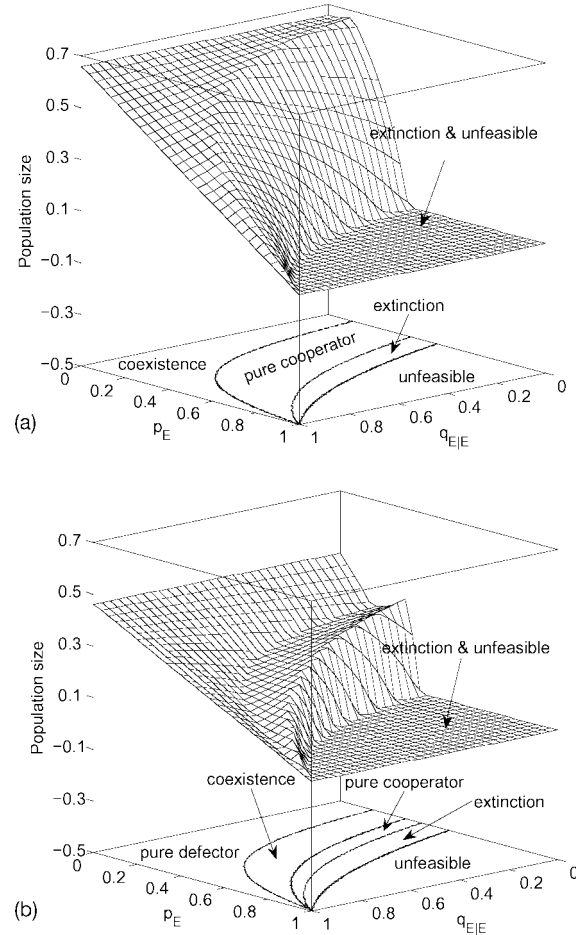


Fig. 2. The effect of habitat loss (p_E) and fragmentation ($q_{E|E}$) on population size at equilibrium. The parameter zones of unfeasible, extinction, pure cooperators, pure defectors, and co-existence are projected on the $p_E - q_{E|E}$ plane. Parameters are $\mu_0 = 0.2$, $\delta = 0.1$, $b = 1$, $c = 0.36$, $n = 4$ for (a) and $n = 8$ for (b).

environment; and (4) the co-existence of multiple strategies in a species provides an efficient way to deal with environmental stress. In the following, we discuss these four propositions in detail.

First, since Axelrod (1984), spatial games have been thoroughly investigated (Nowak and May, 1992; Nowak and Sigmund, 2000; Doebeli and Hauert, 2005), with increasing complexity and reality in modelling rules (Huberman and Glance, 1993; Nowak *et al.*, 1994; Dieckmann *et al.*, 2000). One conclusion of these studies was that the spatial structure of a Prisoner's Dilemma game can indeed promote the evolution of cooperation (Nowak and Sigmund, 2000) even though disagreement remains on the details. Cooperators survive by forming clusters within which they obtain the benefit of mutual cooperation, which balances the exploitation by selfish individuals around these clusters (Doebeli and Hauert, 2005). The spatial structure of local processes is still the main mechanism here that leads to the evolution of cooperation because the Prisoner's

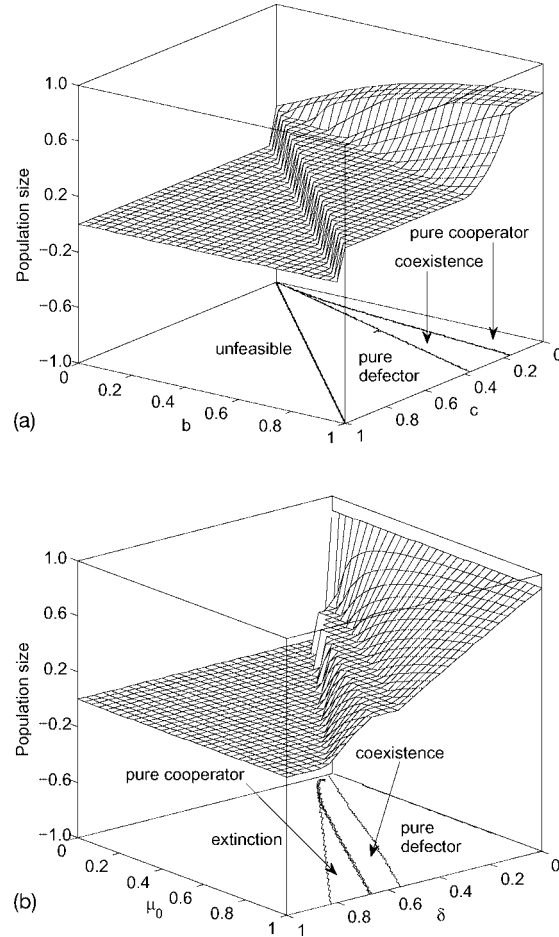


Fig. 3. (a) The effect of the benefits (b) and costs (c) to cooperate, and (b) the effect of the birth rate (μ_0) and death rate (δ) on population size at equilibrium. The parameter zones of unfeasible, extinction, pure cooperators, pure defectors, and co-existence are projected on the $p_E - q_{E|E}$ plane. Parameters are $\mu_0 = 0.3$, $\delta = 0.2$, $p_E - q_{E|E} = 0$ and $n = 8$ for (a), and $p_E - q_{E|E} = 0.1$, $b = 1$, $c = 0.36$ and $n = 8$ for (b).

Dilemma game inhibits the persistence of cooperation under the mean-field assumption (Hauert and Szabo, 2005; Hui *et al.*, 2005). By breaking this assumption and introducing some assortment into the game (here by reducing the number of neighbouring sites from infinite as in the mean-field assumption to only four and eight; Fig. 2), we can expect the successful invasion and persistence of cooperation and even a population with pure cooperators.

Second, the Hamilton rule, as in its initial form in kin selection theory (Hamilton, 1964a, 1964b), states that the cooperation strategy should be selectively favoured if the recipient's benefit (b) weighted by the relatedness (r) of the altruists is greater than the altruistic cost (c), $rb > c$. It is often suggested that kin selection should operate in a viscous population, in which local dispersal promotes interactions among relatives because offspring tend to remain close to their parents. Similar conditions exist in the spatial Prisoner's Dilemma game (van Baalen and

Rand, 1998; Le Galliard *et al.*, 2003; Doebeli and Hauert, 2005). We also derived a Hamilton rule in the spatial Prisoner's Dilemma game (equation 4). Clearly, the proportion of cooperators among the neighbouring individuals of a cooperator (equation 4) serves the same function as relatedness (r) in kinship selection. As mentioned above, both introduce assortment into the game and make the evolution of cooperation possible (Eshel and Cavalli-Sforza, 1982).

Third, spatial saturation (all sites are occupied) is often assumed in spatial games (Axelrod, 1984; Nowak and May, 1992; Huberman and Glance, 1993; Nowak *et al.*, 1994; Lindgren and Nordahl, 1994; Nowak and Sigmund, 2000). This is the same as the frequency of cooperation within a constant population, even though it is impossible to maintain spatial saturation under strong environmental pressure due to enhanced demographic stochasticity (Tilman and Kareiva, 1997; Hanksi, 1998). However, we studied evolution of cooperation in a dynamic population and allowed empty sites through both demographic stochasticity and habitat destruction. Although empty sites due to demographic stochasticity have been shown to promote the evolution of cooperation (Taylor, 1992; Queller, 1992, 1994; Le Galliard *et al.*, 2003), no previous research has focused on a dynamic population in partially suitable habitat due to habitat destruction. Clearly, habitat destruction can promote the evolution of cooperation and even eliminate defectors from the population just before it goes extinct (Fig. 2). Moreover, demographic stochasticity (by increasing the mortality δ and decreasing the birth rate μ_0) has also been shown to promote the evolution of cooperation (Fig. 3b). Overall, a harsh environment, indicated by high levels of habitat destruction and demographic stochasticity, promotes the evolution of cooperation (Hui *et al.*, 2005; Zhang *et al.*, 2005).

Finally, habitat destruction is widely accepted as the main threat to biodiversity conservation (Tilman *et al.*, 1994; Wilcove *et al.*, 1998). However, a very complicated situation was found here for populations with multiple strategies (i.e. when cooperation and defection co-exist within the population). A population can mitigate the damage from habitat destruction by adjusting its proportion of cooperators and defectors within and, as a result, the population size will remain constant regardless of the intensity of habitat destruction (Hui *et al.*, 2005). This self-regulating ability of species (or systems) with multiple interrelated strategies in dealing with environmental changes has also been demonstrated in Lovelock's daisy world (for a review, see Wood *et al.*, 2008). We believe further research is worthy on how behavioural strategies shift in social animals when they are faced with environmental stress.

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