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A mathematical analysis on public goods games in the continuous space

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Abstract

We consider the population dynamics of two competing species sharing the same resource, which is modeled by the carrying capacity term of logistic equation. One species (farmer) increases the carrying capacity in exchange for a decreased survival rate, while the other species (exploiter) does not. As the carrying capacity is shared by both species, farmer is altruistic. The effect of continuous spatial structure on the performance of such strategies is studied using the reaction diffusion equations. Mathematical analysis on the traveling wave solution of the system revealed; (1) Farmers can never expel exploiters in any traveling wave solution. (2) The expanding velocity of the exploiter population invading the farmer population can be analytically determined and it depends only on a cost of altruism and the diffusion coefficients while it is independent of the benefit of altruism. (3) When the effect of altruism is small, the dynamics of the invasion of exploiters obeys the Fisher-KPP equation. Numerical calculations confirm these results.

Keywords: Public goods game; Reaction diffusion; Traveling wave solution; Altruism; Continuous space; Carrying capacity

1. Introduction

Altruistic behavior among unrelated individuals has been widely studied since it cannot be directly explained by the standard kin-selection theory [1]. Spatial structure has been considered

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as a possible mechanism to explain the evolution of altruistic behavior. Most mathematical studies assume discrete spatial structure such as a lattice or randomly connected patches [2–6]. Discretely structured model is advantageous to deal analytically [7,8]. However, the discrete space and the continuous space are essentially different and many creatures in real biology inhabit continuous space. Reaction diffusion equation is one of the simplest models describing spatiotemporal dynamics of continuous entity in the continuous space. Individuals are discrete (countable) entities but their density might be considered as continuous entity if the number of individuals is large enough.

There are a few studies on the evolution of altruistic behavior in the continuous space [9]. Most of them study the reaction diffusion equations modeling the competition among players adopting Tit-For-Tat or All-D strategy in iterated prisoner's dilemma game [10,11]. They showed that, when the corresponding non-spatial model has bistable solutions, the spatial model might have stable coexistence solutions (spatially homogeneous or inhomogeneous). As Tit-For-Tat is a conditional strategy with a memory, it is implicitly assumed that a player can recognize the opponent's last behavior. Such a strategy might evolve if the interaction is direct and observable. In general, however, altruism is not necessarily performed through a direct interaction. In this study we assume that altruism is performed through the investment to the common resource that is shared by all players. The situation is referred to as 'tragedy of commons' or 'public goods game'. Unlike the game played by Tit-For-Tat and All-D, altruistic strategy in public goods games can never win in the non-spatial model, regardless of the initial frequency. Recently, Brandt et al. [12] have studied public goods games in the discrete space but there has been no study in the continuous space. We introduce spatial structure so that each individual moves randomly and that the density distribution obeys a reaction diffusion equation. And we study the performance of the altruistic strategy.

From the mathematical viewpoint, there are a few studies on game models in the continuous space [13–15]. Some useful theorems are derived, especially on the traveling wave solutions. In these models, the local carrying capacity is assumed to be constant and the relative payoff determines the growth rate of each strategy. In our model, the local carrying capacity itself is a function of the density of a strategy, which is different from the preceding works that motivated the author to begin this study.

In this study, we assume two types of strategies (altruistic and non-altruistic) competing in the continuous space. Population dynamics is modeled by the reaction diffusion equations and the behavior of the system is studied. Especially, the existence and the velocity of the traveling wave solutions in which one strategy expels the other are analyzed analytically. The results are confirmed by numerical calculations.

2. Model

We start from the standard logistic equation

$$\frac{\mathrm{d}x}{\mathrm{d}t} = rx\left(1 - \frac{x}{K}\right), \tag{1}$$

where K denotes the carrying capacity. We assume two strategies, namely farmer and exploiter. Farmer increases the carrying capacity in exchange for a decreased survival rate. We assume that all farmers and exploiters share the increased carrying capacity. Therefore, a farmer strategy can be regarded as an altruism strategy. The model is denoted by

$$\begin{aligned}\frac{dx}{dt} &= rx\left(1-\frac{x+y}{K(y)}\right),\\ \frac{dy}{dt} &= ry\left(1-\frac{x+y}{K(y)}\right)-cy,\\ K(y) &= k_0+ky,\end{aligned} \tag{2}$$

where x and y represent the density of exploiters and farmers, respectively. k measures the benefit of altruism given to both strategies while c measures the cost of altruism. We consider the one-dimensional continuous spatial structure by introducing the diffusion of both players.

$$\begin{aligned}\frac{\partial x}{\partial t} &= D_x\frac{\partial^2}{\partial X^2}x+rx\left(1-\frac{x+y}{K(y)}\right),\\ \frac{\partial y}{\partial t} &= D_y\frac{\partial^2}{\partial X^2}y+ry\left(1-\frac{x+y}{K(y)}\right)-cy,\end{aligned} \tag{3}$$

X denotes the coordinates and D_x and D_y denote the diffusion coefficients of exploiters and farmers, respectively. By the following transformation:

$$\begin{aligned}& X'=\sqrt{\frac{r}{D_x}}X, \quad t'=\frac{1}{r}t,\\ & d=\frac{D_y}{D_x}, \quad c'=\frac{c}{r},\\ & x'=\frac{x}{k_0}, \quad y'=\frac{y}{k_0}, \quad k'=\frac{k}{k_0},\end{aligned} \tag{4}$$

the non-dimensionalized system is denoted by

$$\begin{aligned}\frac{\partial x}{\partial t} &= \frac{\partial}{\partial X^2}x+x\left(1-\frac{x+y}{1+ky}\right),\\ \frac{\partial y}{\partial t} &= d\frac{\partial}{\partial X^2}y+y\left(1-\frac{x+y}{1+ky}\right)-cy,\end{aligned} \tag{5}$$

where only d, c and k are independent parameters. Primes are omitted for convenience. Eqs. (5) have two spatially homogeneous equilibriums: $(x,y)=(1,0)$ and $(x,y)=(0,y^*)$ where

$$y^*=\frac{1-c}{1-k+ck}. \tag{6}$$

We presuppose $d>0$, $0<k<1$ and $0<c<1$ in order that y^* is always positive and that the model is biologically realistic. Neglecting the effect on exploiters, the farmer strategy is considered adaptive if $y^*>1$ or $k-c-ck>0$. However, without spatial structure, farmers always go to extinction because the per capita growth rate of exploiters is always larger than that of farmers and because there exists the upper bound of the total population (Fig. 1). In order to study the effect of spatial structure, we consider the case in which exploiters initially inhabit the left half of the space and farmers the right half (Fig. 2). The populations are in the equilibrium states in both ends, while competition occurs at the boundary of two populations (hereafter, we call this 'the front'). The direction of the motion of 'the front' determines which strategy will win the competition. As long as the reaction term is considered, the per capita growth rate of exploiters is always larger than that of farmers at any point in the space. However, the equilibrium density of farmers, y^*,

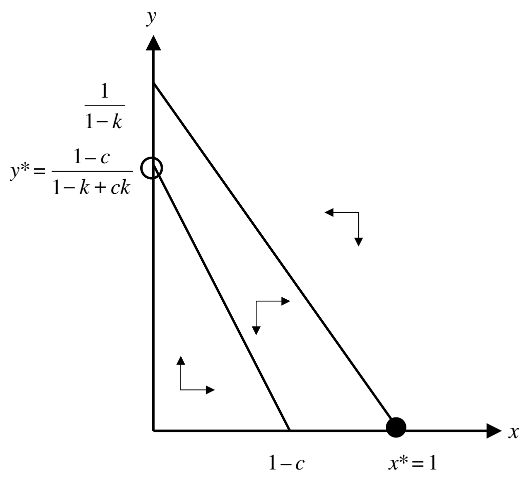

Fig. 1. Phase plane analysis of the dynamics of non-spatial model. Non-dimensionalization denoted by Eq. (4) is applied. Two lines indicate isoclines of x and y. Filled and open circles indicate stable and unstable equilibriums, respectively. As the benefit of altruism is increased (larger k), the monomorphism of farmers can maintain larger population (larger y^*). However, this monomorphism is always unstable against invasion of exploiters.

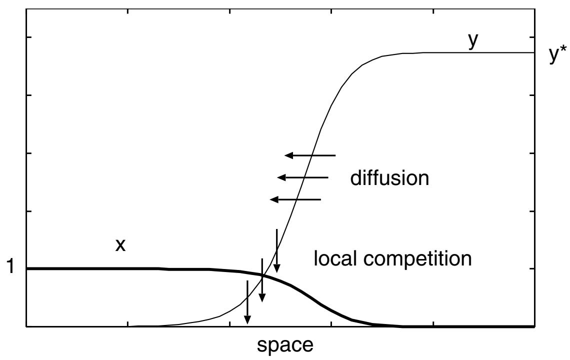

Fig. 2. The schematic illustration of the farmer-exploiter boundary. Solid and bold lines indicate the density of farmers and exploiters, respectively. In general, the equilibrium density of farmers is larger than that of exploiters and thus the disadvantage of farmers in local competition at the boundary area might be compensated by the diffusion from the high-density area (the right half).

can be much greater than that of exploiters when c is very small and k nearly equals one. Under such a condition, the disadvantage of farmers in local competition might be compensated by the diffusion.

3. Analytic result

A traveling wave solution (TWS) is the solution satisfying

$$\begin{aligned} &x(X,t) = x(z),\\ &y(X,t) = y(z),\\ &z = X - vt. \end{aligned} \tag{7}$$

Analysis of a TWS is almost only one analytic tool that is available to study reaction diffusion system. However, the analysis is difficult in multi-species system. One of the simplest models of biological competition in the continuous space is a two-species Lotka–Volterra system with diffusion terms. This is equivalent to the present model with a constant carrying capacity ($k = 0$). Even in this simplest example, the general existence proof of a TWS (as well as a solution itself) is unknown. Only in some special cases, the existence and some characteristics of a TWS are proved [16–19]. Here, we explore the possibility of the existence of a TWS in the present model that is another special case with density dependent carrying capacity.

If there exists a TWS in Eqs. (5), it satisfies

$$\begin{aligned} &-v\dot{x} = \ddot{x} + x\left(1 - \frac{x+y}{1+ky}\right),\\ &-v\dot{y} = d\ddot{y} + y\left(1 - \frac{x+y}{1+ky}\right) - cy \end{aligned}$$

or

$$\begin{aligned} &\dot{x} = p,\\ &\dot{p} = -vp - x\left(1 - \frac{x+y}{1+ky}\right),\\ &\dot{y} = q,\\ &\dot{q} = -\frac{v}{d}q - \frac{y}{d}\left(1 - \frac{x+y}{1+ky}\right) + \frac{c}{d}y, \end{aligned} \tag{8}$$

where a dot symbol represents the derivative with respect to z. Eq. (8) has two equilibriums: $P_x = (1,0,0,0)$ and $P_y = (0,0,y^*,0)$. Jacobian matrix around the point $(x^*,0,y^*,0)$ is

$$\begin{pmatrix} 0 & 1 & 0 & 0\\ A & -v & B & 0\\ 0 & 0 & 0 & 1\\ C & 0 & D & -v/d \end{pmatrix},$$

where

$$A = -1 + \frac{2x^*}{1+ky^*} + \frac{y^*}{1+ky^*},$$
$$B = \frac{x^*(1-kx^*)}{(1+ky^*)^2},$$
$$C = \frac{y^*}{d(1+ky^*)},$$
$$D = \frac{1}{d}\left(c - 1 + \frac{x^*+y^*}{1+ky^*} + \frac{y^*(1-kx^*)}{(1+ky^*)^2}\right)$$

and the characteristic equation is

$$\lambda^4 + (v + v/d)\lambda^3 + (v^2/d - A - D)\lambda^2 - (A/d + D)v\lambda + AD - BC = 0.$$

When $BC = 0$, the equation can be factorized as

$$(\lambda^2 + v\lambda - A)(\lambda^2 + (v/d)\lambda - D) = 0.$$

In the neighborhood of P_x,

$$A = 1,$$
$$B = 1 - k,$$
$$C = 0,$$
$$D = \frac{c}{d}$$

and the eigenvalues are

$$\lambda = \frac{-v \pm \sqrt{v^2+4}}{2},\ \frac{-v \pm \sqrt{v^2+4cd}}{2d},$$

which means P_x is a saddle point. In the neighborhood of P_y,

$$A = -c,$$
$$B = 0,$$
$$C = \frac{1-c}{d},$$
$$D = \frac{1-c}{d(1+ky^*)}$$

and the eigenvalues are

$$\lambda_1^{\pm} = \frac{-v \pm \sqrt{v^2-4c}}{2},$$
$$\lambda_2^{\pm} = \frac{-v \pm \sqrt{v^2+4Dd}}{2d}.$$

As $c, d, D > 0$, P_y has a three-dimensional stable manifold and a one-dimensional unstable manifold.

To proceed further, we introduce the following lemma and definition.

Lemma 1. *Let us consider the four-dimensional dynamical system with a hyperbolic fixed point P (none of the eigenvalues is on the imaginary axis). Assume the hyperplane* $I = \{(x_1, x_2, x_3, x_4) | x_1 = x_2 = 0\}$ *is a two-dimensional invariant manifold of P (if* $x_1 = x_2 = 0$ *holds initially, it holds forever). Assume the only one of the four eigenvalues of P has a positive real part and the corresponding eigenvector is tangent to I. Let* $W^u(P)$ *be the one-dimensional unstable manifold of P. Then,* $W^u(P)$ *is a curve on the invariant hyperplane I.*

Proof. See Appendix A. □

Definition. A realistic TWS is defined as a heteroclinic orbit connecting P_x and P_y in the region $x > 0$ and $y > 0$.

Now we can prove the following theorem.

Theorem 1. *Eqs. (8) do not have any realistic TWS starting from* P_y.

Proof. Consider $W^u(P_y)$, the one-dimensional unstable manifold of P_y. Any orbit which converges to P_y as $z \to -\infty$ must be on $W^u(P_y)$. $W^u(P_y)$ is tangent to the eigenvector for λ_2^+,

$$\vec{e}_2^{\,+} = \begin{pmatrix} 0 \\ 0 \\ 1 \\ \lambda_2^+ \end{pmatrix}$$

at P_y. On the other hand, the hyperplane $I = \{(x, p, y, q) | x = p = 0\}$ is a two-dimensional invariant manifold of Eqs. (8). I is also tangent to $\vec{e}_2^{\,+}$ at P_y. From Lemma 1, $W^u(P_y)$ is a curve on the hyperplane I. As P_x is not on I, $W^u(P_y)$ does not contain P_x. This completes the proof. □

According to this theorem, farmers cannot expel exploiters in any TWS, regardless of parameter values. By the next theorem, we obtain the minimum velocity of the TWS. We empirically know that the TWS of the minimum velocity is most often chosen as a result of a Cauchy problem with a regular initial condition.

Theorem 2. *If Eqs. (8) have a realistic TWS entering* P_y*, the velocity satisfies*

$$v \geqslant 2\sqrt{c}.$$

Proof. We argue by contradiction. Assume there exists a realistic TWS with $v < 2\sqrt{c}$. P_y has three eigenvalues whose real parts are negative. λ_2^- is a negative real and the corresponding eigenvector is

$$\vec{e}_2^- = \begin{pmatrix} 0 \\ 0 \\ 1 \\ \lambda_2^- \end{pmatrix},$$

which is tangent to I. $\lambda_1^\pm$ are complex conjugates ($\mathrm{Im}(\lambda_1^\pm) \neq 0$) with negative real parts and the corresponding eigenvectors are

$$\vec{e}_1^\pm = \begin{pmatrix} 1 \\ \lambda_1^\pm \\ \dfrac{-C}{D-(v/d)\lambda-\lambda^2} \\ \dfrac{-\lambda C}{D-(v/d)\lambda-\lambda^2} \end{pmatrix},$$

which have non-zero components in both x- and p-direction. A realistic TWS must be $W^s_{2^-}(P_y)$, the one-dimensional stable manifold of P_y that is tangent to $\vec{e}_2^-$ at P_y. Otherwise, the orbit has to pass the region $x < 0$ as it approaches P_y. However, as $\vec{e}_2^-$ is tangent to I, $W^s_{2^-}(P_y)$ is a curve on I (this might seem almost trivial from Lemma 1 but see Appendix B for proof). Therefore, $W^s_{2^-}(P_y)$ does not contain P_x. The contradiction completes the proof. □

In addition to these analytic results, we can derive the following conjecture.

Conjecture 1. *Assume $d = 1$. For sufficiently small c and k, the traveling wave solution exists in Eqs. (5) and it approaches to the solution of*

$$\begin{aligned} &y = y^*(1-x), \\ &\frac{\partial x}{\partial t} = \frac{\partial x}{\partial X^2} + cx(1-x) \end{aligned} \tag{9}$$

as $c \to 0$ and $k \to 0$.

Derivation. See Appendix C.

As the second equation is the Fisher-KPP equation, a TWS exists in Eqs. (9) and the system will converge to the TWS with the velocity $v^* = 2\sqrt{c}$ for most regular initial conditions [18]. The conjecture claims that Eqs. (5) is reduced into Eqs. (9).

According to these results, the benefit of altruism (k) has no impact on the final state of the system. However efficient the altruism is, farmers can never expel exploiters. When $k \to 1$ and $c \to 0$, $y^* \to \infty$ and the diffusion of farmers from the right half of the space to 'the front' is expected to diverge to the infinity, while the per capita growth rates in local competition differ only by c. Despite these facts, our result predicts that exploiters will always win. The striking result derived analytically has some limitations. Theorem 1 does not deny the possibility that farmers expel exploiters in any form except TWS. Theorem 2 deals only with the minimum velocity. Only when c and k are small and $d = 1$, we have a reasonable conjecture that the PDE system (Eqs. (5)) develops into a TWS. However, the general PDE problem is difficult to attack. Next, we perform numerical calculations to check the validity of the analysis.

4. Numerical result

We performed the numerical calculation of Eqs. (5) in the region $0 \leqslant X \leqslant L$ with a zero-flux boundary condition. L denotes the size of the space and we fix $L = 4000$. Based on preliminary calculations as well as the analytical result, the initial condition is set as

$$(x,y) = \begin{cases} (1,0), & 0 \leqslant X \leqslant L/10, \\ (0,0), & L/10 < X < L/2, \\ (0,y^*), & L/2 \leqslant X \leqslant L. \end{cases}$$

For all parameters we have tested, a traveling wave is formed in which exploiters expel farmers (Fig. 3). The dependence of the velocity of the TWS on c and k is studied. When $d = 1$, the velocity does not depend on k, as is predicted analytically (Table 1). The dependence on c is quantitatively

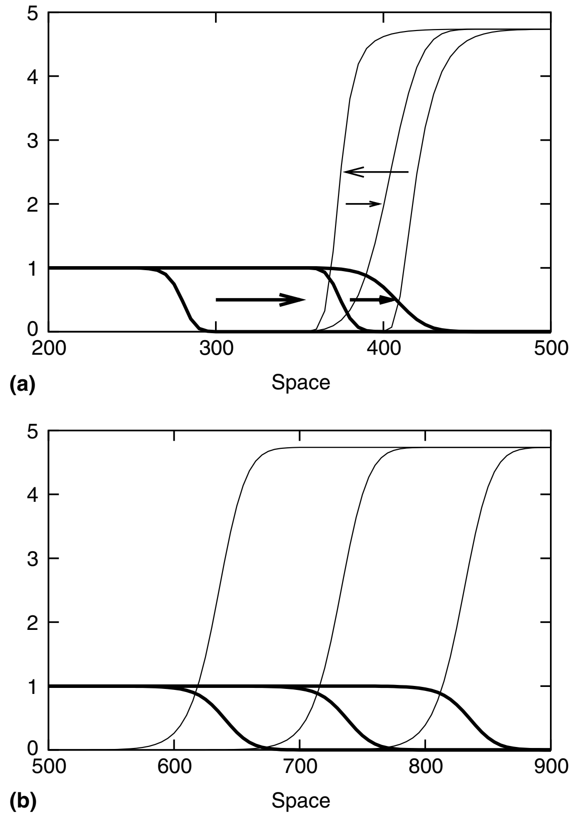

Fig. 3. The profiles of the waves ($k = 0.9$, $c = 0.1$, $d = 0.25$). (a) The propagating waves of farmers (solid) and exploiters (bold) approach each other ($t = 100$) and then collide ($t = 160$) and form the stable boundary ($t = 240$) moving right slowly. (b) After some transient time, the stable traveling wave with the constant velocity is formed ($t = 640, 800, 960$).

Table 1
The velocity of the TWS in Eqs. (5) as a function of c and k

k	c (v^*)				
	0.001 (0.0632)	0.01 (0.2000)	0.1 (0.6325)	0.5 (1.4142)	0.9 (1.8974)
0.01	**0.0583**	0.1946	0.6274	1.4136	1.9044
0.1	**0.0583**	**0.1946**	0.6274	1.4136	1.9044
0.5	**0.0583**	**0.1946**	**0.6274**	1.4137	1.9044
0.9	**0.0583**	**0.1946**	**0.6274**	1.4136	1.9044
0.999	**0.0579**	**0.1946**	**0.6274**	1.4137	1.9044

$d = 1.0$, $v^* = 2\sqrt{c}$. The bold values indicates $y^* > 1$.

Table 2
The velocity of the TWS in Eqs. (5) as a function of d and k

k	d				
	0.01	0.1	1	10	100
0.01	0.6249	0.6260	0.6274	0.6397	0.7933
0.1	0.6249	0.6260	0.6274	0.6395	0.7897
0.5	0.6250	0.6260	0.6274	0.6383	0.7683
0.9	0.6250	0.6261	0.6274	0.6353	0.7251
0.999	0.6251	0.6261	0.6274	0.6353	0.7026

$c = 0.1$. $v^* = 0.6325$.

similar to the predicted value. These results hold when d is decreased, while the discrepancy appears when d is increased (Table 2). Even in the case when $c = 0.001$ and $k = 0.999$ (the corresponding $y^* = 500$), the density of farmers reaches y^* temporally, but exploiters invade the highly efficient population of farmers very slowly and finally expel them. The final realization is always the spatially homogeneous equilibrium state of exploiters, $x = 1$.

We also have a conjecture that the spatiotemporal dynamics of exploiters will converge to that of the Fisher-KPP equation. Our conjecture is valid when c and k are small. In this case, a numerical calculation suggests that the conjecture is true (Fig. 4(a)). When k is not small ($k = 0.9$), the wave is sharper but still affine congruent to the solution of the corresponding Fisher-KPP equation (Fig. 4(b)). If d is increased ($d = 10$), the dynamics behaves quite differently from the Fisher-KPP equation (Fig. 4(c)).

The reason farmers cannot win is also explained by the following verbal discussion. The (local) net per capita growth rate is the sum of the reaction term and the second derivative of spatial distribution. In order to enjoy the diffusion effect, the spatial distribution function must be concave at a focal point. However, due to the nature of a reaction diffusion equation, exploiters instantly spread into the whole space regardless of the initial distribution. Since the zero-flux boundary condition is used, the second derivative cannot be concave for the whole space, which means there is a point where exploiters locally expel farmers. Therefore, farmers cannot expel exploiters in the form of a TWS. The nature (infinite spreading velocity) is a major defect of the reaction diffusion

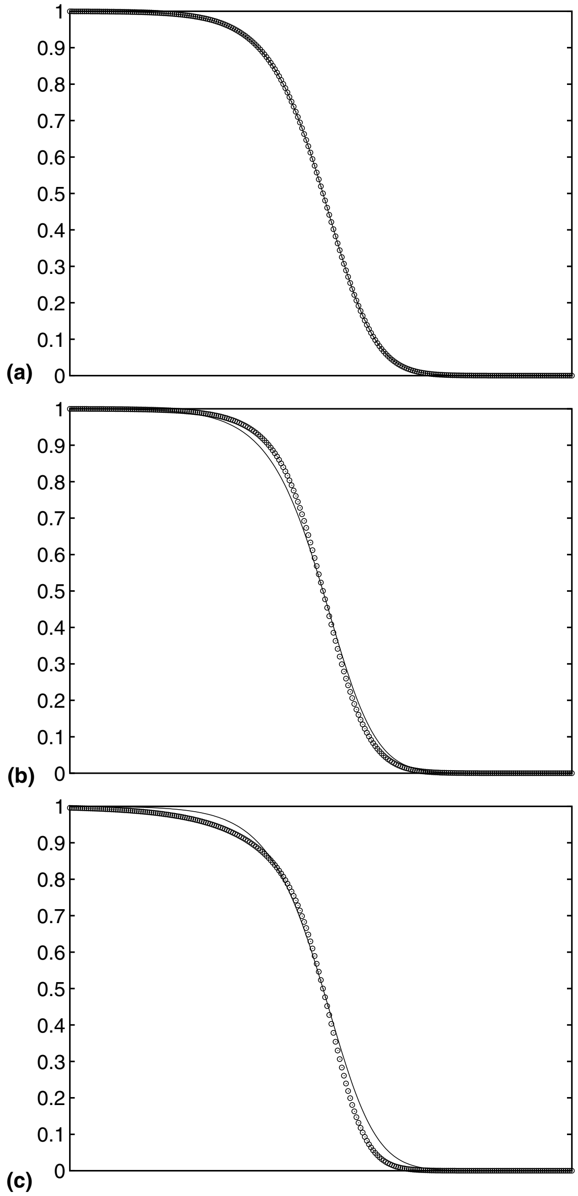

Fig. 4. The comparison between the original model and the Fisher-KPP equation. The solid curve represents the wave profile of Fisher-KPP equation ($c = 0.1$, $d = 1$). The circles represent the wave profile of the solution of Eqs. (5). The two wave profiles are translated so that they intersects at $x = 0.5$. $c = 0.1$ for all figures. (a) Two profiles are almost identical ($d = 1$, $k = 0.1$). (b) They are slightly different but still affine congruent (by rescaling space by a coefficient 1.16) when k is not small ($d = 1$, $k = 0.9$). (c) They are completely different when $d > 1$ ($d = 10$, $k = 0.9$).

equation as a model for biological invasions. The defect might be eliminated by introducing the least viable density ε. In this 'cutoff' model, when the density is below ε, it decreases exponentially. Formally,

Table 3
The velocity of the TWS in the model with cutoff effect

ε	c (v^*)				
	0.001 (0.0632)	0.01 (0.2000)	0.1 (0.6325)	0.5 (1.4142)	0.9 (1.8974)
0.0001	0.0534	0.1778	0.5830	1.3216	1.7759
0.001	0.0437	0.1583	0.5459	1.2548	1.6855
0.01	0.0164	0.1094	0.4599	1.1074	1.4875

$d = 1.0$ and $k = 0.999$.

$$R_x(x,y) = \begin{cases} x\left(1 - \dfrac{x+y}{1+ky}\right) & (x > \varepsilon), \\ -x & (x \leqslant \varepsilon), \end{cases}$$

$$R_y(x,y) = \begin{cases} y\left(1 - \dfrac{x+y}{1+ky}\right) - cy & (y > \varepsilon), \\ -y & (y \leqslant \varepsilon), \end{cases}$$

where R_x and R_y are reaction terms of exploiters and farmers, respectively. The numerical result of the model shows that the cutoff effect decrease the invading velocity of exploiters, however, farmers still cannot win for all parameters we have tested (Table 3).

5. Discussion

We show that the emergence of altruism is impossible in the present model framework. We analytically show that farmers can never expel exploiters in any form of a TWS. Numerical simulation of the reaction diffusion equations shows that exploiters always win. This result is in marked contrast to many studies showing that spatial structure promotes the evolution of cooperative behavior. The discrepancy comes from the essential difference of model, i.e. discrete and continuous spatial structure. Discrete space model is easier to deal with and might be more appropriate for some biological phenomena than continuous space model. However, space is essentially continuous and continuous space model has more applications to the real biological world. If continuous space does not promote the evolution of altruism at all, we must reconsider the effect of spatial structure on the evolution of altruism.

What difference between continuous and discrete space brought the present result? There are many studies on the evolution of altruistic behavior in the population with local interaction and local dispersal (viscous population). Among them, the studies on lattice population using inclusive fitness theory [4,7] may be a clue to the question. Based on the Hamilton's rule, relatedness must be positive for altruism to evolve. In this case, relatedness represents the fact that altruistic individual more likely interacts with altruistic individuals than population average in viscous population. In the lattice models, relatedness is generally positive because the size of local population (patch) is finite. On the other hand, in reaction diffusion models, individuals are represented by density, that is continuous. Thus, relatedness of local population might be always zero, although we do not know any formal definition of relatedness in general reaction diffusion models. This might be the reason why the emergence of altruistic behavior is not promoted in the continuous space.

From the mathematical point of view, we provide the non-existence proof of a TWS in which farmers win. We numerically expect the existence of a TWS in which exploiters win. When $k = 0$, our model falls into a category of the diffusive Lotka–Volterra competition model that has been intensively studied. For example, Hosono [18] shows that the velocity becomes an increasing function of D_y (or d in non-dimensionalized model) for sufficiently large d. This agrees with our numerical result (Table 2) although the present model is not a Lotka–Volterra type. In a realistic situation $d = O(1)$ the velocity does not depend on d, which motivated the analysis of the special case $d = 0$ of the diffusive Lotka–Volterra models. The existence of a TWS in the corresponding three-dimensional phase space is proved by Hosono [17]. We showed that our model might be reduced to the two-dimensional when $d = 1$, but considering the case $d = 0$ of our case might be another way to approach the existence proof.

This study does not positively contribute to the understanding of the evolution of altruistic behavior. Our result suggests that any effort with cost to increase the shared carrying capacity is maladaptive, however efficient it is. One possible explanation for the evolution of altruistic behavior in the continuous space is that the common resource is not allocated evenly. If (for some biological reasons) farmers have the priority to use the addition of the common resource by them, they might be able to resist the invasion of exploiters. This situation might be denoted by the time delay in carry capacity term of exploiters. The author is currently working on this type of model. Although altruism does not spread in the present model, we hope that our analysis will contribute to the understanding of the evolution of altruism in public goods games in the continuous space.

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Appendix A

Proof of Lemma 1. We consider the four-dimensional dynamical system satisfying

$$\dot{\mathbf{x}} = f(\mathbf{x}), \tag{A1}$$

$$f(\mathbf{0}) = \mathbf{0}, \tag{A2}$$

$$\forall x_3, x_4,$$

$$f_1(0, 0, x_3, x_4) = 0, \tag{A3}$$

$$f_2(0, 0, x_3, x_4) = 0,$$

(A3) means the hyperplane $I = \{(x_1, x_2, x_3, x_4) | x_1 = x_2 = 0\}$ is an invariant manifold of O. Jacobian matrix of (A1) around O is generally denoted by

$$J = \begin{pmatrix} \mathbf{A} & \mathbf{0} \\ \mathbf{C} & \mathbf{B} \end{pmatrix},$$

where $\mathbf{A}$, $\mathbf{B}$ and $\mathbf{C}$ are 2×2 square matrices. With proper base transformations in a $x_1 - x_2$ subspace and a $x_3 - x_4$ subspace, $\mathbf{A}$ and $\mathbf{B}$ can be taken as Jordan canonical forms without loss of generality. Thus, we assume

$$J = \begin{pmatrix} \lambda_1 & 0 & 0 & 0 \\ a & \lambda_2 & 0 & 0 \\ c_1 & c_3 & \lambda_3 & 0 \\ c_2 & c_4 & b & \lambda_4 \end{pmatrix}, \tag{A4}$$

where λ_i are eigenvalues. We also assume

$$\mathrm{Re}(\lambda_4) > 0 \quad \text{and} \quad \mathrm{Re}(\lambda_1), \mathrm{Re}(\lambda_2), \mathrm{Re}(\lambda_3) < 0. \tag{A5}$$

This means that the unstable eigenvector is tangent to I. Here we prove the global unstable manifold of O, $W^{\mathrm{u}}(O)$, is contained by I.

Let $W^{\mathrm{u}}_{\mathrm{loc}}(O)$ be the local unstable manifold of O. Let $z \equiv x_4$ then stable manifold theorem ensures that $W^{\mathrm{u}}_{\mathrm{loc}}(O)$ is a curve $(x_1, x_2, x_3) = \varphi(z)$ where $D\varphi(0) = (0, 0, 0)$. The following must be the identity equation of z;

$$f_4(\varphi_1(z), \varphi_2(z), \varphi_3(z), z) \cdot \varphi'(z) = f_i(\varphi_1(z), \varphi_2(z), \varphi_3(z), z), \tag{A6}$$

where $i = 1, 2, 3$. Substituting a Taylor expansion $\varphi_i(z) = a_{ij}z^j + \mathrm{O}(z^{j+1})$ $(j \geqslant 2)$ into a Taylor expansion of f_4 around O, the left hand side of (A6) becomes

$$\left[\sum_{k=1}^{3}\left(\left.\frac{\partial f_4}{\partial x_k}\right|_O \varphi_k(z)\right) + \left.\frac{\partial f_4}{\partial x_4}\right|_O z + \mathrm{O}(z^2)\right](ja_{ij}z^{j-1} + \mathrm{O}(z^j)) = ja_{ij}\lambda_4 z^j + \mathrm{O}(Z^{j+1}).$$

Similarly, for $i = 1$, the right hand side of (A6) becomes

$$\sum_{k=1}^{3}\left(\left.\frac{\partial f_1}{\partial x_k}\right|_O \varphi_k(z)\right) + \left.\frac{\partial f_1}{\partial x_4}\right|_O z + \frac{1}{2}\left.\frac{\partial^2 f_1}{\partial x_4^2}\right|_O z^2 + \cdots = \lambda_1 a_{1j} z^j + \mathrm{O}(Z^{j+1})$$

because $\left.\frac{\partial f_1}{\partial x_k}\right|_O = 0$ for $k = 2, 3, 4$ form (A4) and because $\left.\frac{\partial^l f_i}{\partial x_4^l}\right|_O = 0$ for $i = 1, 2$ from (A3). Comparing the coefficients, we obtain

$$\lambda_1 = j\lambda_4 \quad \text{or} \quad a_{1j} = 0.$$

From (A5), the former condition is impossible and we obtain

$$a_{1j} = 0.$$

For $i = 2$, (A6) becomes

$$ja_{2j}\lambda_4 z^j = aa_{1j}z^j + a_{2j}\lambda_2 z^j + \mathrm{O}(z^3)$$

and we obtain $a_{2j} = 0$. Therefore, we obtain

$$\varphi_i(z) = 0$$

for $i = 1, 2$. Thus, $W^{\mathrm{u}}_{\mathrm{loc}}(O)$ is a curve on the hyperplane I. As $W^{\mathrm{u}}(O)$ is the extension of $W^{\mathrm{u}}_{\mathrm{loc}}(O)$ and I is invariant, $W^{\mathrm{u}}(O)$ is a curve on I. This completes the proof. □

Appendix B

Proof. We consider the same dynamical system denoted by (A1)–(A5). In addition, we assume that λ_1 and λ_2 are complex (corresponding to $\lambda_1^{\pm}$ in the text) and that λ_3 and λ_4 are real (corresponding to $\lambda_2^{\pm}$ in the text), formally,

$$\begin{aligned} &\mathrm{Im}(\lambda_i) \neq 0 \quad \text{for } i = 1, 2, \\ &\mathrm{Im}(\lambda_i) = 0 \quad \text{for } i = 3, 4. \end{aligned} \tag{B1}$$

Let $W^{\mathrm{s}}_{2^-}(O)$ be the one-dimensional stable manifold of O that is tangent to $\vec{e}_2^{\,-}$ at O. Here we prove $W^{\mathrm{s}}_{2^-}(O)$ is contained by I.

Let $z \equiv x_3$ and $W^{\mathrm{s}_{2^-}}_{\mathrm{loc}}(O)$ be $W^{\mathrm{s}_{2^-}}(O)$ in the neighborhood of O. Then $W^{\mathrm{s}_{2^-}}_{\mathrm{loc}}(O)$ is a curve $(x_1, x_2, x_4) = \varphi(z)$ where $D\varphi(0) = (0, 0, 0)$. The following must be the identity equation of z:

$$f_3(\varphi_1(z), \varphi_2(z), z, \varphi_4(z)) \cdot \varphi_i'(z) = f_i(\varphi_1(z), \varphi_2(z), z, \varphi_4(z)), \tag{B2}$$

where $i = 1, 2, 4$. Substituting a Taylor expansion $\varphi_i(z) = a_{ij}z^j + \mathrm{O}(z^{j+1})$ $(j \geqslant 2)$, we obtain

$$ja_{1j}\lambda_3 = a_{1j}\lambda_1$$

and

$$ja_{2j}\lambda_3 = aa_{1j} + a_{2j}\lambda_2.$$

From (B1), neither $\lambda_1 = j\lambda_3$ nor $\lambda_2 = j\lambda_3$ is possible. Thus, we obtain

$$\varphi_i(z) = 0$$

for $i = 1, 2$ and $W^{\mathrm{s}_{2^-}}_{\mathrm{loc}}(O)$ is a curve on the hyperplane I. As $W^{\mathrm{s}_{2^-}}(O)$ is the extension of $W^{\mathrm{s}_{2^-}}_{\mathrm{loc}}(O)$ and I is invariant, $W^{\mathrm{s}_{2^-}}(O)$ is a curve on I. This completes the proof. □

Appendix C

Derivation of Conjecture 1. Here we show that our model reduces to a Fisher-KPP equation if we neglect the second and higher order terms of c and k. The central idea is that the quantity

$$x + \frac{y}{y^*} \tag{C1}$$

will remain one at all points on the orbit when the difference between the property of farmers and that of exploiters is very small, i.e. $c, k \ll 1$. Based on the idea, we apply the following transformation:

$$
\begin{aligned}
m &= x + \frac{y}{y^*} - 1, \\
n &= p + \frac{q}{y^*}, \\
u &= x - \frac{y}{y^*}, \\
w &= p - \frac{q}{y^*}.
\end{aligned} \tag{C2}
$$

We expect that $m = n = 0$ is an invariant manifold of both P_x and P_y. If this is true, the system can be reduced into the two-dimensional dynamics on the manifold. Eqs. (8) can be rewritten by the new four parameters using

$$
\begin{aligned}
x &= \frac{1 + m + u}{2}, \\
y &= \frac{1 + m - u}{2} y^*, \\
p &= \frac{n + w}{2}, \\
q &= \frac{n - w}{2} y^*.
\end{aligned} \tag{C3}
$$

Substituting Eqs. (A3) into Eqs. (8) yields complicated equations. However, linearization around $c = k = 0$ becomes rather simple. To the first order of c and k, we obtain

$$
\begin{aligned}
\dot{u} &= w, \\
\dot{w} &= -\frac{v}{2} Jw - \frac{v}{2} Kn + \frac{c}{4} Ju^2 - \frac{c}{4} J + \mathrm{O}(m), \\
\dot{m} &= n, \\
\dot{n} &= -\frac{v}{2} Jn - \frac{v}{2} Kw + \frac{c}{4} Ku^2 - \frac{c}{4} K + \mathrm{O}(m), \\
J &= 1 + \frac{1}{d}, \\
k &= 1 - \frac{1}{d},
\end{aligned} \tag{C4}
$$

where $\mathrm{O}(m)$ represent the terms including m, which vanish when $m = 0$. Unfortunately, $m = n = 0$ is not invariant in general. However, in the special case $K = 0 \iff d = 1$, the equations become simpler

$$
\begin{aligned}
\dot{u} &= w, \\
\dot{w} &= -vw + \frac{c}{2} u^2 - \frac{c}{2} + \mathrm{O}(m), \\
\dot{m} &= n, \\
\dot{n} &= -vn + \mathrm{O}(m)
\end{aligned} \tag{C4$'$}
$$

and $m = n = 0$ becomes invariant. Hereafter, we assume $d = 1$. The reduced two-dimensional system is

$$\begin{aligned} \dot{u} &= w, \\ \dot{w} &= -vw + \frac{c}{2}(u-1)(u+1). \end{aligned} \tag{C5}$$

The realistic TWS of Eqs. (8) corresponds to the orbit of Eqs. (A5) starting $(u, w) = (1, 0)$ and entering $(-1, 0)$ in the region $-1 < u < 1$. Applying the transformation,

$$\begin{aligned} \widetilde{u} &= \frac{u+1}{2}, \\ \widetilde{w} &= \frac{w}{2}, \end{aligned} \tag{C6}$$

Eqs. (A5) become

$$\begin{aligned} \dot{\widetilde{u}} &= \widetilde{w}, \\ \dot{\widetilde{w}} &= -v\widetilde{w} - c\widetilde{u}(1-\widetilde{u}), \end{aligned} \tag{C7}$$

which is exactly the ODE governing a TWS in the Fisher-KPP equation

$$\frac{\partial \widetilde{u}}{\partial t} = \frac{\partial^2 \widetilde{u}}{\partial X^2} + c\widetilde{u}(1-\widetilde{u}), \tag{C8}$$

with the wave velocity v. We obtain Eq. (9) because $\widetilde{u} = x$ if $m = 0$. The existence of a realistic TWS in Eq. (B2) had been already proved for $v \geqslant 2\sqrt{c}$ [19]. Thus, a realistic TWS exists in Eqs. (C4′). The stability and the convergence to the TWS of the minimum velocity are also proved for the Fisher-KPP equation. To check these in our case, we rewrite Eqs. (5) as

$$\begin{aligned} \frac{\partial u}{\partial t} &= \frac{\partial u}{\partial X^2} - \frac{c}{2}(u-1)(u+1) + \mathrm{O}(m), \\ \frac{\partial m}{\partial t} &= \frac{\partial m}{\partial X^2} - m\left(1 - \frac{c+k}{2}(1-u)\right) + \mathrm{O}(m^2), \end{aligned} \tag{C9}$$

where we used $d = 1$ and neglected the second and higher order terms of c and k. Apparently, $m = 0$ is invariant and we obtain

$$\frac{\partial u}{\partial t} = \frac{\partial u}{\partial X^2} - \frac{c}{2}(u-1)(u+1), \tag{C10}$$

which is essentially identical to the Fisher-KPP equation. Therefore, the stability and the convergence to the TWS for $v = 2\sqrt{c}$ may also hold in our case.

The above argument proves that Eqs. (5) reduces to a Fisher-KPP equation and have the same property (existence and stability of a TWS) if we neglect all the second and higher order terms of c and k. Actually, Eqs. (8) converges to Eqs. (C4′) as $c \to 0$ and $k \to 0$. Unfortunately, however, the existence of a TWS in Eqs. (C4′) does not in general ensure the existence of a TWS in Eqs. (8). We could only show that there is an orbit in Eqs. (8) connecting P_x and P such that $P \to P_y$. However, as we have seen, our system is closely related to Fisher-KPP equation although they look very different.

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