

## TRANSITION OF INTERACTION OUTCOMES IN A FACILITATION-COMPETITION SYSTEM OF TWO SPECIES

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**ABSTRACT.** A facilitation-competition system of two species is considered, where one species has a facilitation effect on the other but there is spatial competition between them. Our aim is to show mechanism by which the facilitation promotes coexistence of the species. A lattice gas model describing the facilitation-competition system is analyzed, in which nonexistence of periodic solution is shown and previous results are extended. Global dynamics of the model demonstrate essential features of the facilitation-competition system. When a species cannot survive alone, a strong facilitation from the other would lead to its survival. However, if the facilitation is extremely strong, both species go extinct. When a species can survive alone and its mortality rate is not larger than that of the other species, it would drive the other one into extinction. When a species can survive alone and its mortality rate is larger than that of the other species, it would be driven into extinction if the facilitation from the other is weak, while it would coexist with the other if the facilitation is strong. Moreover, an extremely strong facilitation from the other would lead to extinction of species. Bifurcation diagram of the system exhibits that interaction outcome between the species can transition between competition, amensalism, neutralism and parasitism in a smooth fashion. A novel result of this paper is the rigorous and thorough analysis, which displays transparency of dynamics in the system. Numerical simulations validate the results.

**1. Introduction.** Natural symbiosis of species is usually a complex combination of positive and negative interactions [6, 7]. For example, one species may receive merit from the other, while there exists competition between them because of spatial or nutrition limitations. The so-called facilitation-competition relationship widely exists in plant-plant, plant-animal and animal-animal interactions in natural environments [4, 5, 9].

Kawai et al. [3] studied two sessile filter-feeders of similar body sizes, the goose barnacle *Capitulum mitella* and mussel *Septifer virgatus*, which live in patches on a moderately wave-exposed rocky shore of south Japan in the western Pacific. The presence of *C. mitella* decreases the washing-away rate of *S. virgatus*, while *S. virgatus* gives no merit to *C. mitella*. Since both species live in the same area, there exists spatial competition between them. In order to understand the pattern of coexistence of the species, Yokoi et al. [12] established a lattice gas model to describe the facilitation-competition system.

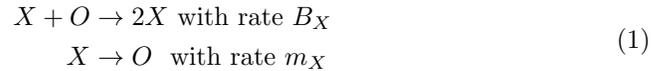
In a lattice gas system of species  $X$  (*S. virgatus*) and  $Y$  (*C. mitella*), individuals of the species live on a square lattice. A site is labeled by  $X$  (or  $Y$ ) if it is occupied

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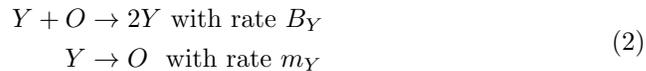
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by an individual of species  $X$  (or  $Y$ ). When it is empty, it is labeled by  $O$ . On the lattice, any pair of sites interact randomly and independently. If sites  $X$  and  $O$  interact, then the site  $O$  will become  $X$  in a birth rate  $B_X$ . If a site is occupied by  $X$ , then it will become  $O$  in a death rate  $m_X$ . Then reactions (contact process) in species  $X$  can be depicted by



where parameter  $B_X$  represents the intrinsic growth rate of species  $X$  and  $m_X$  denotes its mortality rate.

Similarly, the reactions in species  $Y$  can be depicted by



where parameter  $B_Y$  represents the intrinsic growth rate of species  $Y$  and  $m_Y$  denotes its mortality rate. All parameters in (1)-(2) are positive.

The interaction outcome between species  $X$  and  $Y$  is determined by positive (+), neutral (0), or negative (−) effects of one species on the other [1, 8, 11]. Assume that species  $X$  can approach a density of  $x_1$  in the absence of  $Y$ , while in the presence of  $Y$ , species  $X$  approaches a density of  $x_2$ . Similarly, assume that species  $Y$  can approach a density of  $y_1$  in the absence of  $X$ , while in the presence of  $X$ , species  $Y$  approaches a density of  $y_2$ . Here, the density of a species represents the number of the species in a certain area. When  $x_2 - x_1 > 0$  and  $y_2 - y_1 < 0$ , the interaction outcome between species  $X$  and  $Y$  is parasitism (+ −). When  $x_2 - x_1 = 0$  and  $y_2 - y_1 = 0$ , the interaction outcome becomes neutralism (0 0). When  $x_2 - x_1 = 0$  and  $y_2 - y_1 < 0$ , the interaction outcome is amensalism (0 −). When  $x_2 - x_1 < 0$  and  $y_2 - y_1 = 0$ , the interaction outcome becomes the other amensalism (− 0). When  $x_2 - x_1 < 0$  and  $y_2 - y_1 < 0$ , the interaction outcome is competition (− −).

Based on the reactions in (1)-(2), Yokoi et al. [12] established a facilitation-competition model. Local stability analysis and numerical simulations of the model exhibit novel transition of interaction outcomes between the species. In order to show global stability in the system and display all possible transitions of outcomes, it is necessary to give rigorous and thorough analysis and transparency of the results.

In this paper, we analyze global dynamics of the model established by Yokoi et al. [12], in which our results consolidate and extend those by Yokoi et al. [12]. Moreover, dynamical behavior of the facilitation-competition system demonstrates that interaction outcomes between the species can transition between competition (− −), amensalism (0 −), amensalism (− 0), neutralism (0 0) and parasitism (+ −) in a smooth fashion. Numerical simulations validate our results.

**2. Model.** When the lattice size is sufficiently large, the reactions of (1)-(2) are usually described by differential equations, which are called the mean-field theory of lattice model [10]:

$$\begin{aligned} \frac{dx}{dt} &= B_X x(1 - x - y) - m_X x \\ \frac{dy}{dt} &= B_Y y(1 - x - y) - m_Y y \end{aligned} \tag{3}$$

where parameter  $m_X = \bar{m}_X/(1 + cy)$  denotes the mortality rate of species  $X$  in the presence of  $Y$ . Parameter  $\bar{m}_X$  represents the mortality rate of species  $X$  in

the absence of  $Y$ , and  $c$  measures the degree of facilitation. The term  $1 - x - y$  represents the density of empty sites. For simplicity, system (3) is rewritten as

$$\begin{aligned} \frac{dx}{dt} &= r_1x\left(1 - x - y - \frac{d_1}{1 + cy}\right) \\ \frac{dy}{dt} &= r_2y(1 - d_2 - x - y) \end{aligned} \tag{4}$$

where

$$r_1 = B_X, \quad d_1 = \frac{\bar{m}_X}{B_X}, \quad r_2 = B_Y, \quad d_2 = \frac{m_Y}{B_Y}. \tag{5}$$

We consider solutions  $(x(t), y(t))$  of (4) with initial values  $x(0) > 0, y(0) > 0$ . Then we have  $x(t) > 0, y(t) > 0$  as  $t > 0$ .

The following result demonstrates boundedness of solutions and non-existence of periodic solutions of (4).

**Theorem 2.1.** (i) *Solutions of (4) are bounded.*

(ii) *System (4) admits no periodic solution.*

*Proof.* (i) When  $x + y \geq 1$ , we have  $dx/dt < 0$  and  $dy/dt < 0$ , which implies all solutions of (4) will satisfy  $x(t) + y(t) < 1$  as  $t$  is sufficiently large. Thus solutions of (4) are bounded.

(ii) Let  $H(x, y) = 1/(xy)$ , which is called the Dulac function. Let  $\phi(x, y)$  and  $\psi(x, y)$  be the righthand sides of equations in (4), respectively. Then we have

$$\frac{\partial(H\phi)}{\partial x} + \frac{\partial(H\psi)}{\partial y} = -\frac{r_1}{y} - \frac{r_2}{x} < 0$$

for all  $x > 0, y > 0$ . It follows from Bendixson-Dulac Theorem [2] that system (4) admits no periodic solution. □

It follows from Theorem 2.1 that all solutions of (4) converge to equilibria. When  $d_2 \geq 1$ , we have  $dy/dt < 0$ , which implies  $\lim_{t \rightarrow \infty} y(t) = 0$ . Thus  $\lim_{t \rightarrow \infty} x(t) = 1 - d_1$  as  $1 - d_1 > 0$ , and  $\lim_{t \rightarrow \infty} x(t) = 0$  as  $1 - d_1 \leq 0$ . Therefore, we assume  $d_2 < 1$  in the following analysis.

**3. Dynamics.** In this section, we consider dynamics of system (4), which are determined by the relative positions of isoclines. Denote the isoclines of (4) by

$$\begin{aligned} L_1 : 1 - x - y - \frac{d_1}{1 + cy} &= 0, \\ L_2 : 1 - d_2 - x - y &= 0. \end{aligned}$$

Then  $L_1$  is a hyperbola with asymptotes  $1 - x - y = 0$  and  $y = -1/c$ . In the first quadrant,  $L_1$  can be rewritten as

$$x = f(y) = 1 - y - \frac{d_1}{1 + cy}.$$

Thus we have

$$\frac{d^2 f(y)}{dy^2} = -\frac{2c^2 d_1}{(1 + cy)^3} < 0$$

which implies that  $L_1$  is convex rightward in the first quadrant.

On the other hand,  $L_2$  is a line, which is parallel to the asymptote  $1 - x - y = 0$ . Thus, there is at most one interior equilibrium of system (4) as shown in Figs. 1-2.

The Jacobian matrix  $A$  of (4) is

$$A = \begin{pmatrix} a_{11} & a_{12} \\ a_{21} & a_{22} \end{pmatrix} \tag{6}$$

where

$$a_{11} = r_1[1 - 2x - y - d_1/(1 + cy)], \quad a_{12} = r_1x[-1 + cd_1/(1 + cy)^2],$$

$$a_{21} = -r_2y, \quad a_{22} = r_2(1 - d_2 - x - 2y).$$

The equilibria of (4) are considered as follows, while their local stability is determined by eigenvalues of Jacobian matrix  $A$  of (4) at the equilibria.

(a) The trivial equilibrium  $O(0, 0)$  always exists and has eigenvalues  $r_1(1 - d_1), r_2(1 - d_2)$ .

(b) The semi-trivial equilibrium  $P_1(1 - d_1, 0)$  exists if  $d_1 < 1$ , while  $P_2(0, 1 - d_2)$  exists since it is assumed that  $d_2 < 1$ . The eigenvalues of  $P_1$  are  $-r_1(1 - d_1), r_2(d_1 - d_2)$ . The eigenvalues of  $P_2$  are

$$\lambda_2^{(1)} = r_1[d_2 - \frac{d_1}{1 + c(1 - d_2)}], \quad \lambda_2^{(2)} = -r_2(1 - d_2).$$

(c) There is at most one interior equilibria  $P^*(x^*, y^*)$  with

$$x^* = 1 - d_2 - \frac{d_1 - d_2}{cd_2}, \quad y^* = \frac{d_1 - d_2}{cd_2} \tag{7}$$

which implies that  $P^*$  exists if and only if  $d_1 > d_2$  and  $c > c^*$  with

$$c^* = \frac{d_1 - d_2}{(1 - d_2)d_2}. \tag{8}$$

The following result exhibits stability of  $P^*$ .

**Theorem 3.1.** *Assume  $d_1 > d_2$  and  $c > c^*$ . The interior equilibria  $P^*$  is globally asymptotically stable.*

*Proof.* A direct computation shows that the Jacobian matrix  $A$  of (4) at  $P^*$  is

$$A^* = \begin{pmatrix} -r_1x^* & r_1x^*[-1 + cd_1/(1 + cy^*)^2] \\ -r_2y^* & -r_2y^* \end{pmatrix}. \tag{9}$$

Thus the eigenvalues  $\lambda_1$  and  $\lambda_2$  of  $A^*$  satisfies

$$\lambda_1 + \lambda_2 = -r_1x^* - r_2y^* < 0, \quad \lambda_1\lambda_2 = r_1r_2x^*y^* \frac{cd_1}{(1 + cy^*)^2} > 0$$

which implies that the real parts of  $\lambda_1$  and  $\lambda_2$  are negative and  $P^*$  is asymptotically stable. It follows from Theorem 2.1 that  $P^*$  is globally asymptotically stable.  $\square$

We consider dynamics of system (4) in two cases:  $d_1 \geq 1$  and  $d_1 < 1$ , which represents that species  $X$  cannot/can survive in the absence of species  $Y$ , respectively.

**Case 1.**  $d_1 \geq 1$

When  $d_1 > 1$ , equilibrium  $O$  is a saddle point. When  $d_1 = 1$ ,  $O$  has a zero eigenvalue. Since the isocline  $L_1$  is convex rightward,  $O$  is unstable in the first quadrant by phase-portrait analysis, as shown in Fig. 1a.

Since  $d_1 \geq 1$ , equilibrium  $P_1$  does not exist. When  $c < c^*$ , equilibrium  $P_2$  is a stable node. When  $c = c^*$ ,  $P_2$  has a zero eigenvalue and isoclines  $L_1$  and  $L_2$  intersect at  $P_2$ . Since  $L_1$  is below  $L_2$  as shown in Fig. 1b,  $P_2$  is asymptotically stable in the first quadrant by phase-portrait analysis. It follows from  $c \leq c^*$  that system (4)

has no interior equilibrium. Therefore,  $P_2$  is globally asymptotically stable when  $c \leq c^*$ .

When  $c > c^*$ , equilibrium  $P_2$  is a saddle point and system (4) has a unique interior equilibrium  $P^*$ , which is globally asymptotically stable by Theorem 3.1.

**Case 2.**  $d_1 < 1$

Since  $d_1 < 1$ , the equilibrium  $O$  is an unstable node and  $P_1$  exists. When  $d_1 \leq d_2$ ,  $P_1$  is asymptotically stable and  $P_2$  is a saddle point. From  $d_1 \leq d_2$ , we have  $y^* \leq 0$  and system (4) has no interior equilibrium. Thus  $P_1$  is globally asymptotically stable.

When  $d_1 > d_2$ , equilibrium  $P_1$  is a saddle point. If  $c \leq c^*$ , system (4) has no interior equilibrium and  $P_2$  is globally asymptotically stable. If  $c > c^*$ , both equilibria  $P_1$  and  $P_2$  are saddle points. System (4) has a unique interior equilibrium  $P^*$ . It follows from Theorem 3.1 that  $P^*$  is globally asymptotically stable.

Therefore, we conclude the following result.

**Theorem 3.2.** *Assume  $d_2 < 1$ .*

- (i) *Let  $d_1 \geq 1$ . If  $c \leq c^*$ , then equilibrium  $P_2$  is globally asymptotically stable, as shown in Figs. 1a-b. If  $c > c^*$ , then equilibrium  $P^*$  is globally asymptotically stable, as shown in Figs. 1c-d.*
- (ii) *Let  $d_1 < 1$ . If  $d_1 \leq d_2$ , then equilibrium  $P_1$  is globally asymptotically stable, as shown in Figs. 2a-b. If  $d_1 > d_2$  and  $c \leq c^*$ , then equilibrium  $P_2$  is globally asymptotically stable, as shown in Fig. 2c. If  $d_1 > d_2$  and  $c > c^*$ , then equilibrium  $P^*$  is globally asymptotically stable, as shown in Fig. 2d.*

**4. Transition of outcomes.** In this section, we consider transition of interaction outcomes between the species when parameters vary. We focus on parameters  $c$  and  $d_1$ , which denote the the facilitation from species  $Y$  to  $X$  and the mortality of  $X$  respectively.

**4.1. Transition with parameter  $c$ .** *First*, we consider the case of  $d_1 \geq 1$ , which implies that species  $X$  cannot survive in the absence of  $Y$ . As shown in Theorem 3.2(i) and Figs. 1a-b, when the facilitation from  $Y$  is weak ( $c \leq c^*$ ), species  $X$  still goes extinct while  $Y$  approaches its carrying capacity ( $1 - d_2$ ), in which interaction outcomes between them are neutralism (0 0). The biological reason is that the facilitation from  $Y$  is so weak that it cannot lead to the survival of  $X$  with high mortality.

However, as shown in Theorem 3.2(ii) and Figs. 1c-d, when the facilitation from  $Y$  is strong ( $c > c^*$ ), species  $X$  can persist while  $X$  and  $Y$  coexist at a steady state  $(x^*, y^*)$  with  $y^* < 1 - d_2$ . Thus, the interaction outcome becomes parasitism (+ -). The biological reason is that the strong facilitation from  $Y$  largely decreases the mortality  $-d_1/(1 + cy)$  of  $X$  and leads to persistence of  $X$ , while the persistence of  $X$  forms spatial competition with  $Y$  but provides no merit to  $Y$ . Since species  $X$  cannot persist alone, it is the facilitation from  $Y$  that leads to its survival, where species  $X$  can be regarded as a parasite of  $Y$ .

Moreover, when the facilitation is extremely strong ( $c \rightarrow \infty$ ), we have  $y^* \rightarrow 0$  by (7) and then species  $Y$  goes extinct, which implies the extinction of species  $X$  since  $X$  cannot persist alone. Thus, interaction outcome between the species is changed to amensalism (0 -). The biological reason is that an extremely strong facilitation from species  $Y$  results in rapid growth of  $X$ , which would occupy most sites on the lattice and result in the extinction of  $Y$  and finally results in the extinction of  $X$

in return. Since species  $Y$  can persist alone, it is the extremely strong facilitation from  $Y$  that leads to the extinction of both species.

*Second*, we consider the case of  $d_1 < 1$ , which implies that species  $X$  can survive alone. As shown in Theorem 3.2(ii) and Fig. 2a, when  $d_1 < d_2$ , species  $Y$  goes extinct while  $X$  approaches its carrying capacity. Then interaction outcome between the species is amensalism (0 -). The biological reason is that the low mortality of  $X$  leads to an advantage of  $X$  over  $Y$  in spatial competition. Since species  $Y$  can survive alone, it is the competition from  $X$  that results in its extinction.

As shown in Theorem 3.2(ii) and Fig. 2b, even when  $d_1 = d_2$ , species  $Y$  still goes extinct and  $X$  approaches its carrying capacity. The reason is as follows. Suppose  $c = 0$ , which implies that there is no facilitation from species  $Y$ . Then system (4) becomes

$$\begin{aligned}\frac{dx}{dt} &= r_1x(1 - d_1 - x - y) \\ \frac{dy}{dt} &= r_2y(1 - d_1 - x - y)\end{aligned}\tag{10}$$

which has a line segment of stable interior equilibria and all positive solutions of (4) converge to the equilibria. Thus, when there is no facilitation from  $Y$ , the two species coexist. Therefore, the biological reason under the extinction of  $Y$  is the facilitation from  $Y$ , which decreases the mortality of  $X$  and leads to the advantage of  $X$  over  $Y$  in spatial competition. Since species  $Y$  and  $X$  can coexist without facilitation, it is the facilitation from species  $Y$  that results in the extinction of  $Y$  itself.

When  $d_1 > d_2$ , Theorem 3.2(ii) and Fig. 2c exhibits that if the facilitation from  $Y$  is weak ( $c \leq c^*$ ), species  $X$  goes extinct and  $Y$  approaches its carrying capacity, while interaction outcome between the species becomes amensalism (- 0). The biological reason is that the low mortality of  $Y$  leads to an advantage of  $Y$  over  $X$  in spatial competition under the weak facilitation from  $Y$  to  $X$ . Since species  $X$  can survive alone, it is the competition from  $Y$  that results in its extinction.

Moreover, if the facilitation from  $Y$  is strong ( $c > c^*$ ), the two species coexist at a steady state  $(x^*, y^*)$  with  $y^* < 1 - d_2$ . The biological reason under the coexistence is that although the low mortality of  $Y$  leads to an advantage of  $Y$  over  $X$ , the strong facilitation from  $Y$  to  $X$  decreases the mortality of  $X$ , which results in a balance between its positive and negative effects on  $X$ . The transition of interaction outcomes is as follows. From  $x^* = 1 - d_1$  we obtain

$$c^{**} = \frac{1}{d_2}.$$

Then if  $c < c^{**}$ , interaction outcome between the species is changed to competition (- -). The biological reason is that the positive effect from  $Y$  to  $X$  is larger than the negative effect. If  $c = c^{**}$ , interaction outcome between the species is changed to amensalism (0 -). If  $c > c^{**}$ , interaction outcome between the species is parasitism (+ -). The biological reason is that the positive effect from  $Y$  to  $X$  is equal to or less than the negative effect. Since species  $X$  goes extinct in the absence of facilitation, it is the the strong facilitation from  $Y$  that results in its persistence.

Furthermore, when the facilitation is extremely strong ( $c \rightarrow \infty$ ), we have  $y^* \rightarrow 0$  by (7), which implies that species  $Y$  goes extinct and  $X$  approaches its carrying capacity. Then interaction outcome between the species becomes amensalism (0 -). The biological reason is that an extremely strong facilitation from species  $Y$  would

result in rapid growth of species  $X$ , which leads to extinction of  $Y$  because there is spatial competition between them. Since species  $Y$  can persist alone, it is the extremely strong facilitation from  $Y$  that leads to the extinction of itself.

**4.2. Transition with parameter  $d_1$ .** Since parameter  $d_1$  represents the effect of environmental conditions on the mortality rate of species  $X$ , it plays an important role in transitions of interaction outcomes from the viewpoint of biology. For simplicity, we assume that  $c$  and  $d_2$  are fixed. If  $c$  and  $d_2$  vary with environmental conditions, a similar discussion can be given.

Denote

$$d_1^* = d_2[1 + c(1 - d_2)].$$

Then  $c < c^*$  can be rewritten as  $d_1 > d_1^*$ .

*First*, we consider the case of  $d_1 \geq 1$ , which implies that species  $X$  cannot persist in the absence of  $Y$ . As shown in Theorem 3.2(i) and Fig. 3a, when  $d_1$  is large ( $d_1 \geq \max\{1, d_1^*\}$ ), species  $X$  goes extinct and  $Y$  approaches its carrying capacity, while interaction outcome between the species is neutralism (0 0). The biological reason is that the mortality of  $X$  is so large that the facilitation from species  $Y$  cannot drive  $X$  into survival.

However, as shown in Theorem 3.2(i) and Fig. 3b, when  $d_1$  is intermediate ( $1 \leq d_1 < d_1^*$ ), species  $X$  and  $Y$  coexist at a steady state  $(x^*, y^*)$  and the interaction outcome is parasitism (+ -). The biological reason is that the facilitation from species  $Y$  decreases the mortality of  $X$ , which leads to the survival of  $X$ . Since species  $X$  cannot survive alone, an intermediate mortality can be decreased by the facilitation of species  $Y$ , which can lead to the survival of  $X$ .

*Second*, we consider the case of  $d_1 < 1$ , which means that species  $X$  can survive alone. When  $d_1 > d_2$  and  $d_1 \geq d_1^*$ , Theorem 3.2(ii) exhibits that species  $X$  goes extinct and interaction outcome between the species is amensalism (- 0). The biological reason is that the low mortality of  $Y$  leads to an advantage of  $Y$  over  $X$  in spatial competition under the large mortality of  $X$ . Since species  $X$  can survive alone, it is the large mortality that results in its extinction in the competition with  $Y$ .

However, if  $d_2 < d_1 < d_1^*$ , Theorem 3.2(ii) and Fig. 3c show that the species coexist at a steady state  $(x^*, y^*)$  and the interaction outcome between the species is competition (- -). The biological reason under the coexistence is that although the low mortality of  $Y$  leads to an advantage of  $Y$  over  $X$ , the strong facilitation from  $Y$  to  $X$  decreases the mortality of  $X$ , which results in a balance between its positive and negative effects on  $X$ . Since species  $X$  with large mortality ( $d_1 \geq d_1^*$ ) goes extinct in the competition with species  $Y$ , it is the intermediate mortality that makes the facilitation from  $Y$  to drive  $X$  into persistence.

As shown in Theorem 3.2(ii) and Fig. 3d, when  $d_1 \leq d_2$ , species  $Y$  would be driven into extinction by  $X$  and the interaction outcome between the species is amensalism (0 -). The biological reason is that the low mortality of  $X$  and facilitation from  $Y$  leads to an advantage of  $X$  over  $Y$  in spatial competition. Since species  $Y$  can survive alone, it is the low mortality of  $X$  that results in the extinction of  $Y$  in the spatial competition with  $X$ .

**Remark 1.** Transition of interaction outcomes can be shown by the bifurcation diagram in Fig. 4. Here, we fix  $r_1 = r_2 = 1, d_2 = 0.2$ . Then

$$c^* = \frac{25}{4}(d_1 - 0.2), \quad c^{**} = 5.$$

The lines  $d_1 = 0.2$ ,  $d_1 = 1.0$ ,  $c = c^*$  and  $c = c^{**}$  divide the first quadrant of  $d_1 - c$  plane into 6 regions. In the region  $d_1 \leq 0.2$ , the interaction outcome remains amensalism (0 -). In the regions  $0.2 < d_1 < 1.0$ , the interaction outcome changes from amensalism (- 0), to competition (- -), to the other amensalism (- 0) and to parasitism (+ -) in a smooth fashion when the facilitation  $c$  increases. Even on the line  $d_2 = 1$ , the interaction outcome changes from neutralism (0 0) to parasitism (+ -) as  $c$  increases. Similarly, in the regions  $d_1 > 1.0$ , the interaction outcome changes from neutralism (0 0) to parasitism (+ -) in a smooth fashion when the facilitation  $c$  increases.

**5. Discussion.** In this paper, we consider a lattice gas model describing facilitation-competition systems. Global dynamics of the model demonstrate mechanisms by which facilitation can lead to persistence/extinction of species.

The facilitation in our discussion from species  $Y$  (*C. mitella*) to  $X$  (*S. virgatus*) is observed in real situations since *C. mitella* decreases the washing-away rate of *S. virgatus* [12]. Thus the presence of species  $Y$  is crucial for the persistence of  $X$  when the environmental condition is harsh. Indeed, as shown in Theorem 3.1, when species  $X$  cannot survive under a harsh environmental condition ( $d_1 \geq 1$ ), the facilitation provided by species  $Y$  would drive it into persistence if the facilitation is sufficient ( $c > c^*$ ). However, an extremely large facilitation from species  $Y$  would result in extinction of both species as discussed in Section 4.1. Moreover, when both species can survive under the harsh environmental conditions ( $d_1 < 1$  and  $d_2 < 1$ ), an extremely large facilitation from species  $Y$  would result in extinction of species  $Y$  itself, as discussed in Section 4.1.

While we focus on mortality rates  $d_1$  and  $d_2$  in Section 4, a similar discussion can be given for birth rates. The reason is that from (5) and (8), we have

$$d_1 = \bar{m}_X/B_X, \quad d_2 = m_Y/B_Y, \quad c^* = (d_1 - d_2)/[(1 - d_2)d_2]$$

in which the birth rates  $B_X$  and  $B_Y$  are included in expressions of  $d_1$  and  $c^*$ . For example, when the birth rate of species  $X$  is low under a harsh environmental condition ( $B_X \leq \bar{m}_X$ ), species  $X$  cannot survive alone. However, when the facilitation is sufficient ( $c > c^*$ ), species  $X$  would be driven into persistence as shown in Theorem 3.1.

Numerical simulations validate the results in this paper. Here, we let  $r_1 = r_2 = 1$ . In Fig. 1, we fix  $d_1 = 1$ ,  $d_2 = 0.1$ , and let  $c$  vary. Thus, species  $X$  cannot survive in the absence of  $Y$ , which is discussed in Theorem 3.1. As shown in Figs. 1a-b, when the facilitation from species  $Y$  is not sufficient ( $c = 6, 10 \leq 10 = c^*$ ), species  $X$  goes extinct and  $Y$  approaches its carrying capacity 0.9. As shown in Figs. 1c-d, when the facilitation is sufficient ( $c = 15, 90 > c^*$ ), species  $X$  and  $Y$  coexist at steady states (0.3, 0.6) and (0.8, 0.0995), respectively. Fig. 1d also predicts the tendency of extinction of species  $Y$  when the facilitation is extremely large.

In Fig. 2, we fix  $d_2 = 0.1$ , and let  $d_1 (< 1)$  and  $c$  vary. Thus, species  $X$  can survive in the absence of  $Y$ , which is discussed in Theorem 3.2. As shown in Figs. 2a-b, when  $d_1 = 0.08, 0.1 \leq d_2$ , species  $Y$  goes extinct and  $X$  approaches its carrying capacity 0.92. As shown in Fig. 2c, when  $d_1 = 0.2 > d_2$  and the facilitation is not sufficient ( $c = 1 < 1.11 = c^*$ ), species  $X$  goes extinct and  $Y$  approaches its carrying capacity 0.9. As shown in Fig. 2d, when  $d_1 = 0.2 > d_2$  and the facilitation is sufficient ( $c = 20 > 1.11 = c^*$ ), species  $X$  and  $Y$  coexist at a steady state (0.85, 0.049). Fig. 2d also predicts the tendency of extinction of species  $Y$  when the facilitation is extremely large.

In Fig. 3, we fix  $d_2 = 0.1, c = 20$ , and let  $d_1$  vary. As shown in Fig. 3a, when  $d_1 = 2 > d_2$  and  $c = 20 < 21.11 = c^*$ , species  $X$  goes extinct and  $Y$  approaches its carrying capacity 0.9. As shown in Fig. 3b, When  $d_1 = 1.1 > d_2$  and  $c = 20 > 11.11 = c^*$ , the species coexist at a steady state (0.4, 0.5). As shown in Fig. 3c, when  $d_1 = 0.2 > d_2$  and  $c = 20 > 1.11 = c^*$ , the species coexist at a steady state (0.85, 0.048) and species  $Y$  approaches a density extremely less than its carrying capacity 0.9. As shown in Fig. 3d,  $d_1 = 0.08 < d_2$ , species  $Y$  goes extinct and  $X$  approaches its carrying capacity.

The difference between our work and that by Yokoi et al. [12] is as follows. First, we show boundedness of solutions and nonexistence of periodic orbits of system (4) which leads to global dynamics of the system, while Yokoi et al. [12] focused on local stability analysis of equilibria. Second, we give a complete analysis on model (4) including critical situations such as  $d_1 = 1$  and  $c = c^*$ , which are not shown by Yokoi et al. [12]. Finally, we display five interaction outcomes in system (4) such as competition (– –), amensalism (0 –), amensalism (– 0), neutralism (0 0) and parasitism (+ –), while Yokoi et al. [12] exhibited two outcomes of competition (– –) and parasitism (+ –). Here, parasitism (+ –) corresponds to the commensalism defined by Yokoi et al. [12] since they considered the facilitation from  $Y$  to  $X$ , but did not include spatial competition in their definition.

Because there is no real data, it is difficult to check that variation of parameters could result in persistence/extinction of species. However, we can see that in some situations, dynamics of the model and ecological phenomena are consistent. For example, in the facilitation-competition system of and as mentioned in Section 1, the simulations shown in Fig. 2d displays that species  $X$  can approach a density higher than its carrying capacity in the absence of  $Y$ . Thus, this model might be helpful in the study of facilitation-competition system like *S. virgatus* and *C. mitella*. While the model is simple, its dynamics demonstrate essential features of facilitation-competition interactions, which may be useful for understanding the complexity of facilitation-competition systems in real situations.

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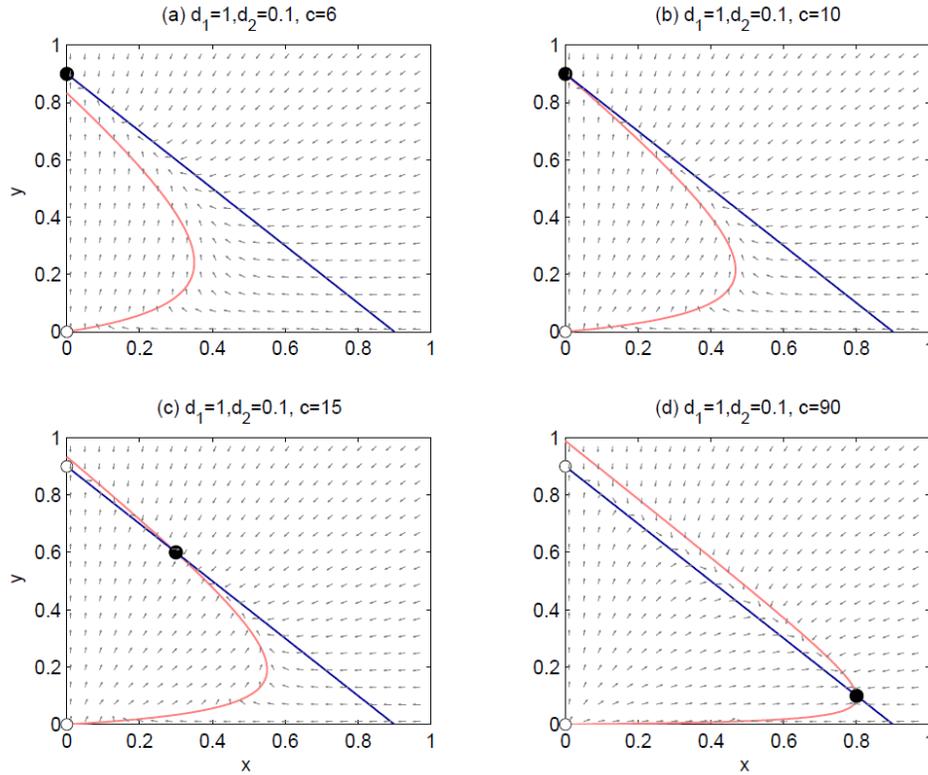


FIGURE 1. Phase-plane diagrams of (4) with  $d_1 \geq 1$ . Red and blue lines are the isoclines for  $x$  and  $y$ , respectively. Grey arrows display the direction and strength of the vector fields in the phase-plane space. Fix  $r_1 = r_2 = 1$ ,  $d_1 = 1$ ,  $d_2 = 0.1$  and let the facilitation  $c$  vary. (a-b) When  $c(= 6, 10)$  is small, species  $X$  goes to extinction and  $Y$  approaches its carrying capacity. (c) When  $c(= 15)$  is large, the species coexist. (d) When  $c(= 90)$  is very large, the species coexist and species  $Y$  approaches a density extremely less than its carrying capacity.

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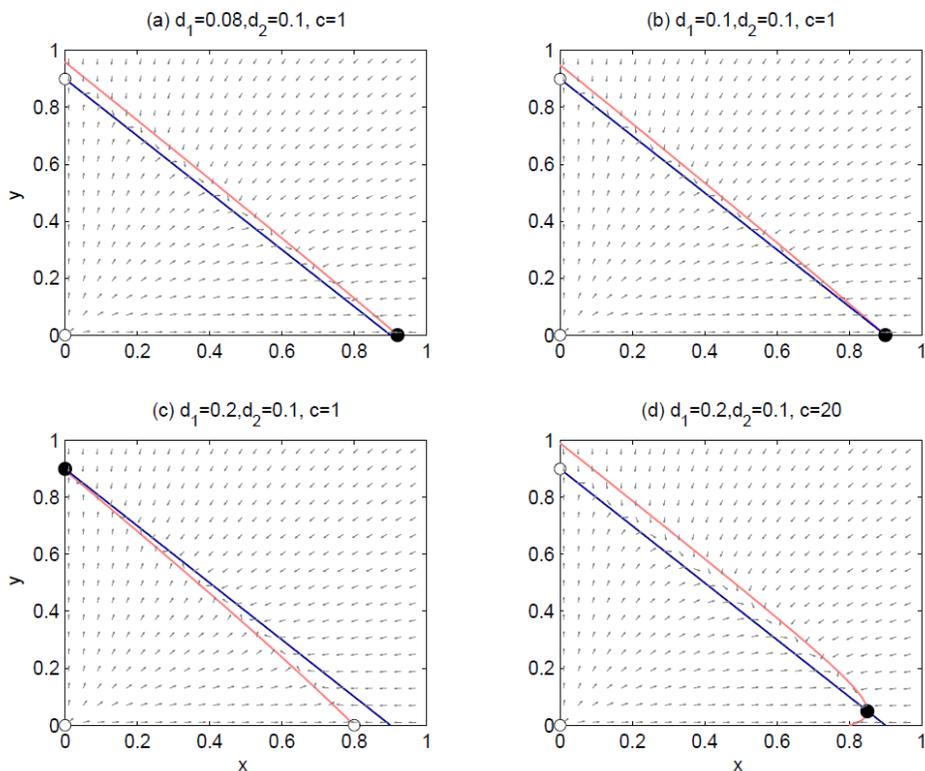


FIGURE 2. Phase-plane diagrams of (4) with  $d_1 < 1$ . Red and blue lines are the isoclines for  $x$  and  $y$ , respectively. Grey arrows display the direction and strength of the vector fields in the phase-plane space. Fix  $r_1 = r_2 = 1, d_2 = 0.1$  and let  $d_1$  and  $c$  vary. (a-b) When  $d_1 = 0.08, 0.1$  and  $c = 1$ , species  $Y$  goes to extinction and  $X$  approaches its carrying capacity. (c) When  $d_1 = 0.2$  and  $c = 1$ , species  $X$  goes to extinction and  $Y$  approaches its carrying capacity. (d) When  $d_1 = 0.2$  and  $c = 20$ , the species coexist.

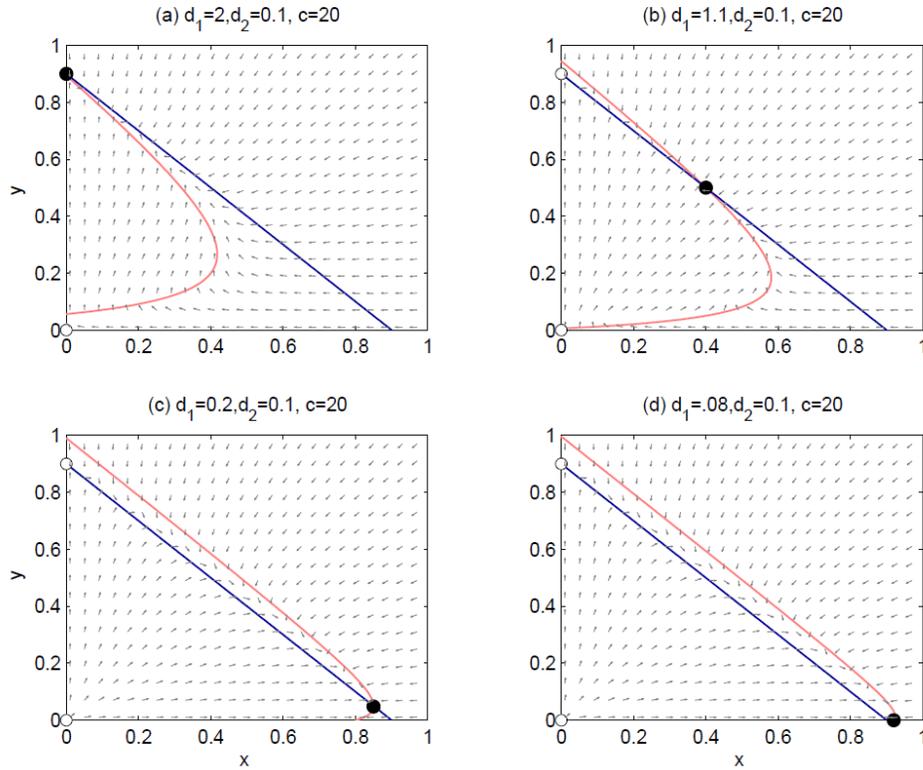


FIGURE 3. Phase-plane diagrams of (4) when the mortality  $d_1$  varies. Red and blue lines are the isoclines for  $x$  and  $y$ , respectively. Grey arrows display the direction and strength of the vector fields in the phase-plane space. Fix  $r_1 = r_2 = 1, d_2 = 0.1, c = 20$ . (a) When  $d_1 (= 2)$  is large, species  $X$  goes to extinction and  $Y$  approaches its carrying capacity. (b) When  $d_1 (= 1.1)$  is intermediate, the species coexist. (c) When  $d_1 (= 0.2)$  is small, the species coexist and species  $Y$  approaches a density extremely less than its carrying capacity. (d) When  $d_1 (= 0.08)$  is extremely small, species  $Y$  goes to extinction and  $X$  approaches its carrying capacity.

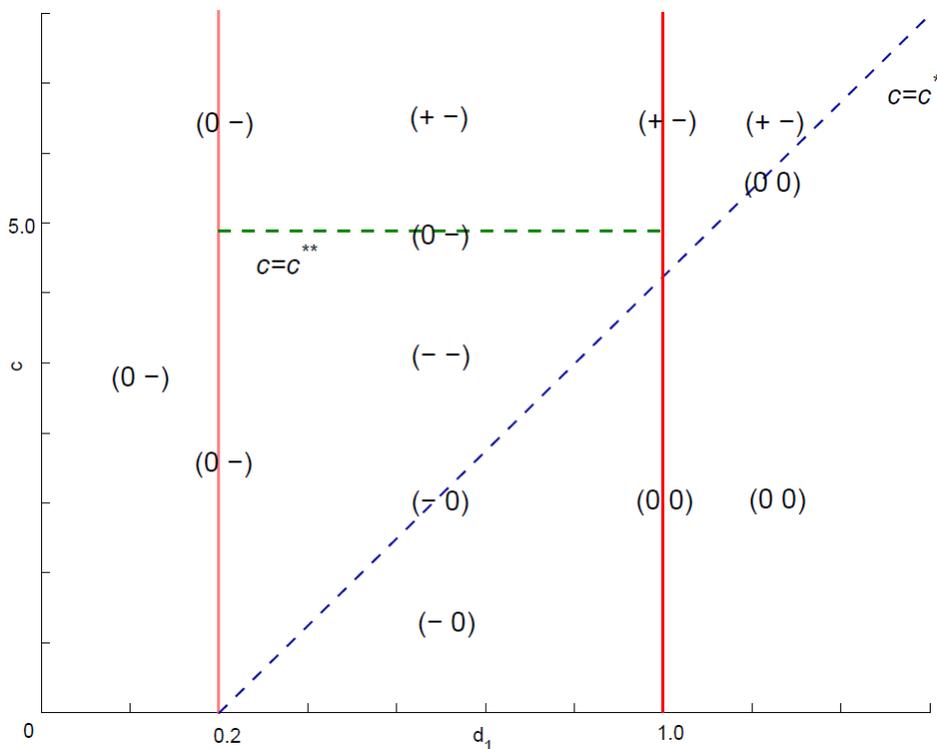


FIGURE 4. Bifurcation diagram of system (4) on the  $d_1 - c$  plane. Fix  $r_1 = r_2 = 1, d_2 = 0.2$ . Then lines  $d_1 = 0.2, d_1 = 1.0, c = 6.25(d_1 - 0.2)$  and  $c = 5$  divide the first quadrant into 6 regions. In the region  $d_1 \leq 0.2$ , the interaction outcome remains amensalism  $(0 -)$ . In the regions  $0.2 < d_1 < 1.0$ , the interaction outcome changes from amensalism  $(- 0)$ , to competition  $(- -)$ , to the other amensalism  $(- 0)$  and to parasitism  $(+ -)$  in a smooth fashion when the facilitation  $c$  increases. Similarly, in the regions  $d_1 \geq 1.0$ , the interaction outcome changes from neutralism  $(0 0)$  to parasitism  $(+ -)$  in a smooth fashion when the facilitation  $c$  increases.