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A simple population theory for mutualism by the use of lattice gas model

Shigehide Iwata[1], Kazuyuki Kobayashi[2], Shinichiro Higa[2], Jin Yoshimura[2,3,4] and Kei-ichi Tainaka[2]*

[1]Bluefin Tuna Resources Division, National research institute of far seas fisheries, 5-7-1 Orito, Shimizu-ku, Shizuoka, Shizuoka, 424-8633, Japan

[2]Department of Systems Engineering, Shizuoka University, 3-5-1 Johoku, Naka-ku, Hamamatsu 432-8561, Japan

[3]Marine Biosystems Research Center, Chiba University, 1 Uchiura, Kamogawa 299-5502, Japan.

[4]Department of Environmental and Forest Biology, State University of New York College of Environmental Science and Forestry, Syracuse, New York 13210, USA.

*Corresponding author: Kei-ichi Tainaka (tainaka@sys.eng.shizuoka.ac.jp)

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Abstract

The population dynamics of species interactions provides valuable information for life sciences. Lotka–Volterra equations (LVEs) are known to be the most popular model, and they are mainly applied to the systems of predation and competition. However, LVEs often fail to catch the population dynamics of mutualism; the population sizes of species increase infinitely under certain condition (divergence problem). Furthermore, LVEs never predicts the Allee effect in the systems of obligate mutualism. Instead of LVEs, several models have been presented for mutualism; unfortunately, they are rather complicated. It is, therefore, necessary to introduce a simpler theory for mutualism. In the present paper, we apply the lattice gas model which corresponds to the mean-field theory of the usual lattice model. The derived equations are cubic and contain only essential features for mutualism. In the case of obligate mutualism, the dynamics exhibits the Allee effect, and it is almost the same as in the male-female systems. In our model, the population sizes never increase infinitely, because our model contains not only intra- but also inter-specific competitions. If the density of one species increases disproportionately in respect of its mutual partners, then this might imply downward pressure on the population abundance of the mutual partner species and such feedback would eventually act as a controlling influence on the population abundance of either species. We discuss several assumptions in our model; in particular, if both species can occupy in each cell simultaneously, then the interspecific competition disappears.

1. Introduction

All species on the earth are closely related to other species. In a simple view, the interaction between a pair of species can be classified into three typical categories: predation (one gains and the other suffers: " + , − "), competition (− , −) and mutualism (+ , +) (Begon et al.2006). In recent years, the concern for mutualism is growing, since most of the World's biomass is dependent on mutualism (e.g., Pellmyr and Huth 2002; Bashary and Bronstein 2004; Begon et al. 2006). For example, microbial species influence on the abundances and ecological functions of related species (Madigan et al. 2000; Keller and Surette 2006; Goto et al. 2010). Many bacterial species coexist in a syntrophic association (obligate mutualism); that is, one species lives off the products of another species. So far, mathematical models for mutualisms have often been neglected in many ecological textbooks.

The most famous model of population dynamics is a series of Lotka-Volterra equations (LVEs) (e.g., Lotka 1925;Volterra 1926;Takeuchi 1996; Hofbauer and Sigmund 1998). In many textbooks, LVEs are referred as basic models for both predation and competition. When LVEs were applied to mutualism, they were given by

$$\frac{dx}{dt} = r_X x(K_X - x + \alpha_Y y)/K_X , \tag{1a}$$

$$\frac{dy}{dt} = r_Y y(K_Y - y + \alpha_X x)/K_Y \tag{1b}$$

where x and y indicate the population sizes (densities) of symbiotic species X and Y, respectively, and r_j K_j, α_j are parameters ($j = X, Y$). It is known that the positive stable equilibrium exists, only when $\alpha_X \alpha_Y < 1$ (Takeuchi 1996). However, if $\alpha_X \alpha_Y > 1$, the population sizes of both x and y increase infinitely ("divergence problem"). Moreover, LVEs never predict Allee effects for obligate mutualism. These problems can be avoided by several models (Wright 1989; Doebeli 2002; Tainaka et al. 2003; Hammerstein, 2003; Amarasekare 2004; Courchamp et al. 2008; Holland and DeAngelis 2010). However, these models are rather complicated; they use fractional equations or nonlinear equations of higher order; not only the analytic solutions are difficult to obtain, but also the resultant solutions are difficult to interpret. In order to understand the basic features of mutualism, it is necessary to build a simpler mathematic model.

The Allee effect has been first introduced for a single species by W. C. Allee

(Allee 1930). His main interest was the influence of density on population dynamics, especially in aquatic organisms. When the population size of a species becomes below a critical number, the risk of extinction increases drastically. Such a threshold effect is termed Allee effect (Odum 1953; Courchamp et al. 2008). Since his pioneering work, many ecologists studied the Allee effect (Lamont et al. 1993; Groom 1998; Davis et bal. 2002; Angulo et al. 2007; Tanaka et al. 2009; Nariai et al. 2011). The most typical population model for an Allee effect has been represented by

$$\frac{dx}{dt} = Rx(x-a)(b-x) \tag{2}$$

where x indicates the population size of a species, and the parameres R, a and b are positive ($a < b$) (Lewis and Kareiva 1993; Courchamp et al. 2008). Equation (2) has three equilibriums; both $x = 0$ and $x = b$ are stable, while $x = a$ is unstable. The species survives (goes extinct) for $x > a$ ($x \le a$). Hence, the parameter a means a minimum size of viable population and b the stable equilibrium density. Note R is a parameter related to the initial growth rate (discussed later). Our theory for obligate mutualism can derive equation (2) for both species.

In the present paper, we apply "lattice gas model" or "lattice gas automaton" which is a kind of individual-based models on a lattice (Frisch et al. 1986; Dieter 2000; Hagiwara et al. 2011). The lattice gas model (lattice gas automaton) differs from the usual "lattice model". The difference between lattice and lattice gas models lies in the range of interaction: in lattice model, the interaction occurs between adjacent lattice sites ("local interaction"), whereas in lattice gas model it occurs between any pair of lattice sites ("global interaction"). In most cases, the dynamics of lattice models cannot be expressed by mathematical equations. In contrast, that of lattice gas model is usually represented by differential equations that are called the mean-field theory of lattice model. Such equations are served for multiple uses. In order to build a simple mathematical model of mutualism, we here apply the lattice gas model.

In the next section, we review the correspondence relation between lattice and lattice gas models. In ecology, the lattice gas model (mean-field theory of lattice model) usually correspond to LVEs (Tainaka 1988; Matsuda et al. 1992). We apply such a correspondence to mutualism. In section 3, we build a simple lattice gas model for mutualism. In sections 4 and 5, we derive the mean-field theories which are represented by cubic equations. Section 5 is devoted to report the results for obligate mutualism. In section 5, we deal with general cases of mutualism. The phase diagram and typical types

of population dynamics are elucidated.

2. Theoretical Rationale

In recent years, lattice models are widely applied in the field of ecology. On a lattice, simulations are performed under either local or global interactions. In the former case, an interaction occurs between adjacent lattice sites. The latter case is called lattice gas model, where an interaction occurs between any pair of lattice sites.

For simplicity, we first consider a single-species system. It is well known that the most canonical model is the logistic equation (Verhulst 1845). A lattice version of logistic equation is called "contact process" (Harris 1974; Liggett 1985; Konno 1994) which is defined as follows:

$$\mathrm{X} + \mathrm{O} \rightarrow 2\mathrm{X}, \qquad \text{(reproduction rate } r\text{)} \tag{3a}$$

$$\mathrm{X} \rightarrow \mathrm{O} \qquad \text{(mortality rate } m\text{)} \tag{3b}$$

where X denotes an individual of a species (or the site occupied by a species), and O is the empty site. The first (second) reaction means the birth (death) processes of X. In the lattice model, the first reaction occurs between adjacent lattice sites. In the lattice gas model, it occurs between any pair of sites, and its dynamics can be represented by the following rate equation:

$$\frac{dx}{dt} = rx(1-x) - mx\,, \tag{4}$$

where x and $(1-x)$ are the densities of species and empty sites, respectively. The first and second terms in the right hand side come from the birth and death processes. Equation (4) can be rewritten by the logistic equation $dx/dt = Rx(1-x/K)$, where $R = r - m$ and $K = r/(r-m)$.

For two-species system, the lattice version of Lotka-Volterra models have been studied by several authors (Satulovsky and Tome 1994; Nakagiri et al. 2001). A typical lattice version of prey-predator system has been introduced as follows (Tainaka and Fukazawa 1992):

$$\mathrm{X} + \mathrm{Y} \rightarrow 2\mathrm{Y}, \quad \mathrm{X} + \mathrm{O} \rightarrow 2\mathrm{X}, \quad \mathrm{Y} \rightarrow \mathrm{O}$$

where X and Y denote prey and predator, respectively. The above reactions represent

the predation of Y, reproduction of X, and death of Y, in order. The mean-field theory corresponds to LVEs in prey-predator system with density effect. Similarly, lattice versions of competition system have been presented by several authors (Matsuda et al. 1992; Neuhauser 1992; Tainaka et al. 2004; Kawai et al. 2008). Their mean-field theories correspond to the LVEs of competition. Hence, it is expected that a canonical theory for mutualism can be derived from a canonical lattice gas model.

3. Model

Let us consider a system consisting of two species X and Y. Each lattice site is labeled by X, Y or O, where O means the empty site. The reactions are defined by

$$\mathrm{X} + \mathrm{O} \rightarrow 2\,\mathrm{X}, \qquad (\text{rate } B_X) \tag{5a}$$

$$\mathrm{Y} + \mathrm{O} \rightarrow 2\,\mathrm{Y}, \qquad (\text{rate } B_Y) \tag{5b}$$

$$\mathrm{X} \rightarrow \mathrm{O} \qquad (\text{rate } m_X) \tag{5c}$$

$$\mathrm{Y} \rightarrow \mathrm{O} \qquad (\text{rate } m_Y) \tag{5d}$$

where the reactions (5a) and (5c) respectively denote the birth and death processes of species X, and B_X (m_X) denotes the birth (mortality) rate of species X. Similarly, the reactions (5b) and (5d) have the same meanings for species Y. The birth rates should be indicated as follows:

$$B_X = r_X + \varepsilon_X y \tag{6a}$$

$$B_Y = r_Y + \varepsilon_Y x \tag{6b}$$

where x (y) is the density of species X (Y). The parameters r_X and r_Y are the reproduction rates without the other species, and ε_X and ε_Y denote mutualistic effects on the reproduction rates. Hence, the birth rate of one species increases with the density of the other species. If species Y is absent, then the reaction (5) is equivalent to the contact process [the reaction (3)]. In the limiting case $(\varepsilon_X, \varepsilon_Y) \rightarrow (0,0)$, the system (5) becomes a competition model called "multiple contact process" (Neuhauser 1992). In this case, two species cannot coexist; because of reaction (5a), both species compete with each other to get empty sites (exploitative competition).

We explain the simulation procedure of lattice gas model for mutualism. Reaction processes are performed in the following two steps:

i) Two lattice sites are chosen randomly and independently. The pair sites obey the

reaction (5a). For example, if chosen sites are X and O, then the site O will become X by the rate B_X defined by equation (6a).

ii) Next, we perform reaction (5b). Choose one lattice point randomly; if the point is occupied by X (or Y), then it becomes O by the rate m_X (or m_Y).

We repeat above steps i) and ii) until the system reaches a stationary state. It is emphasized that the reaction (5a) occurs between any pair of lattice sites.

4. Theory for Obligate Mutualism

4. 1. Basic equations for mutualism

We carry out simulations for lattice gas model. The simulation results agree with the predictions of mean-field theory (rate equation), if the lattice size is sufficiently large. The population dynamics of lattice gas model for reaction (5) is described by

$$\frac{dx}{dt} = B_X(1-x-y)x - m_X x, \tag{7a}$$

$$\frac{dy}{dt} = B_Y(1-x-y)y - m_Y y, \tag{7b}$$

where the factor $(1-x-y)$ in the right hand sides denotes the density of empty site. The first and second terms in equation (7) come from birth and death processes, respectively. In this case the divergence problem can be avoided, because the growth factors in (7) need the density of empty site. This means the effect of carrying capacity: both species compete to take the limited resources (empty sites).

4. 2. Population model for obligate mutualism

Let us consider typical case of obligate mutualism. For simplicity, we put $r_X = 0$ and $r_Y = 0$. In this case, each species cannot survive without the other species. Inserting these relations and equation (6) into equation (7), we have

$$\frac{dx}{dt} = \varepsilon_X y(1-x-y)x - m_X x, \tag{8a}$$

$$\frac{dy}{dt} = \varepsilon_Y x(1-x-y)y - m_Y y. \tag{8b}$$

This is a basic model for obligate mutualism. Note that equation (8) is the same as in the

male-female system presented by Tainaka et al. (2007), and it is very similar to the equations presented by Berec et al. (2001). Hereafter, we deal with equation (8) in two cases: i) $m_X = m_Y$ and ii) $m_X \neq m_Y$.

4. 3. Case for $m_X = m_Y$

Tainaka et al. (2007) has derived Allee equation (2) for the special case that $m_X = m_Y$ ($= m$). We briefly explain their procedures. Equation (8) has both fast and slow dynamics. Insert $z = B_X - B_Y$ into (8), then we have $dz/dt = \varepsilon_X dy/dt - \varepsilon_Y dx/dt = -mz$. This is the fast dynamics, and z rapidly approaches zero. Namely, the relation $\varepsilon_X y \approx \varepsilon_Y x$ is rapidly satisfied. Inserting this relation into equation (8a), we get the slow dynamics as follows:

$$\frac{dx}{dt} = \varepsilon_Y (1 - x - y)x^2 - mx \quad . \tag{9}$$

This equation is formally rewritten as

$$\frac{dx}{dt} = \varepsilon_Y x(x - x_-)(x_+ - x), \tag{10}$$

where the parameters x_+ and x_- are given by

$$x_\pm = \frac{1 \pm \sqrt{1 - 4D_m m/\varepsilon_Y}}{2D_m} \quad , \quad D_m = 1 + \varepsilon_Y / \varepsilon_X$$

When $x_\pm$ are real, or when $\varepsilon_X \varepsilon_Y > 4(\varepsilon_X + \varepsilon_Y)m$, then equation (10) becomes equivalent to equation (2); the dynamics thus exhibits the Allee effect. On the contrary, when $\varepsilon_X \varepsilon_Y < 4(\varepsilon_X + \varepsilon_Y)m$, there is no survival equilibrium: both species always go extinct. In summary, basic equation (8) has two phases. One is an extinction phase: both species always go extinct. The other is the Allee-effect phase represented by equation (2). Here the phase boundary is represented by

$$\varepsilon_X \varepsilon_Y = 4(\varepsilon_X + \varepsilon_Y)m . \tag{11}$$

4. 4. Case for $m_X \neq m_Y$

Next, we consider a general case for obligate mutualism; that is $m_X \neq m_Y$. We put

$$\frac{dx}{dt} = \varepsilon_X y(1 - x - y)x - m_X x = f_X(x, y)x , \tag{12a}$$

$$\frac{dy}{dt} = \varepsilon_Y x(1 - x - y)y - m_Y y = f_Y(x, y)y . \tag{12b}$$

Applying the quasi steady state approximation (Segel, 1988; Borghans et al., 1996), we have the following slow dynamics:

$$f_X(x,\hat{y}) = (x-\alpha)(-x+\beta) \Bigg/ \left\{ \frac{\varepsilon_y}{m_y \varepsilon_x} \left(1 + \frac{m_x \varepsilon_Y}{m_y \varepsilon_x} \right) x^2 \right\} \quad , \tag{13}$$

where y satisfy $f_Y(x,y)=0$, that is

$$y = 1 - x - {m_Y}/{\varepsilon_Y x} \quad . \tag{14}$$

The parameters α and β are the roots of the following quadratic equation ($\alpha < \beta$):

$$\{-({m_X}^2+1)x^2 + x - {m_Y}^2\}/({m_X}^2+1) = 0$$

The denominator of equation (13) is always positive, so that equation (13) also exhibits the Allee effect (Allee et al. 1949; Stephens et al. 1999; Amaraskare 2004). Namely, $f_X(x,y)>0$ holds, if $\alpha < x < \beta$. In contrast, $f_X(x,y)<0$ holds, if $0<x<\alpha$ or $\beta > x$. Thus, $x=\alpha$ means the threshold density. In Table 1, the values of equilibriums and the conditions for both existence and stability are listed.

In Fig. 1, a typical phase diagram is displayed. There are two phases A and B. In phase A, both species always go extinct. On the other hand, phase B exhibits the Allee effect (survival/extinction phase). The condition for the phase boundary is represented by

$$\frac{1}{4} = \frac{m_X}{\varepsilon_X} + \frac{m_Y}{\varepsilon_Y} \tag{15}$$

(see case 2 in Table 1). This is a generalized expression of equation (11). Typical population dynamics are illustrated in Fig. 2, where Fig. 2(a) and (b) correspond to phases A and B, respectively. In Fig. 2(b), each orbit is roughly composed of both fast and slow dynamics; the orbit is immediately attracted to the line connecting three equilibriums (fast dynamics), and then the orbit is gradually attracted into one of two stable equilibriums (slow dynamics). It should be emphasized that the results described here include all profiles in subsection 4.3 (case $m_X = m_Y$).

5. General cases for mutualism

5. 1. Basic equation

We start from basic equation (7) for $r_X \neq 0$ and $r_Y \neq 0$. Let us substitute the following parameters into equation (7):

$$\frac{m_X}{r_X} = m_1 \quad , \quad \frac{m_Y}{r_Y} = m_2 \quad , \quad \frac{\varepsilon_X}{r_X} = \varepsilon_1 \quad , \quad \frac{\varepsilon_Y}{r_Y} = \varepsilon_2 . \tag{16}$$

Then equation (7) will be reduced as

$$\frac{dx}{dt} = r_x \{ -m_1 + (1+\varepsilon_1 y)(1-x-y) \} x \quad , \tag{17a}$$

$$\frac{dy}{dt} = r_y \{ -m_2 + (1+\varepsilon_2 x)(1-x-y) \} y \quad , \tag{17b}$$

where the coefficients ε_1 and ε_2 are the measures of "relative mutualistic strength" for the reproduction rate. This is because mutualistic interaction becomes strong, if ε_j takes a large value. Now let us consider the characteristics of basic equation (17). We define $f_x(x,y)$ and $f_y(x,y)$ by

$$\frac{dx}{dt} \equiv f_x(x,y)x , \quad \frac{dy}{dt} \equiv f_y(x,y)y . \tag{18}$$

The equation (17) include the meaning of intra-specific competition, because

$$\partial f_x / \partial x = -(1+\varepsilon_1 y) < 0 , \tag{19a}$$

$$\partial f_y / \partial x = -(1+\varepsilon_2 y) < 0 \tag{19b}$$

Both species do not always gain merits with each other. From equations (17), we have

$$\partial f_x / \partial y = \varepsilon_1 (1-x-y) - (1+\varepsilon_1 y) , \tag{20a}$$

$$\partial f_y / \partial x = \varepsilon_2 (1-x-y) - (1+\varepsilon_2 x) . \tag{20b}$$

When $\partial f_x(x,y)/\partial y$ is positive, the abundance of species X increases by the existence of species Y. Namely, the species X gains merit from species Y, when y is small. Similarly, the species Y gains merit from X, when x takes a small value. If the population size of both species X and Y becomes large, both inter- and intra-specific competitions become dominant. When all the empty sites are taken, the effective growth rates of both species become zero.

We explore the local stability around the equilibrium. Equation (17) allows the four categories of equilibrium points. Type1: $(x,y)=(0,0)$, where both species go extinct. Type 2 (survival of both species): $(x,y)=(x_{\pm},y_{\pm})$. Type3: $(x,y)=(1-m_1,0)$. In this case, only species X goes extinct. Type 4: $(x,y)=(0,1-m_1)$, where only species Y goes extinct. The important difference from the obligate mutualism is that there are the equilibrium points that one species survives but the other is extinct. The results of stability for these equilibriums are summarized in Table 2.

5. 2. Phase diagram

Phase diagram for equation (17) depends on the values of parameters. In general, there are seven phases. For the simplicity, let's us set $(\varepsilon_1,\varepsilon_2)=(8,8)$. In Fig. 3, the phase diagram is shown. The horizontal axis (resp. vertical axis) represents the death rate $m_1=m_x/r_x$ (resp. $m_2=m_y/r_y$) of species X (resp. Y). With the increase of m_1 (or m_2), the species X (or Y) tends to go extinct. The basic equation (17) has seven phases in population dynamics. In this section, we explain each phase (region) in Fig. 3.

-Region A

In region A, both species always go extinct. There is a stable equilibrium point $(x,y)=(0,0)$ in x-y plain.

-Regions B and C

In region B (resp. C), there are two types of equilibrium points; one is unstable extinction and the other is a stable equilibrium. In the latter case only one species X (resp. Y) survives.

-Region D

Except the coexistence point (x_+,y_+), all the other equilibrium points are unstable (extinction and one species surviving equilibrium points). Furthermore, the stable equilibrium corresponds to the case 1 in Table 2, so that interior

equilibrium exists only (x_+, y_+).

-Region E

In this region, there are two types of equilibrium points. One is the extinction equilibrium which is stable. The other points are interior equilibriums. The point (x_+, y_+) is stable, but (x_-, y_-) is unstable. This phase corresponds to the phase B in Fig. 1. Both species will extinct if the initial densities are smaller than the separatrix (Allee effect).

- Regions F and G

In region F or G, there are four types of equilibrium points. The points respectively mean the extinction of both species (unstable), the survival of only one species (stable), and two coexistence states $(x_\pm, y_\pm)$. The point (x_+, y_+) is stable, but (x_-, y_-) is unstable.

Hence, the case of obligate mutualism is included in general case of equation (17).

Typical population dynamics are shown in Fig. 4. In cases A-D, Allee effect never occurs. In contrast, in the regions E, F and G, we find the Allee effect; the system reaches either the extinction of one species or survival of both species.

Next, we consider the case of weak mutualism. If ε_1 and ε_2 take small values, the phases E, F and G in Fig. 3 disappear. With the decrease of mutualistic strength, the phase diagram in Fig. 3 should be changed; both upper leaves in phase D shrink and combine. In Fig. 5, the phase diagram for $(\varepsilon_1, \varepsilon_2) = (2,2)$ is shown. This figure resembles the phase diagram for competition. In the limiting case $(\varepsilon_1, \varepsilon_2) \to (0,0)$, both species cannot coexist (Neuhauser 1992).

6. Discussions

Even though the most famous model of population dynamics is Lotka-Volterra equations (LVEs), they fail to describe the dynamics incorporating mutualism. In the LVEs with mutualism, the population sizes of species increase infinitely causing divergence. In order to avoid this divergence problem, many authors have proposed various models of mutualisms (e.g., Vandermeer 1978; Goh 1979; Wolin and Lower 1984; Boucher 1985; Hammerstein 2003). However, they are not so simple; they use fractional equations or nonlinear equations of higher order. Due to such mathematical

complications, their analytic solutions are rather difficult and often include some artificial phases or effects not related to mutualistic relationships.

In the present paper, we have applied the lattice gas model, and introduced equation (17) for mutualism or equation (8) for obligate mutualism. In our modeling, the divergence problem is solved simply by the main feature of lattice gas model. The population size of each species never exceeds the total number of lattice sites. Such an idea for carrying capacity is similar to Dean (1983) and Holland et al. (2002). The advantage of our model is the cubic equations which include only mutualistic relations. The previous models also contained all phases in Fig. 3 (see e.g., Wright 1989; Doebeli 2002; Tainaka et al. 2003; Hammerstein, 2003; Amarasekare 2004; Courchamp et al. 2008; Holland and DeAngelis 2010).

The simulation results for lattice gas model agree with the predictions of mean-field theory, when the lattice size is sufficiently large. The basic model [equation (8)] for obligate mutualism predicts two phases (regions A and B) as illustrated in Fig. 1. In the region B, the dynamics exhibits an Allee effect [see Fig 2(b)]; the slow dynamics is represented by the equation (2). Note that equation (8) has the similar behavior as in the male-female systems (Berec et al. 2001; Tainaka et al. 2007). The similarity comes from the fact that one species (male) cannot produce offspring without the other (female).

The generalized model [equation (17)] shows various phases (regions A-G) as illustrated in Figs. 3 and 4. The phase E in Fig. 3 is similar to the phase B for obligate mutualism (Fig. 1). This phase has been predicted by many authors (e.g., Tainaka et al. 2003; Amarasekare 2004; Courchamp et al. 2008). In real systems of obligate mutualism, the Allee effect as shown in Fig. 4(e) can be observed (Amarasekare 2004; Katsuyama et al. 2009). Phases F and G may correspond to the dynamics for commensalism. A concrete example is a two-shellfish (mussel-goose barnacle) system in the upper intertidal zone (Kawai and Tokeshi 2004). The mussel could not survive without goose barnacle, while the latter was not influenced by the presence of mussel. The dynamics of commensalism can be obtained from our model. So far, we omit the cases (i) $r_X = 0$, $r_Y \neq 0$ and (ii) $r_X \neq 0$, $r_Y = 0$. If we take into account these cases, we may obtain both phases F and G.

The previous models contained all phases in Fig. 3 (Wright 1989; Doebeli 2002; Tainaka et al. 2003; Hammerstein, 2003; Amarasekare 2004; Courchamp et al. 2008; Holland and DeAngelis 2010). However, they are not so simple; they use fractional equations or nonlinear equations of higher order. Due to the mathematical complications, the analytic solutions are rather difficult and often include some artificial

phases or effects not related to mutualistic relationships. The advantage of our model is the cubic equations which include only mutualistic relations.

We discuss the relation between mutualism and competition. The basic equation (10) contains the feature of competition [see equation (13)]. Such a competition is originated in the individual-based model. Reactions (5a) and (5b) mean that an individual is created only from an empty site, so that the divergence (infinite population size) never occurs. These reactions contain both inter- and intra-species competitions: individuals compete to take the limited empty sites. When we consider the case that the mutualistic strength is relatively weak (see Fig. 5), then the phase diagram becomes similar to that of competition models. In the cases of small values of ε_1 and ε_2, the phases E, F and G in general case disappear (Fig. 3).

As described in section 4, the degree of competition in our model depends upon the density of partner species. If the density of one species becomes too high, then the other species may receive damages. Such density-dependent competition is very popular in real ecosystems (Addicott 1979; Begon et al. 2006). For example, in a yucca-yucca moth system, too many yucca moths become harmful for yucca plant (Fiegna et al. 2006). Another example is a coral-algae system; when the density of algae is too high, the excess algae are excluded from coral (Rosenberg et al. 2007). Many two-species systems of obligate mutualism have some mechanism to avoid an abrupt increase of one species (Begon et al. 2006).

Finally, we discuss two assumptions in our model. One is the assumption that both species cannot coexist in each site simultaneously. This may be inadequate, especially for obligate mutualism. If we assume that both species can coexist in each cell, then no competition occurs. To prove this, the factor $(1-x-y)$ in equations (8a) and (8b) should be respectively changed by $(1-x)$ and $(1-y)$. Then we have $\partial f_x / \partial y > 0$ and $\partial f_y / \partial x > 0$. Hence, each species always increases with the abundance of the other species. Note that this modification never changes the qualitative properties of phase diagram in Fig. 1 (see Berec et al. 2001). Another assumption in our model is the global interaction. If we precisely explore real systems, the application of local interaction between adjacent sites may be necessary. It is, however, emphasized for local interaction that there is no equation to describe the population dynamics.

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Table 1. The result of stability for obligate mutualism ($r_X = 0$ and $r_Y = 0$)

Equilibrium Points	Existence Conditions	Stability Conditions
(0,0)	always exists	always stable
$(x_{\pm}, y_{\pm})$	Case 1: (x_{+}, y_{+}) $\frac{1}{4} = \frac{m_X}{\varepsilon_X} + \frac{m_Y}{\varepsilon_Y}$ Case 2: $(x_{\pm}, y_{\pm})$ $\frac{1}{4} > \frac{m_X}{\varepsilon_X} + \frac{m_Y}{\varepsilon_Y}$	Case 1: Unstable Case 2: (x_{+}, y_{+}) : stable (x_{-}, y_{-}) : unstable

$x_{\pm} = \frac{1 \pm \sqrt{1 - 4D\frac{m_y}{\varepsilon_y}}}{2D}, y_{\pm} = \frac{m_x \varepsilon_y}{m_y \varepsilon_x} x_{\pm}$ and $\mathrm{D} = 1 + \frac{m_x \varepsilon_y}{m_y \varepsilon_x}$.

Table 2. The result of the local stability analysis in general case

Equilibrium Points	Existence Conditions	Stability Conditions
$(0,0)$	always	$m_1 > 1 \quad and \quad m_2 > 1$
$(1-m_1,0)$	$0 < m_1 < 1$	$M_1 < 0$
$(0,1-m_2)$	$0 < m_2 < 1$	$M_2 < 0$
$(x_\pm, y_\pm)$	Case1: $M_1 > 0 \quad , \quad m_2 > m_1$ or $M_2 > 0 \quad , \quad m_1 > m_2$ Case2: $C_1 < M_1 < 0 \quad , \quad C_2 < M_2 < 0$ $B_1 < 0 \quad , \quad B_2 < 0$	Case1: stable Case2: (x_+^*, y_+^*) : stable (x_-^*, y_-^*) : unstable

$$M_1 = -m_2 + \{1 + \varepsilon_2(1-m_1)\}m_1,$$
$$M_2 = -m_1 + \{1 + \varepsilon_1(1-m_2)\}m_2,$$
$$x_\pm^* = \frac{-B_1 \pm m_2\sqrt{A}}{2\varepsilon_2(\varepsilon_1 m_2 + \varepsilon_2 m_1)}, y_\pm^* = \frac{-B_2 \pm m_1\sqrt{A}}{2\varepsilon_1(\varepsilon_1 m_2 + \varepsilon_2 m_1)},$$

Here

$$A = (\varepsilon_1 + \varepsilon_2 + \varepsilon_1\varepsilon_2)^2 - 4\varepsilon_1\varepsilon_2(\varepsilon_1 m_2 + \varepsilon_2 m_1),$$
$$B_i = 2\varepsilon_j m_i + \{\varepsilon_i - \varepsilon_j(1+\varepsilon_i)\}m_j,$$
$$C_i = (4\varepsilon_j\varepsilon_i^2 - 1)m_j + \{1 + \varepsilon_j(1 - m_i + 4\varepsilon_i\varepsilon_j)\}m_i - (\varepsilon_i + \varepsilon_j + \varepsilon_i\varepsilon_j)^2,$$

and $i, j = 1,2 \quad (i \neq j)$.

Figure Captions

Fig. 1. Phase diagram for obligate mutualism. Model parameters are $\varepsilon_x = \varepsilon_y = 0.8$ and $m_x = m_y = 0.1$. The population dynamics can be categorized into two regions. The boundary is given by equation (15). Both species go extinct in region A, while an Allee effect can be observed in region B.

Fig. 2. Typical dynamics for obligate mutualism. The thin curves denote the orbits calculated from equation (8) by the use of Mathematica. The orbits start from various initial densities, and reach the stable equilibriums as symbolically represented by thick arrows.

Fig. 3. Phase diagram for general case: equation (17). The population dynamics can be categorized into seven regions (from A to G). The values of mutualistic strengths are set $(\varepsilon_1, \varepsilon_2) = (8,8)$.

Fig. 4. Typical population dynamics for mutualism. The curves and arrows have the same meaning as in Fig. 2.

Fig. 5. Same as Fig. 3, but the mutualistic strengths take small values: $(\varepsilon_1, \varepsilon_2) = (2,2)$. The phases A-D are the same as in Fig. 3.

Fig. 1

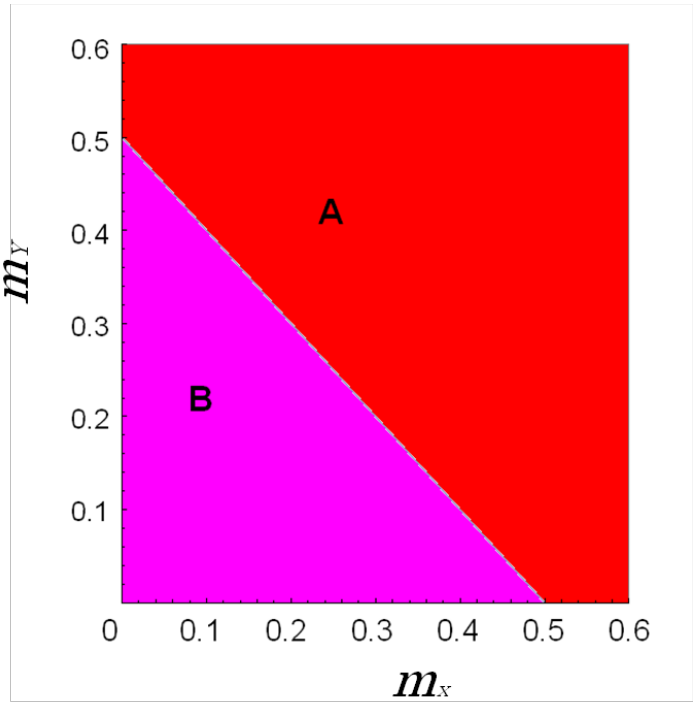


Fig. 2

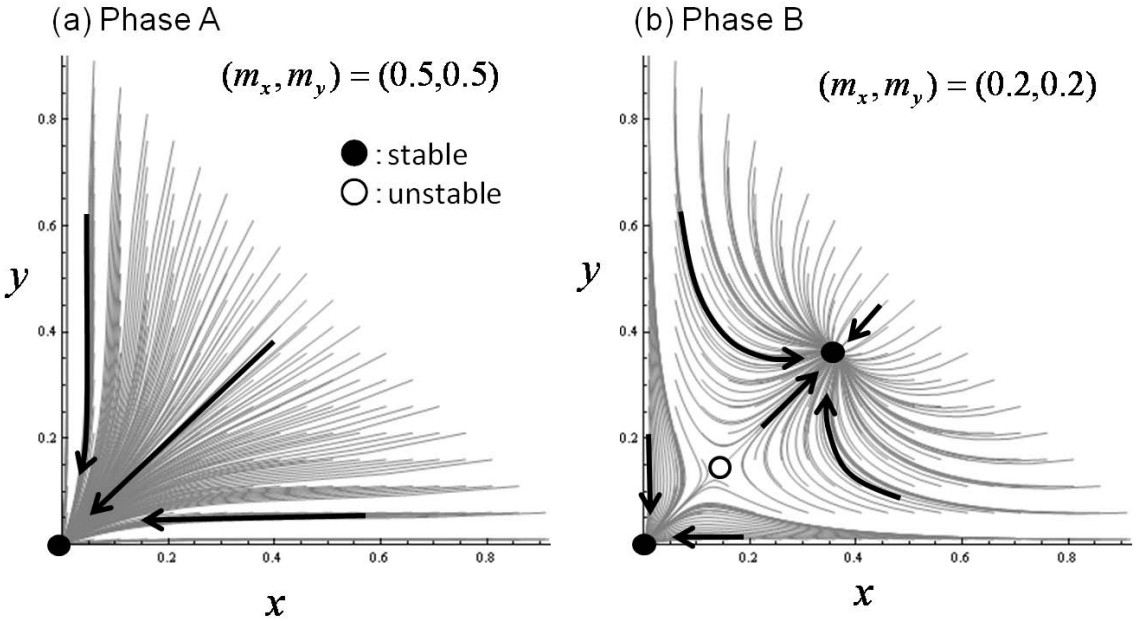

(a) Phase A
$(m_x, m_y) = (0.5, 0.5)$
: stable
: unstable
y
x
0.2
0.4
0.6
0.8
(b) Phase B
$(m_x, m_y) = (0.2, 0.2)$
y
x
0.2
0.4
0.6
0.8

Fig. 3

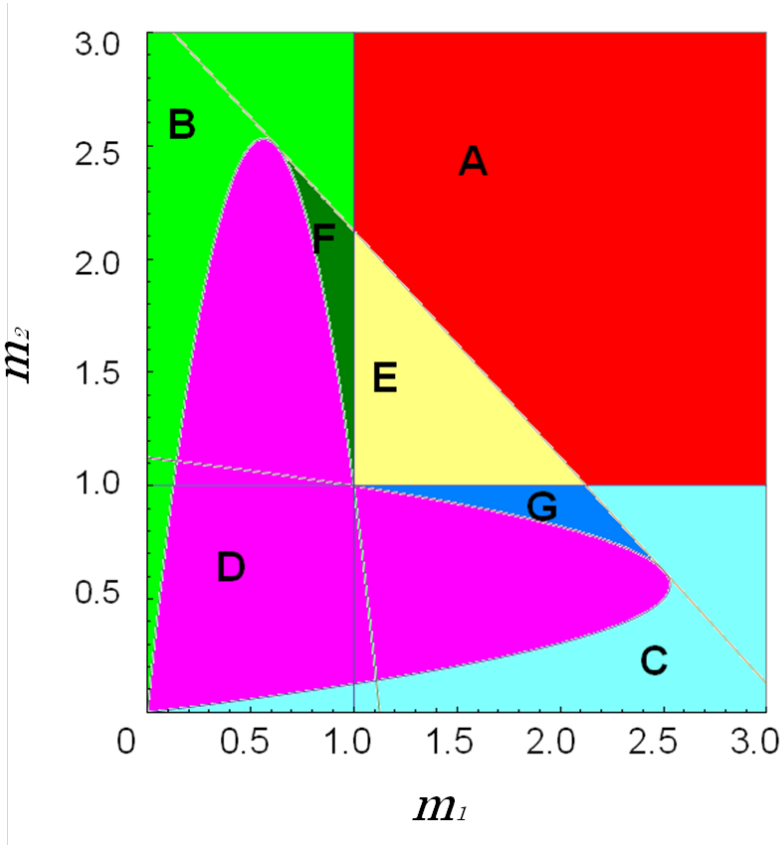
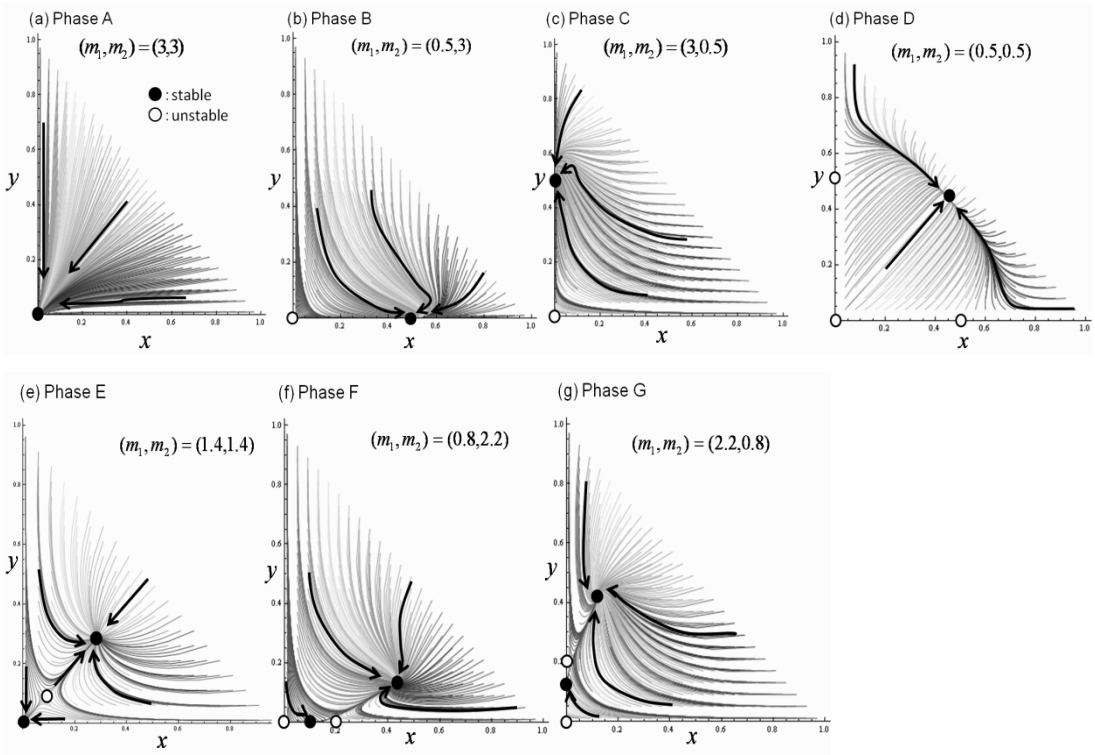


Fig. 4


(a) Phase A
$(m_1, m_2) = (3,3)$
●: stable
○: unstable
(b) Phase B
$(m_1, m_2) = (0.5,3)$
(c) Phase C
$(m_1, m_2) = (3,0.5)$
(d) Phase D
$(m_1, m_2) = (0.5,0.5)$
(e) Phase E
$(m_1, m_2) = (1.4,1.4)$
(f) Phase F
$(m_1, m_2) = (0.8,2.2)$
(g) Phase G
$(m_1, m_2) = (2.2,0.8)$
x
y

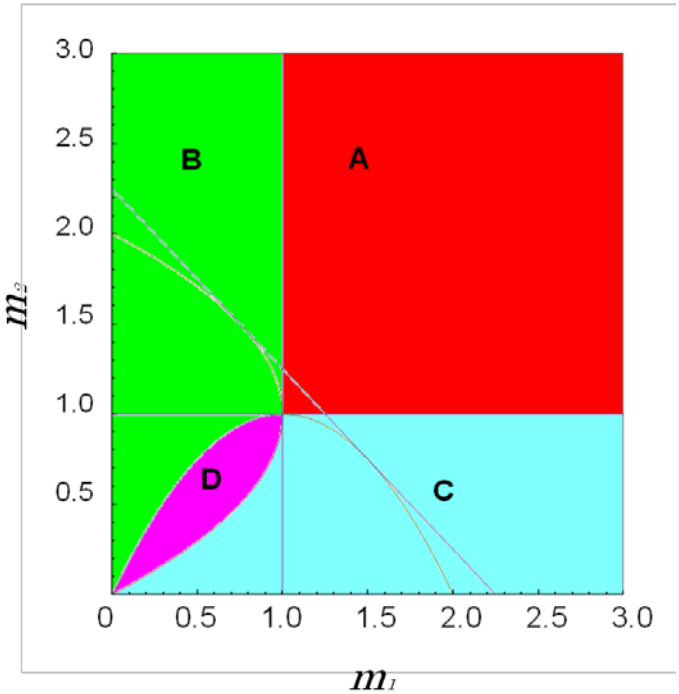



Fig. 5