

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

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

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18 mutualism

19

1 **Abstract**

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

21

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

$$\frac{dx}{dt} = r_x x (K_x - x + \alpha_y y) / K_x, \quad (1a)$$

$$\frac{dy}{dt} = r_y y (K_y - y + \alpha_x x) / K_y \quad (1b)$$

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

1 (Allee 1930). His main interest was the influence of density on population dynamics,
2 especially in aquatic organisms. When the population size of a species becomes below a
3 critical number, the risk of extinction increases drastically. Such a threshold effect is
4 termed Allee effect (Odum 1953; Courchamp et al. 2008). Since his pioneering work,
5 many ecologists studied the Allee effect (Lamont et al. 1993; Groom 1998; Davis et al.
6 2002; Angulo et al. 2007; Tanaka et al. 2009; Nariai et al. 2011). The most typical
7 population model for an Allee effect has been represented by

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

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

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

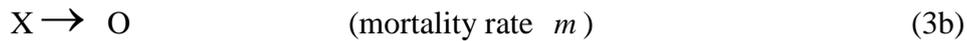
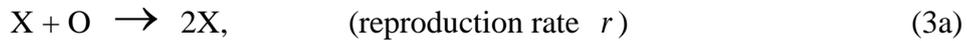
29 In the next section, we review the correspondence relation between lattice and
30 lattice gas models. In ecology, the lattice gas model (mean-field theory of lattice model)
31 usually correspond to LVEs (Tainaka 1988; Matsuda et al. 1992). We apply such a
32 correspondence to mutualism. In section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

1 of population dynamics are elucidated.

2. Theoretical Rationale

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

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



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

$$20 \quad \frac{dx}{dt} = rx(1-x) - mx, \quad (4)$$

21 where x and $(1-x)$ are the densities of species and empty sites, respectively. The
22 first and second terms in the right hand side come from the birth and death processes.
23 Equation (4) can be rewritten by the logistic equation $dx/dt = Rx(1-x/K)$, where
24 $R = r - m$ and $K = r/(r - m)$.

25
26 For two-species system, the lattice version of Lotka-Volterra models have been
27 studied by several authors (Satulovsky and Tome 1994; Nakagiri et al. 2001). A typical
28 lattice version of prey-predator system has been introduced as follows (Tainaka and
29 Fukazawa 1992):

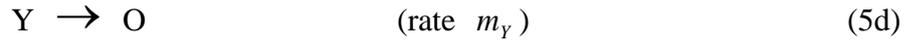
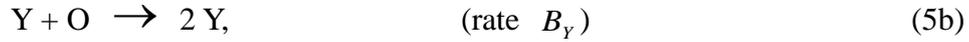
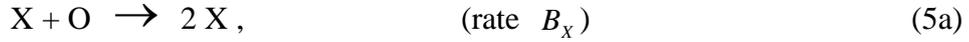


31 where X and Y denote prey and predator, respectively. The above reactions represent

1 the predation of Y, reproduction of X, and death of Y, in order. The mean-field theory
 2 corresponds to LVEs in prey-predator system with density effect. Similarly, lattice
 3 versions of competition system have been presented by several authors (Matsuda et al.
 4 1992; Neuhauser 1992; Tainaka et al. 2004; Kawai et al. 2008). Their mean-field
 5 theories correspond to the LVEs of competition. Hence, it is expected that a canonical
 6 theory for mutualism can be derived from a canonical lattice gas model.

8 3. Model

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



15
 16 where the reactions (5a) and (5c) respectively denote the birth and death processes of
 17 species X, and B_X (m_X) denotes the birth (mortality) rate of species X. Similarly, the
 18 reactions (5b) and (5d) have the same meanings for species Y. The birth rates should be
 19 indicated as follows:
 20

$$21 \quad B_X = r_X + \varepsilon_X y \quad (6a)$$

$$22 \quad B_Y = r_Y + \varepsilon_Y x \quad (6b)$$

23
 24 where x (y) is the density of species X (Y). The parameters r_X and r_Y are the
 25 reproduction rates without the other species, and ε_X and ε_Y denote mutualistic
 26 effects on the reproduction rates. Hence, the birth rate of one species increases with the
 27 density of the other species. If species Y is absent, then the reaction (5) is equivalent to
 28 the contact process [the reaction (3)]. In the limiting case $(\varepsilon_X, \varepsilon_Y) \rightarrow (0,0)$, the system
 29 (5) becomes a competition model called "multiple contact process" (Neuhauser 1992).
 30 In this case, two species cannot coexist; because of reaction (5a), both species compete
 31 with each other to get empty sites (exploitative competition).
 32

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

35 i) Two lattice sites are chosen randomly and independently. The pair sites obey the
 36

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

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

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

9 **4. Theory for Obligate Mutualism**

11 **4.1. Basic equations for mutualism**

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

$$16 \quad \frac{dx}{dt} = B_X(1-x-y)x - m_X x, \quad (7a)$$

$$17 \quad \frac{dy}{dt} = B_Y(1-x-y)y - m_Y y, \quad (7b)$$

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

25 **4.2. Population model for obligate mutualism**

26 Let us consider typical case of obligate mutualism. For simplicity, we put
27 $r_X = 0$ and $r_Y = 0$. In this case, each species cannot survive without the other species.
28 Inserting these relations and equation (6) into equation (7), we have

$$30 \quad \frac{dx}{dt} = \varepsilon_X y(1-x-y)x - m_X x, \quad (8a)$$

$$31 \quad \frac{dy}{dt} = \varepsilon_Y x(1-x-y)y - m_Y y. \quad (8b)$$

32
33 This is a basic model for obligate mutualism. Note that equation (8) is the same as in the

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

4 3. Case for $m_X = m_Y$

6 Tainaka et al. (2007) has derived Allee equation (2) for the special case that
 7 $m_X = m_Y (=m)$. We briefly explain their procedures. Equation (8) has both fast and
 8 slow dynamics. Insert $z = B_X - B_Y$ into (8), then we have
 9 $dz/dt = \varepsilon_X dy/dt - \varepsilon_Y dx/dt = -mz$. This is the fast dynamics, and z rapidly
 10 approaches zero. Namely, the relation $\varepsilon_X y \approx \varepsilon_Y x$ is rapidly satisfied. Inserting this
 11 relation into equation (8a), we get the slow dynamics as follows:

$$13 \quad \frac{dx}{dt} = \varepsilon_Y (1 - x - y)x^2 - mx \quad . \quad (9)$$

14 This equation is formally rewritten as

$$16 \quad \frac{dx}{dt} = \varepsilon_Y x(x - x_-)(x_+ - x), \quad (10)$$

17 where the parameters x_+ and x_- are given by

$$18 \quad x_{\pm} = \frac{1 \pm \sqrt{1 - 4D_m m / \varepsilon_Y}}{2D_m}, \quad D_m = 1 + \varepsilon_Y / \varepsilon_X$$

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

$$26 \quad \varepsilon_X \varepsilon_Y = 4(\varepsilon_X + \varepsilon_Y)m. \quad (11)$$

28 4.4. Case for $m_X \neq m_Y$

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

$$32 \quad \frac{dx}{dt} = \varepsilon_X y(1 - x - y)x - m_X x = f_X(x, y)x, \quad (12a)$$

$$33 \quad \frac{dy}{dt} = \varepsilon_Y x(1 - x - y)y - m_Y y = f_Y(x, y)y. \quad (12b)$$

34

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

$$3 \quad f_x(x, \hat{y}) = (x - \alpha)(-x + \beta) / \left\{ \frac{\varepsilon_y}{m_y \varepsilon_x} \left(1 + \frac{m_x \varepsilon_y}{m_y \varepsilon_x} \right) x^2 \right\}, \quad (13)$$

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

$$6 \quad y = 1 - x - \frac{m_y}{\varepsilon_y x}. \quad (14)$$

7
 8 The parameters α and β are the roots of the following quadratic equation ($\alpha < \beta$):

$$9 \quad \{-(m_x^2 + 1)x^2 + x - m_y^2\} / (m_x^2 + 1) = 0$$

10 The denominator of equation (13) is always positive, so that equation (13) also exhibits
 11 the Allee effect (Allee et al. 1949; Stephens et al. 1999; Amaraskare 2004). Namely,
 12 $f_x(x, y) > 0$ holds, if $\alpha < x < \beta$. In contrast, $f_x(x, y) < 0$ holds, if $0 < x < \alpha$ or
 13 $\beta > x$. Thus, $x = \alpha$ means the threshold density. In Table 1, the values of
 14 equilibriums and the conditions for both existence and stability are listed.

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

$$20 \quad \frac{1}{4} = \frac{m_x}{\varepsilon_x} + \frac{m_y}{\varepsilon_y} \quad (15)$$

21
 22 (see case 2 in Table 1). This is a generalized expression of equation (11). Typical
 23 population dynamics are illustrated in Fig. 2, where Fig. 2(a) and (b) correspond to
 24 phases A and B, respectively. In Fig. 2(b), each orbit is roughly composed of both fast
 25 and slow dynamics; the orbit is immediately attracted to the line connecting three
 26 equilibriums (fast dynamics), and then the orbit is gradually attracted into one of two
 27 stable equilibriums (slow dynamics). It should be emphasized that the results described
 28 here include all profiles in subsection 4.3 (case $m_x = m_y$).

31 5. General cases for mutualism

32

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):

$$\frac{m_x}{r_x} = m_1, \quad \frac{m_y}{r_y} = m_2, \quad \frac{\varepsilon_x}{r_x} = \varepsilon_1, \quad \frac{\varepsilon_y}{r_y} = \varepsilon_2. \quad (16)$$

Then equation (7) will be reduced as

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

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

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

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

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

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

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

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

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

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

1

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

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

16 5. 2. Phase diagram

17 Phase diagram for equation (17) depends on the values of parameters. In
18 general, there are seven phases. For the simplicity, let's us set $(\varepsilon_1, \varepsilon_2) = (8, 8)$. In Fig. 3,
19 the phase diagram is shown. The horizontal axis (resp. vertical axis) represents the death
20 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
21 (or m_2), the species X (or Y) tends to go extinct. The basic equation (17) has seven
22 phases in population dynamics. In this section, we explain each phase (region) in Fig. 3.

23 -Region A

24 In region A, both species always go extinct. There is a stable equilibrium point
25 $(x, y) = (0, 0)$ in x-y plain.

26 -Regions B and C

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

30 -Region D

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

1 equilibrium exists only (x_+, y_+) .

2 -Region E

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

8 - Regions F and G

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

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

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

17 Next, we consider the case of weak mutualism. If ε_1 and ε_2 take small
18 values, the phases E, F and G in Fig. 3 disappear. With the decrease of mutualistic
19 strength, the phase diagram in Fig. 3 should be changed; both upper leaves in phase D
20 shrink and combine. In Fig. 5, the phase diagram for $(\varepsilon_1, \varepsilon_2) = (2, 2)$ is shown. This
21 figure resembles the phase diagram for competition. In the limiting case
22 $(\varepsilon_1, \varepsilon_2) \rightarrow (0, 0)$, both species cannot coexist (Neuhauser 1992).

25 6. Discussions

26 Even though the most famous model of population dynamics is Lotka-Volterra
27 equations (LVEs), they fail to describe the dynamics incorporating mutualism. In the
28 LVEs with mutualism, the population sizes of species increase infinitely causing
29 divergence. In order to avoid this divergence problem, many authors have proposed
30 various models of mutualisms (e.g., Vandermeer 1978; Goh 1979; Wolin and Lower
31 1984; Boucher 1985; Hammerstein 2003). However, they are not so simple; they use
32 fractional equations or nonlinear equations of higher order. Due to such mathematical

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

3 In the present paper, we have applied the lattice gas model, and introduced
4 equation (17) for mutualism or equation (8) for obligate mutualism. In our modeling,
5 the divergence problem is solved simply by the main feature of lattice gas model. The
6 population size of each species never exceeds the total number of lattice sites. Such an
7 idea for carrying capacity is similar to Dean (1983) and Holland et al. (2002). The
8 advantage of our model is the cubic equations which include only mutualistic relations.
9 The previous models also contained all phases in Fig. 3 (see e.g., Wright 1989; Doebeli
10 2002; Tainaka et al. 2003; Hammerstein, 2003; Amarasekare 2004; Courchamp et al.
11 2008; Holland and DeAngelis 2010).

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

20 The generalized model [equation (17)] shows various phases (regions A-G) as
21 illustrated in Figs. 3 and 4. The phase E in Fig. 3 is similar to the phase B for obligate
22 mutualism (Fig. 1). This phase has been predicted by many authors (e.g., Tainaka et al.
23 2003; Amarasekare 2004; Courchamp et al. 2008). In real systems of obligate
24 mutualism, the Allee effect as shown in Fig. 4(e) can be observed (Amarasekare 2004;
25 Katsuyama et al. 2009). Phases F and G may correspond to the dynamics for
26 commensalism. A concrete example is a two-shellfish (mussel-goose barnacle) system
27 in the upper intertidal zone (Kawai and Tokeshi 2004). The mussel could not survive
28 without goose barnacle, while the latter was not influenced by the presence of mussel.
29 The dynamics of commensalism can be obtained from our model. So far, we omit the
30 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,
31 we may obtain both phases F and G.

32 The previous models contained all phases in Fig. 3 (Wright 1989; Doebeli
33 2002; Tainaka et al. 2003; Hammerstein, 2003; Amarasekare 2004; Courchamp et al.
34 2008; Holland and DeAngelis 2010). However, they are not so simple; they use
35 fractional equations or nonlinear equations of higher order. Due to the mathematical
36 complications, the analytic solutions are rather difficult and often include some artificial

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

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

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

21 Finally, we discuss two assumptions in our model. One is the assumption that
22 both species cannot coexist in each site simultaneously. This may be inadequate,
23 especially for obligate mutualism. If we assume that both species can coexist in each
24 cell, then no competition occurs. To prove this, the factor $(1-x-y)$ in equations (8a)
25 and (8b) should be respectively changed by $(1-x)$ and $(1-y)$. Then we have

26 $\partial f_x / \partial y > 0$ and $\partial f_y / \partial x > 0$. Hence, each species always increases with the abundance

27 of the other species. Note that this modification never changes the qualitative properties
28 of phase diagram in Fig. 1 (see Berec et al. 2001). Another assumption in our model is
29 the global interaction. If we precisely explore real systems, the application of local
30 interaction between adjacent sites may be necessary. It is, however, emphasized for
31 local interaction that there is no equation to describe the population dynamics.

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1 **References**

- 2 Addicott, J.F. 1979. A multispecies aphid-ant association: density-dependence and
3 species-specific effects. *Canadian Journal of Zoology* 57, 558-559.
- 4 Amarasekare, P. 2004. Spatial dynamics of mutualistic interactions. *Journal of Animal*
5 *Ecology* 73, 128–142.
- 6 Allee, W. C., 1930. *Animal aggregations*. University of Chicago Press.
- 7 Allee, W.C., Emerson, A.E., Park, O. 1949. *Principles of animal ecology*. W. B.
8 Saunders, Philadelphia, PA.
- 9 Angulo, E. Roemer, G.W. Berc, L. Gascoigne, J. Courchamp, F. 2007. Double Allee
10 effects and extinction in the island fox. *Conservation Biology* 21, 1082-1091.
- 11 Bashary R and Bronstein, J. L. 2004. Game structures in mutualisms: what can the
12 evidence tell us about the kind of models we need? *Advances in the Study of*
13 *Behavior* 34, 59-101.
- 14 Begon, M., Townsend, C.R. and Harper, J.L. 2006. *Ecology: From Individuals to*
15 *Ecosystems*. Wiley, New York.
- 16 Berc, L., Boukal D.S. and Berc, M. 2001. Linking the Allee effect, sexual
17 reproduction and temperature-dependent sex determination via spatial dynamics.
18 *American Naturalist* 157, 217-230.
- 19 Borghans, J.A.M., De Boer, R.J. and Segel, L.A. 1996. Extending the quasi-steady state
20 approximation by changing variables. *Bulletin of mathematical biology* 58, 43–63.
- 21 Boucher, D. H. 1985. Lotka-Volterra models of mutualism and positive density
22 dependence. *Ecological Modelling* 27, 251-270.
- 23 Courchamp, F., Berc, L. and Gascoigne, J. 2008. *Allee effects in ecology and*
24 *conservation*, Oxford University Press, Oxford.
- 25 Davis, H.G. Taylor C.M. Lambrinos, J.G. Strong, D.R. 2002. Pollen limitation causes
26 an Allee effect in a wind-pollinated invasive grass (*Spartina alterniflora*). *Proc. Natl.*
27 *Acad. Sci. USA* 101, 13804-7.
- 28 Dean, M.A. 1983. A simple model of mutualism. *American Naturalist* 121, 409-418
- 29 Dieter, A.W. 2000. *Lattice-Gas Cellular Automata and Lattice Boltzmann Models*.
30 Springer, Berlin.
- 31 Doebeli, M. 2002. A model for the evolutionary dynamics of cross-feeding
32 polymorphisms in microorganisms. *Population Ecology* 44, 59–70.
- 33 Fiegna, F., Yu, Y-T. N. Kadam, S.V. Velicer, G.J. 2006. Evolution of an obligate social
34 cheater to a superior cooperator Francesca, *Nature* 441, 310-314.
- 35 Frisch, U., Hasslacher, B. and Pomeau, Y. 1986. Lattice-gas automata for the
36 Navier-Stokes equation. *Physical Review Letters* 56, 1505–1508.

- 1 Goh, B.S. 1979, Stability in models of mutualism. *American Naturalist* 113, 261-276
- 2 Goto, R. Okamoto, T. Kiers, E.T. Kawakita, A. and Kato, M. 2010. Selective flower
3 abortion maintains moth cooperation in a newly discovered pollination mutualism.
4 *Ecology Letters* 13, 321-329.
- 5 Groom, M. 1998. Allee effects limit population viability of an annual plant. *American*
6 *Naturalist* 151, 487-496.
- 7 Hagiwara, T. Ushimaru T. Tainaka, K. Kurachi, H. Yoshimura, J. 2011. Apoptosis and
8 inflection point in liquid culture of budding yeasts. *PLoS ONE* in press.
- 9 Harris, T. E., 1974. Contact interaction on a lattice. *Annals of Probability* 2, 969-988.
- 10 Hammerstein, P. 2003. Genetic and cultural evolution of cooperation, MIT press.
- 11 Hofbauer, J. and Sigmund, K. 1998. Evolutionary games and population dynamics,
12 Cambridge University Press.
- 13 Holland, J.N. and DeAngelis, D.L. 2010. A consumer–resource approach to the
14 density-dependent population dynamics of mutualism. *Ecology* 91, 1286–1295.
- 15 Holland, J. N., DeAngelis, D. L. and Bronstein, J. L. 2002. Population dynamics and
16 mutualism: functional responses of benefits and costs. *American Naturalist* 159,
17 231-244.
- 18 Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore.
- 19 Katsuyama, C. Nakaoka, S, Takeuchi, Y. Tago, K. Hayatsu, M. and Kato, K. 2009.
20 Complementary cooperation between two syntrophic bacteria in pesticide degradation.
21 *Journal of Theoretical Biology* 256, 644–654.
- 22 Kawai, T. and Tokeshi, M. 2004. Variable modes of facilitation in the upper intertidal:
23 goose barnacles and mussels. *Marine Ecology Progress Series* 272, 203–213
- 24 Kawai, T., Tadokoro, Y., Tainaka, K., Hayashi, T. and Yoshimura, J. 2008. A lattice
25 model of fashion propagation with correlation analysis. *International Journal of*
26 *Systems Science* 39, 947-957.
- 27 Keller, L., Surette, M.G., 2006. Communication in bacteria: an ecological and
28 evolutionary perspective. *Nature Reviews Microbiology*. 4, 249–258.
- 29 Konno, N. 1994. Phase transition of interacting particle systems. World Scientific,
30 Singapore.
- 31 Lamont, B.B. Klinkhamer, P.G.L. Witkowski, E.T.F et al. 1993. Population
32 fragmentation may reduce fertility to zero in *Banksia goodie*: a demonstration of the
33 Allee effect. *Oecologia*, 94, 446-460.
- 34 Lewis M. A. and Kareiva P. 1993. Allee dynamics and the spread of invading
35 organisms. *Theoretical Population Biology* 43, 141-158.
- 36 Liggett, T. M. 1985. *Interacting Particle Systems*. Springer-Verlag, Berlin.

- 1 Madigan, M.T. Martinko, J.M. Parker, J. 2000. *Biology of microorganisms*. Prentice
2 Hall, Inc., New Jersey.
- 3 Matsuda, H. Ogita, N. Sasaki, A. and Sato, K. 1992. Statistical mechanics of population:
4 the lattice Lotka-Volterra model. *Progress of Theoretical Physics* 88, 1035-1049.
- 5 Nakagiri, N. Tainaka, K. and Tao, T. 2001. Indirect relation between extinction and
6 habitat destruction. *Ecological Modelling* 137, 109-118.
- 7 Nariai, Y. Hayashi, S. Morita, S. Umemura, Y. Tainaka K., Sota, T. Cooley, J.R.
8 Yoshimura, J. 2011. Life cycle replacement by gene introduction under an Allee effect
9 in periodical cicadas. *PLoS ONE* in press.
- 10 Neuhauser, C. 1992. Ergodic theorems for the multitype contact process. *Probability*
11 *Theory Related Fields* 91, 467–506.
- 12 Odum, E.P. 1953. *Fundamentals of Ecology*. Saunders, Pennsylvania.
- 13 Pellmyr, O. and Huth, C.J. 2002. Evolutionary stability of mutualism between yuccas
14 and yucca moths. *Nature* 372, 257 – 260.
- 15 Rosenberg, E. Koren, O. Reshef, L. Efrony, R. and Zilber-Rosenberg, I. 2007. The role
16 of microorganisms in coral health, disease and evolution. *Nature Reviews* 5, 255-262.
- 17 Satulovsky, J. E. and Tome, T., 1994. Stochastic lattice gas model for a predator-prey
18 system. *Physical Review E* 49, 5073-5079.
- 19 Segel, L. A. 1988. On the validity of the steady state assumption of enzyme kinetics.
20 *Bulletin of Mathematical Biology* 50, 579–593.
- 21 Stephens, P. A., Sutherland, W. J. and Freckleton, R.P. 1999. What is the Allee effect?.
22 *Oikos* 87, 185-190.
- 23 Tainaka, K. 2003. Perturbation expansion and optimized death rate in a lattice
24 ecosystem, *Ecological Modelling* 163, 73-85.
- 25 Tainaka, K. 1988. Lattice model for the Lotka-Volterra system. *Journal of the Physical*
26 *Society of Japan* 57, 2588-2590.
- 27 Tainaka, K. 1989. Stationary pattern of vortices or strings in biological systems: lattice
28 version of the Lotka-Volterra model. *Physical Review Letters* 63, 2688-2691.
- 29 Tainaka, K. and Fukazawa, S. 1992. Spatial pattern in a chemical reaction system: prey
30 and predator in the position-fixed limit. *Journal of the Physical Society of Japan* 61,
31 1891-1894.
- 32 Tainaka, K. Kushida, M. Ito, Y. and Yoshimura, J. 2004. Phase interspecific segregation
33 in a lattice ecosystem with intraspecific competition. *Journal of the Physical Society of*
34 *Japan* 73, 2914-2915.
- 35 Tainaka, K. Terazawa, N. Yoshida, N. Nakagiri, N. Takeuchi, Y. and Yoshimura J. 2003.
36 The effect of mutualism on community stability. *Journal of the Physical Society of*

1 Japan 68, 956-961.

2 Tainaka, K., Yoshimura, J. and Rosenzweig, M. L. 2007. Do male orangutans play a
3 hawk-dove game? *Evolutionary Ecology Research* 9, 1043-1049.

4 Takeuchi, Y., 1996. *Global dynamical properties of Lotka-Volterra systems*. World
5 Scientific, Singapore.

6 Tanaka, Y. Yoshimura, J, Simon, C. Cooley, J.R. Tainaka, K. 2009. The Allee effect in
7 the selection for prime-numbered cycles in periodical cicadas. *Proc. Natl. Acad. Sci.*
8 USA 106, 8975–8979.

9 Volterra, V. 1926. Pages 409-448 in Chapman R.N. 1931. *Animal ecology*. McGraw-Hill,
10 New York.

11 Vandermeer, J. H. and Douglas H. Boucher. 1978. Varieties of mutualistic interaction in
12 population models. *Journal of Theoretical Biology* 74, 549-558.

13 Wolin, C. L. and Lawlor, L R. 1984, Models of facultative mutualism: Density effects.
14 *American Naturalist* 124, 843-862.

15 Wright, D.H. 1989. A simple stable model of mutualism incorporating handling time.
16 *American Naturalist* 134, 664-667.

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18

1 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})	<p>Case 1: (x_+, y_+)</p> $\frac{1}{4} = \frac{m_x}{\varepsilon_x} + \frac{m_y}{\varepsilon_y}$ <p>Case 2: (x_{\pm}, y_{\pm})</p> $\frac{1}{4} > \frac{m_x}{\varepsilon_x} + \frac{m_y}{\varepsilon_y}$	<p>Case 1: Unstable</p> <p>Case 2: (x_+, y_+) : stable (x_-, y_-) : unstable</p>

2

3
$$x_{\pm} = \frac{1 \pm \sqrt{1 - 4D \frac{m_y}{\varepsilon_y}}}{2D}, y_{\pm} = \frac{m_x \varepsilon_y}{m_y \varepsilon_x} x_{\pm} \text{ and } D = 1 + \frac{m_x \varepsilon_y}{m_y \varepsilon_x} .$$

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

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

2

3
$$M_1 = -m_2 + \{1 + \varepsilon_2(1 - m_1)\}m_1,$$

4
$$M_2 = -m_1 + \{1 + \varepsilon_1(1 - m_2)\}m_2,$$

5
$$x_{\pm}^* = \frac{-B_1 \pm m_2 \sqrt{A}}{2\varepsilon_2(\varepsilon_1 m_2 + \varepsilon_2 m_1)}, y_{\pm}^* = \frac{-B_2 \pm m_1 \sqrt{A}}{2\varepsilon_1(\varepsilon_1 m_2 + \varepsilon_2 m_1)},$$

6
7 Here

$$A = (\varepsilon_1 + \varepsilon_2 + \varepsilon_1 \varepsilon_2)^2 - 4\varepsilon_1 \varepsilon_2 (\varepsilon_1 m_2 + \varepsilon_2 m_1),$$

8
$$B_i = 2\varepsilon_j m_i + \{\varepsilon_i - \varepsilon_j(1 + \varepsilon_i)\}m_j,$$

$$C_i = (4\varepsilon_j \varepsilon_i^2 - 1)m_j + \{1 + \varepsilon_j(1 - m_i + 4\varepsilon_i \varepsilon_j)\}m_i - (\varepsilon_i + \varepsilon_j + \varepsilon_i \varepsilon_j)^2,$$

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

1 **Figure Captions**

2 **Fig. 1.** Phase diagram for obligate mutualism. Model parameters are $\varepsilon_x = \varepsilon_y = 0.8$ and

3 $m_x = m_y = 0.1$. The population dynamics can be categorized into two regions. The
4 boundary is given by equation (15). Both species go extinct in region A, while an
5 Allee effect can be observed in region B.

6
7 **Fig. 2.** Typical dynamics for obligate mutualism. The thin curves denote the orbits
8 calculated from equation (8) by the use of Mathematica. The orbits start from various
9 initial densities, and reach the stable equilibriums as symbolically represented by thick
10 arrows.

11
12 **Fig. 3.** Phase diagram for general case: equation (17). The population dynamics can be
13 categorized into seven regions (from A to G). The values of mutualistic strengths are
14 set $(\varepsilon_1, \varepsilon_2) = (8, 8)$.

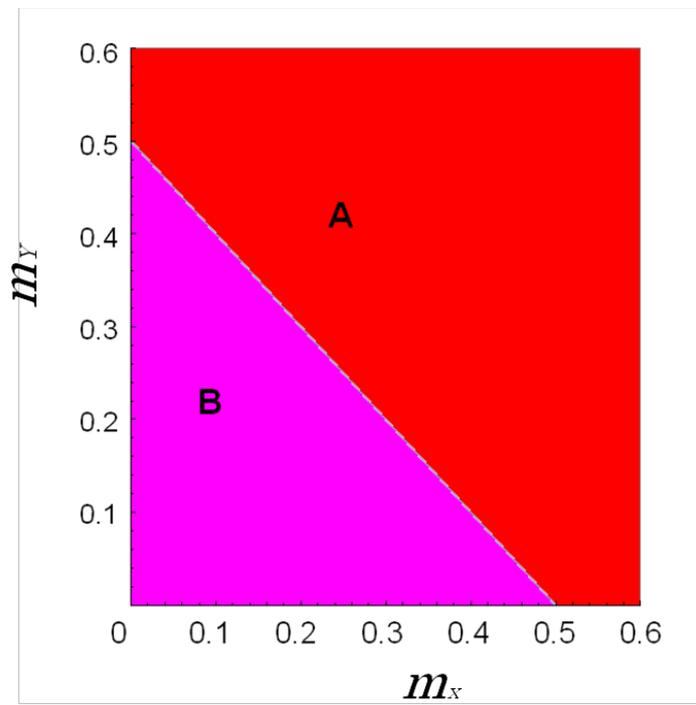
15
16 **Fig. 4.** Typical population dynamics for mutualism. The curves and arrows have the
17 same meaning as in Fig. 2.

18
19 **Fig. 5.** Same as Fig. 3, but the mutualistic strengths take small values: $(\varepsilon_1, \varepsilon_2) = (2, 2)$.
20 The phases A-D are the same as in Fig. 3.

21
22

1 Fig. 1

2



3

4

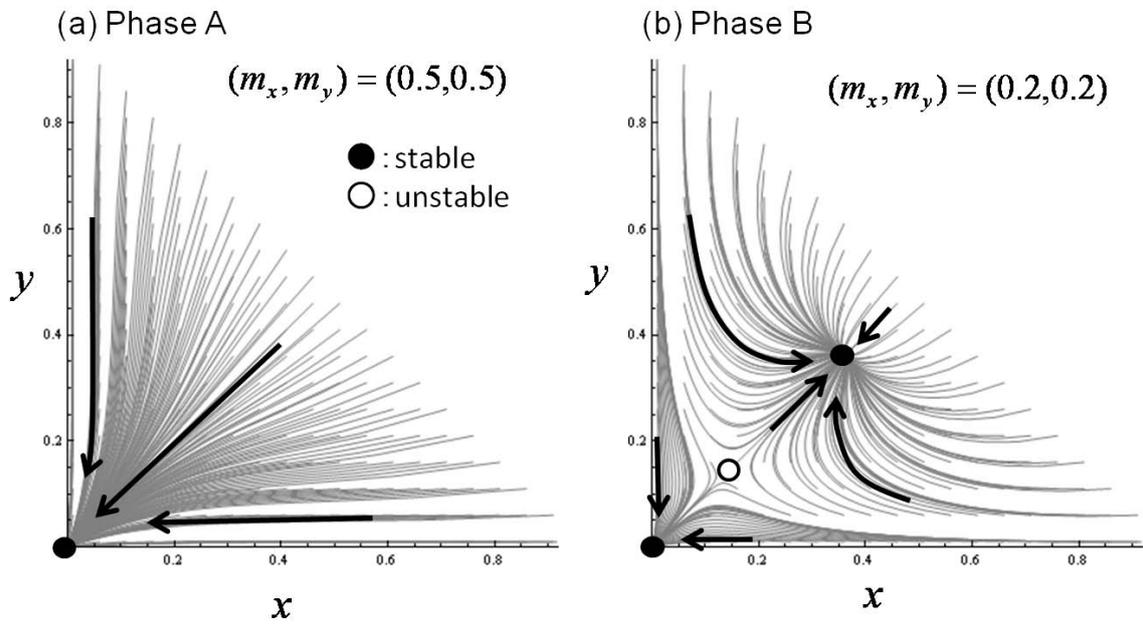
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2 Fig. 2

3



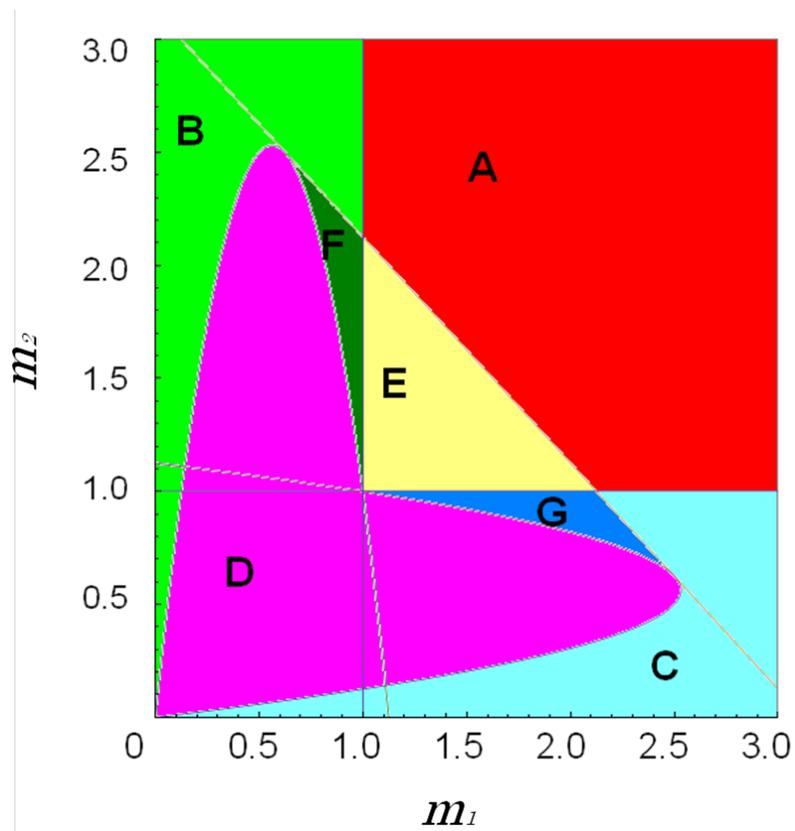
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1 Fig. 3

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3



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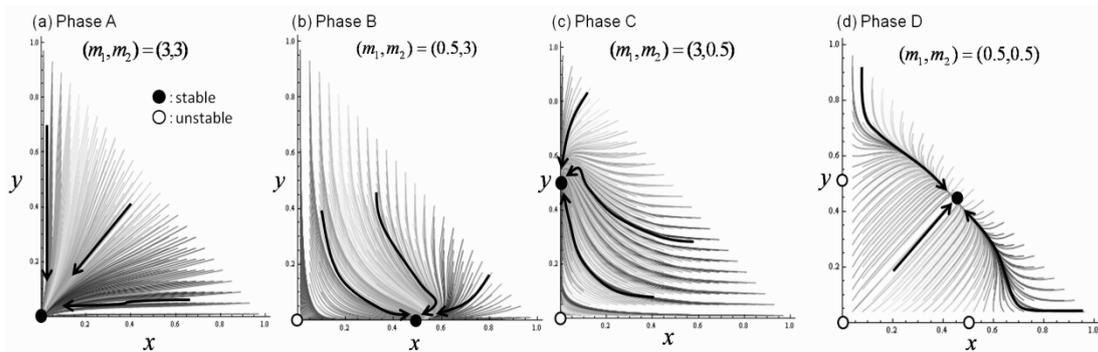
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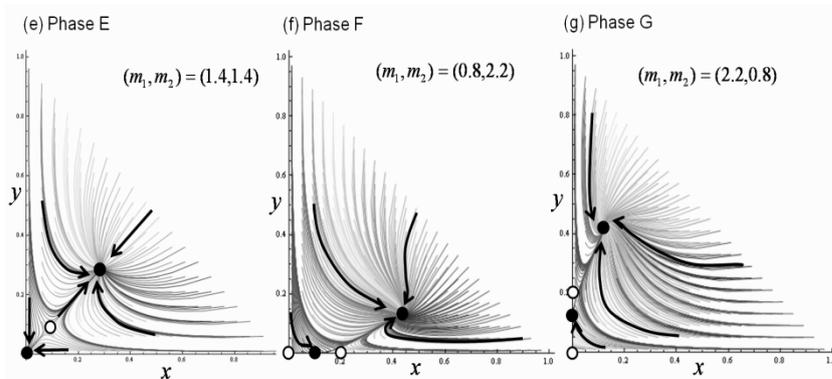
1 Fig. 4

2

3

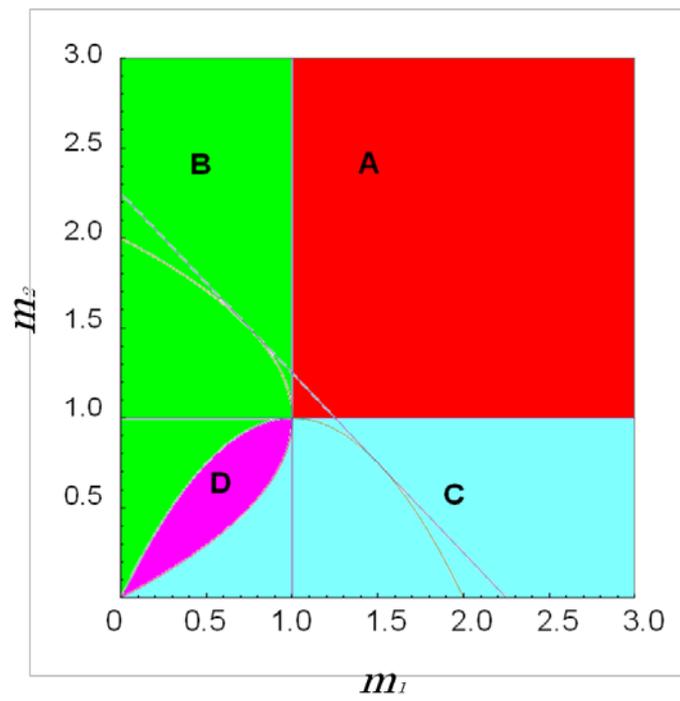


4



1 Fig. 5

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