STABILITY OF MUTUALISMS IN A LATTICE GAS SYSTEM OF TWO SPECIES

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ABSTRACT. This article considers mutualisms in a lattice gas system of two species. The species are mutualistic since each one can provide resources to the other. They are also competitive since they compete for empty sites on the same lattice. The mutualisms are assumed to have a saturated response, and the intraspecific competition is considered because of self-limitation. The mutualism system is characterized by differential equations, which are derived from reactions on lattice and are extension of a previous model. Global stability analysis demonstrates that (i) When neither species can survive alone, they can coexist if mutualisms between them are strong and population densities are large, which exhibits the Allee effect in obligate mutualism; (ii) When one species can survive alone but the other cannot, the latter one will survive if the mutualistic effect from the former is strong. Even if the effect is intermediate, the latter species can survive by strengthening its mutualistic effect on the former and enhancing its population density; (iii) When either species can survive alone, a weak mutualism will lead to extinction of one species. When in coexistence, intermediate strength of mutualism is shown to be beneficial under certain parameter range, while over- or under- mutualism is not good. Furthermore, extremely strong/weak mutualism is exhibited to result in extinction of one/both species. While seven typical dynamics are displayed by numerical simulation in a previous work, they are proved in this work and the eighth one is exhibited. Numerical simulations validate and extend our conclusions.

1. INTRODUCTION

Mutualistic interactions are ubiquitous in nature since most biomass survive by cooperating with the others [4]. For example, many microbial species are observed to play a role in the abundance of interrelated species [10, 12], while various bacterial species coexist in syntrophic colonies, in which one species consumes resources produced by another (obligate mutualisms) [2, 17]. Many models have been presented to characterize mutualisms, among which Lotka-Volterra equations (LVEs)

are the most famous [18, 19]. The LVEs can be modeled by

$$
\begin{aligned}
\frac{dx_1}{dt} &= x_1(r_1 - d_1 x_1 + e_1 x_2) \\
\frac{dx_2}{dt} &= x_2(r_2 - d_2 x_2 + e_2 x_1),
\end{aligned}
\tag{1.1}
$$

where variable x_i represents population density of species i, while parameters r_i and d_i denote the intrinsic growth rate and self-competition degree in species i, respectively ($i = 1, 2$). e_i represents the mutualistic effect of species j on i, $i \neq j$, $i, j = 1, 2$. It is known that the two species can coexist at a steady state if mutualistic effects between them are weak ($e_1 e_2 < d_1 d_2$). Otherwise, population densities of both species tend to infinity, which is called the convergence problem [14]. Moreover, model (1.1) cannot characterize the Allee effect which predicts that when the population density of a species is below a threshold, the species goes to extinction [3]. In order to avoid these problems, several models have been established, but most of them are very complicated such that their global dynamics cannot be shown [3, 6, 8, 11, 14, 16, 21, 22, 23]. Therefore, it is necessary to form an appropriate model to exhibit basic properties of mutualisms [1].

In a recent study, Iwata et al [9] established a lattice gas model of mutualisms, which is derived from reactions on lattice and has a form similar to that of LVEs. Numerical simulations and local stability analysis demonstrate interesting features of mutualisms. However, global dynamics of the model are not shown and the model is given in a simplified form. To demonstrate more properties of mutualisms, it is important to extend the model and analyze its global stability.
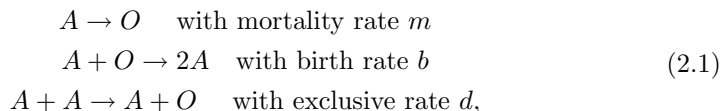
In this article, we consider a lattice gas model of mutualisms, which is extended from the model established by Iwata et al [9]. In the extended model, the mutualisms are assumed to have a saturated response, while intraspecific competition is considered because of self-limitation. Population densities of the species will not tend to infinity because of spatial limitation on the lattice. Global stability analysis demonstrates that (i) When neither species can survive alone, they can coexist if mutualisms between them are strong and population densities are large, which exhibits the Allee effect in obligate mutualism; (ii) When one species can survive alone but the other cannot, the latter one will survive if the mutualistic effect from the former is strong. Even if the effect is intermediate, the latter species can survive by strengthening its mutualistic effect on the former and enhancing its population density; (iii) When either species can survive alone, a weak mutualism will lead to extinction of one species. When in coexistence, intermediate mutualisms are exhibited to be favorable under certain parameter conditions, and over-mutualism or under-mutualism is not good. Furthermore, extremely strong/weak mutualisms are demonstrated to lead to extinction of one/both species. While seven typical dynamics are displayed by Iwata et al [9], they are proved in this paper and the eighth one is exhibited (see section 6 and Figure 3a).

The article is organized as follows. Section 2 describes the model. Sections 3-5 consider obligate mutualism, obligate-facultative mutualism and facultative mutualism, respectively. Discussion is in section 6.

2. Model

In this section, we characterize the lattice gas model of mutualisms. First, we describe the lattice gas system of one species. On a lattice of species A, a site is

labeled by A if it is occupied by an individual of A, while an empty site is labeled by O. The site A will become site O in a mortality rate m. Any pair of sites on the lattice contact in a random and independent way. The "contact process" can be described as follows [5, 20]
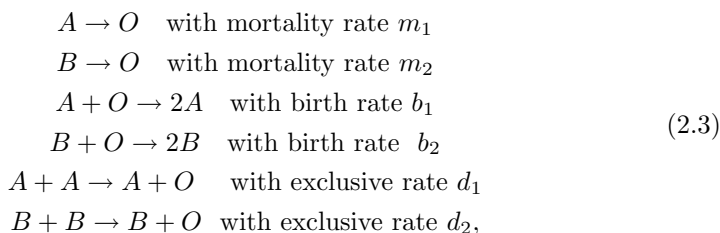
$$
\begin{aligned}
A &\to O \quad \text{with mortality rate } m \\
A + O &\to 2A \quad \text{with birth rate } b \\
A + A &\to A + O \quad \text{with exclusive rate } d,
\end{aligned}
\tag{2.1}
$$

where A represents the site occupied by species A and O denotes the empty one. The first (second) reaction describes the death (birth) process of species A, while the third one characterizes the self-competition in A. Dynamics of lattice gas systems are usually described by differential equations, which are called the mean-field theory of lattice model [13]. Based on the models in [9, 20], dynamics of reactions in (2.1) can be represented by the rate equation

$$
\frac{dx}{dt} = x[-m + b(1 - x) - dx]
\tag{2.2}
$$

where x and $1 - x$ represent densities of the species and empty sites, respectively. Let $\tilde{r} = b - m, \tilde{d} = b + d$. Then (2.2) can be rewritten as the logistic equation $dx/dt = x(\tilde{r} - \tilde{d}x)$.

Second, we consider a lattice gas system of two species A and B. The site on lattice is labeled by A (B) if it is occupied by an individual of species A (B), while an empty site is labeled by O. Reactions occur between any pair of sites randomly and independently. Thus the reactions on a lattice of two species can be described as follows

$$
\begin{aligned}
A &\to O \quad \text{with mortality rate } m_1 \\
B &\to O \quad \text{with mortality rate } m_2 \\
A + O &\to 2A \quad \text{with birth rate } b_1 \\
B + O &\to 2B \quad \text{with birth rate } b_2 \\
A + A &\to A + O \quad \text{with exclusive rate } d_1 \\
B + B &\to B + O \quad \text{with exclusive rate } d_2,
\end{aligned}
\tag{2.3}
$$

where the first (third) reaction describes the death (birth) process of species A, while the fifth characterizes the self-competition in A. The second, fourth and sixth reactions have similar meanings for species B. The birth rates can be described by

$$
b_1 = r_1 + \frac{e_1 x_2}{1 + c_1 x_2}, \quad b_2 = r_2 + \frac{e_2 x_1}{1 + c_2 x_1},
$$

where x_i represents population density of species i and r_i is the intrinsic growth rate of species i in the absence of species j, $i \neq j$, $i, j = 1, 2$. The term $e_1 x_2/(1 + c_1 x_2)$ represents the functional response in the mutualisms: e_1/c_1 denotes the saturation level in the Holling Type II functional response, while $1/c_1$ is the half-saturation constant. For convenience, we focus on parameter e_1, which represents the mutualistic effect of species 2 on 1. e_1 can be defined by $e_1 = \mu_1 \nu_2$, where ν_2 denotes resources (energy, service, etc.) provided by species 2 and μ_1 is the efficiency of species 1 in converting the resources/services into fitness. A similar discussion can be given for $e_2 x_1/(1 + c_2 x_1)$.

Therefore, dynamics of reactions in (2.3) can be described by

$$\frac{dx_1}{dt} = x_1[-m_1 + b_1(1 - x_1 - x_2) - d_1 x_1],$$
$$\frac{dx_2}{dt} = x_2[-m_2 + b_2(1 - x_1 - x_2) - d_2 x_2],$$
$$(2.4)$$

where the factor $(1 - x_1 - x_2)$ in the righthand sides represents the density of empty sites.

Model (2.4) is an extension of the model in [9] Since it considers saturated response and intraspecific competition. Indeed, let $c_i = d_i = 0, i = 1, 2$, then model (2.4) becomes the model in [9]. On the other hand, we can see that model (2.4) has the same form as that of LVEs since in the brackets of its righthand sides, the three terms represent death, birth and exclusive rates, respectively.

In the following analysis, we focus on the case of $r_1 > 0, r_2 > 0$, while cases of $r_1 > 0, r_2 = 0$ and $r_1 = r_2 = 0$ are considered in Appendices A and B respectively.
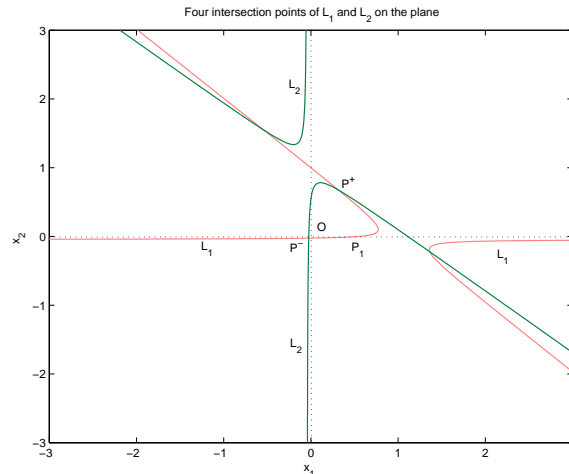

FIGURE 1. Intersection points of parabolas L_1 and L_2 on the whole plane. Let $m_1 = m_2 = 0.02$, $e_1 = e_2 = 40$, $c_1 = c_2 = 0.001$, $d_1 = 0.8$, $d_2 = 0.75$. Then L_1 and L_2 have four intersection points, while two of them are in the second and fourth quadrants, respectively.

Assume $r_1 > 0, r_2 > 0$. Then each species can reproduce in the absence of the other as shown in [9]. Denote

$$m_1 := \frac{m_1}{r_1}, \quad m_2 := \frac{m_2}{r_2}, \quad e_1 := \frac{e_1}{r_1}, \quad e_2 := \frac{e_2}{r_2}. \qquad (2.5)$$

Then model (1.1) can be rewritten as

$$\frac{dx_1}{dt} = r_1 x_1[-m_1 + (1 + \frac{e_1 x_2}{1 + c_1 x_2})(1 - x_1 - x_2) - d_1 x_1],$$
$$\frac{dx_2}{dt} = r_2 x_2[-m_2 + (1 + \frac{e_2 x_1}{1 + c_2 x_1})(1 - x_1 - x_2) - d_2 x_2].$$
$$(2.6)$$

Equilibria of (2.6) are determined by their relative positions of isoclines L_i, which can be described as

$$L_1 : -m_1 + (1 + \frac{e_1 x_2}{1 + c_1 x_2})(1 - x_1 - x_2) - d_1 x_1 = 0$$

$$L_2 : -m_2 + (1 + \frac{e_2 x_1}{1 + c_2 x_1})(1 - x_1 - x_2) - d_2 x_2 = 0. \tag{2.7}$$

The expression of L_1 can be rewritten as

$$(\alpha_1 - x_1 - \beta_1 x_2)[1 + d_1 + (e_1 + c_1 + c_1 d_1)x_2] = \gamma_1,$$

$$x_1 = x_1(x_2, e_1) = \alpha_1 - \beta_1 x_2 - \frac{\gamma_1}{1 + d_1 + (e_1 + c_1 + c_1 d_1)x_2}, \tag{2.8}$$

where

$$\alpha_i = \frac{e_i d_i + (e_i + c_i - m_i c_i)(e_i + c_i + c_i d_i)}{(e_i + c_i + c_i d_i)^2}, \quad \beta_i = \frac{e_i + c_i}{e_i + c_i + c_i d_i},$$

$$\gamma_i = \frac{e_i m_i}{e_i + c_i + c_i d_i} + \frac{e_i d_i (1 + d_i + e_i + c_i + c_i d_i)}{(e_i + c_i + c_i d_i)^2}, \quad i = 1, 2.$$

Thus, $P_1((1 - m_1)/(1 + d_1), 0) \in L_1$ as shown in the first quadrant of Figure 1. L_1 is a parabola which is convex rightward and has a vertex $\bar{P}(\bar{x}_1, \bar{x}_2)$ with

$$\bar{x}_1 = x_1(\bar{x}_2, e_1), \quad \bar{x}_2 = \sqrt{\frac{\gamma_1}{\beta_1(e_1 + c_1 + c_1 d_1)}} - \frac{1 + d_1}{e_1 + c_1 + c_1 d_1}.$$

The asymptotes of L_1 are

$$L_{11} : \alpha_1 - x_1 - \beta_1 x_2 = 0, \quad L_{12} : x_2 = -\frac{1 + d_1}{e_1 + c_1 + c_1 d_1}.$$

Since

$$\frac{\partial x_1}{\partial e_1} = \frac{x_2(1 - x_1 - x_2)}{1 + d_1 + (e_1 + c_1 + c_1 d_1)x_2} > 0 \quad \text{as } 1 - x_1 - x_2 > 0 \tag{2.9}$$

the function $x_1 = x_1(x_2, e_1)$ increases monotonously as e_1 increases. From (2.8), we have

$$\lim_{e_1 \to +\infty} x_1(x_2, e_1) = 1 - x_2, \quad \lim_{e_1 \to 0} x_1(x_2, e_1) = (1 - m_1 - x_2)/(1 + d_1).$$

If $\alpha_1 \leq 0$, then $L_1 \cap \text{int } R_+^2 = \emptyset$ by (2.8) and $dx_1/dt < 0$ by (2.6), which implies that species 1 goes to extinction. A similar discussion can be given for species 2. Thus, we assume the following hypothesis in this work

$$\alpha_i > 0, \quad i = 1, 2.$$

When $1 - m_1 > 0$, we have $L_1 \cap \text{int } R_+^2 \neq \emptyset$ since $P_1 \in L_1$ and L_1 has an asymptote $\alpha_1 - x_1 - \beta_1 x_2 = 0$. When $1 - m_1 \leq 0$, we have $L_1 \cap \text{int } R_+^2 \neq \emptyset$ if and only if L_1 and the positive x_2-axis have two intersection points. That is, the following equation has two positive roots

$$G(x_2) \equiv \tilde{a} x_2^2 + \tilde{b} x_2 + \tilde{c} = 0,$$

where

$$\tilde{a} = e_1 + c_1, \quad \tilde{b} = 1 - e_1 + c_1(m_1 - 1), \quad \tilde{c} = m_1 - 1.$$

Let $\tilde{\Delta} = \tilde{b}^2 - 4\tilde{a}\tilde{c}$, then

$$\tilde{\Delta} = e_1^2 - 2e_1[c_1(m_1 - 1) + 2m_1 - 1] + [c_1(m_1 - 1) - 1]^2.$$

Thus the equation $G(x_2) = 0$ has two positive roots if and only if $\tilde{b} < 0$ and $\tilde{\Delta} > 0$. From $\tilde{b} < 0$ we have $e_1 > \tilde{e}_1 = c_1(m_1 - 1) + 1$. From $\tilde{\Delta} > 0$ we have $e_1 > e_1^+$ or $e_1 < e_1^-$ with

$$e_1^{\pm} = c_1(m_1 - 1) + 2m_1 - 1 \pm 2\sqrt{m_1(m_1 - 1)(1 + c_1)}.$$

Since

$$e_1^- - \tilde{e}_1 = 2(m_1 - 1) - 2\sqrt{m_1(m_1 - 1)(1 + c_1)} < 0,$$
$$e_1^+ - \tilde{e}_1 = 2(m_1 - 1) + 2\sqrt{m_1(m_1 - 1)(1 + c_1)} > 0,$$

the equation $G(x_2) = 0$ has two positive roots if and only if $e_1 > e_1^{(1)}$ with

$$e_i^{(1)} = c_i(m_i - 1) + 2m_i - 1 + 2\sqrt{m_i(m_i - 1)(1 + c_i)}, \quad i = 1, 2. \tag{2.10}$$

Similarly, the expression of L_2 can be rewritten as

$$(\alpha_2 - x_2 - \beta_2 x_1)[1 + d_2 + (e_2 + c_2 + c_2 d_2)x_1] = \gamma_2$$
$$x_2 = x_2(x_1, e_2) = \alpha_2 - \beta_2 x_1 - \frac{\gamma_2}{1 + d_2 + (e_2 + c_2 + c_2 d_2)x_1}. \tag{2.11}$$

Thus, $P_2(0, (1 - m_2)/(1 + d_2)) \in L_2$ and L_2 is a parabola and convex upward, which has a vertex $\hat{P}(\hat{x}_1, \hat{x}_2)$. The asymptotes of L_2 are

$$L_{21} : \alpha_2 - x_2 - \beta_2 x_1 = 0, \quad L_{22} : x_1 = -\frac{1 + d_2}{e_2 + c_2 + c_2 d_2}.$$

From equations (2.6)-(2.8) we have

$$\frac{\partial x_2}{\partial e_2} > 0 \quad \text{as } 1 - x_1 - x_2 > 0$$
$$\lim_{e_2 \to +\infty} x_2(x_1, e_2) = 1 - x_1, \quad \lim_{e_2 \to 0} x_2(x_1, e_2) = (1 - m_2 - x_1)/(1 + d_2). \tag{2.12}$$

When $1 - m_2 > 0$, then $L_2 \cap \operatorname{int} R_+^2 \neq \emptyset$ since $P_2 \in L_2$ and L_2 has an asymptote $\alpha_2 - x_2 - \beta_2 x_1 = 0$. When $1 - m_2 \leq 0$, we have $L_2 \cap \operatorname{int} R_+^2 \neq \emptyset$ if and only if $e_2 > e_2^{(1)}$.

Lemma 2.1. *The parabolas L_1 and L_2 have at most four intersection points on the plane, while system (2.6) has at most two positive equilibria $P^+(x_1^+, x_2^+)$ and $P^-(x_1^-, x_2^-)$ with $x_1^+ > x_1^-$.*

Proof. Let $P(x_1, x_2)$ be the intersection point of L_1 and L_2. From (2.8) and (2.11), a direct computation shows that $P(x_1, x_2)$ satisfies

$$a_0 x_1^4 + a_1 x_1^3 + a_2 x_1^2 + a_3 x_1 + a_4 = 0, \quad a_0 = \beta_2(1 - \beta_1 \beta_2)(e_1 + c_1 + c_1 d_1)(e_2 + c_2 + c_2 d_2)^2.$$

Thus, the parabolas L_1 and L_2 have at most four intersection points on the plane.

Assume asymptotes L_{11} and L_{21} coincide. From (2.8) and (2.11), x_1 is a linear function of x_2. By (2.8), x_1 satisfies a quadratic equation, which implies that system (2.6) has at most two positive equilibria.

Assume asymptotes L_{11} and L_{21} do not coincide but are parallel. Then we have $1 - \beta_1 \beta_2 = 0$ and $a_0 = 0$. Thus, x_1 satisfies a cubic equation, which implies that the parabolas L_1 and L_2 have at most three intersection points on the plane. If L_{11} is above L_{21}. then L_1 and L_2 have an intersection point in the second quadrant. If L_{11} is below L_{21}. then L_1 and L_2 have an intersection point in the fourth quadrant. Thus, system (2.6) has at most two positive equilibria.

Assume asymptotes L_{11} and L_{21} intersect. Without loss of generality, we suppose $\beta_2 < 1/\beta_1$ as shown in Figure 1. Let L_1^+ be the part of L_1 above L_{11}. Let L_2^- be the part of L_2 below L_{21}. Then L_1^+ divide the fourth quadrant into two parts. If L_2^- starts at a point above L_1^+, then L_2^- and L_1^+ have an intersection point in the fourth quadrant since they have asymptotes L_{21} and L_{12}, respectively. If L_2^- starts at a point below L_1^+, then L_2^- and L_1^+ have an intersection point in the fourth quadrant since they have asymptotes L_{22} and L_{11}, respectively. Thus, L_1 and L_2 always have an intersection point in the fourth quadrant. A similar discussion could show that L_1 and L_2 always have an intersection point in the second quadrant. Therefore, system (2.6) has at most two positive equilibria. □

Lemma 2.2. *There is no periodic orbit of system* (2.6) *and solutions of* (2.6) *are bounded.*

Proof. Let $f_i(x_1, x_2)$ be the right-hand sides of the equalities in (2.6), respectively. Denote $g(x_1, x_2) = 1/x_1 x_2$. Then we obtain

$$\frac{\partial(gf_1)}{\partial x_1} + \frac{\partial(gf_2)}{\partial x_2} = -\frac{\gamma_1}{x_2}\left(1 + \frac{e_1 x_2}{1 + c_1 x_2}\right) - \frac{\gamma_2}{x_1}\left(1 + \frac{e_2 x_1}{1 + c_2 x_1}\right) < 0.$$

By Bendixson-Dulac Theorem [7], there is no periodic orbit of (2.6).

If $x_1 + x_2 \geq 1$, then $dx_1/dt < 0$ and $dx_2/dt < 0$ by (2.6). Thus, all solutions of (2.6) satisfy $x_1 + x_2 \leq 1$ as t is sufficiently large, which implies that solutions of (2.6) are bounded. □

The equilibria of (2.6) on axes are analyzed as follows, while their local stability is determined by eigenvalues of Jacobian matrix of (2.6) at these equilibria.

(a) The trivial equilibrium $O(0, 0)$ always exists and has eigenvalues $r_1(1 - m_1)$, $r_2(1 - m_2)$.

(b) The semi-trivial equilibrium $P_1((1 - m_1)/(1 + d_1), 0)$ exists if $1 - m_1 > 0$, while $P_2(0, (1 - m_2)/(1 + d_2))$ exists if $1 - m_2 > 0$. The eigenvalues of P_i are $-r_i(1 - m_i), -r_j D_j$ with

$$D_j = m_j - \frac{d_i + m_i}{1 + d_i}\left[1 + \frac{e_j(1 - m_i)}{1 + d_i + c_j(1 - m_i)}\right], \quad i, j = 1, 2, \ i \neq j.$$

Stability analysis of system (2.6) is considered in three situations: (i) obligate mutualisms, i.e., $1 - m_1 \leq 0, 1 - m_2 \leq 0$; (ii) obligate-facultative mutualisms, i.e., $1 - m_1 > 0, 1 - m_2 \leq 0$; (iii) facultative mutualisms, i.e., $1 - m_1 > 0, 1 - m_2 > 0$.

3. Obligate mutualisms

In this section, we consider the situation $1 - m_1 \leq 0, 1 - m_2 \leq 0$, which means that neither species can survive in the absence of the other. Denote

$$k_i = \frac{\gamma_i(e_i + c_i + c_i d_i)}{(1 + d_i)^2} - \beta_i, \quad i = 1, 2.$$

Theorem 3.1. *Assume* $1 - m_1 = 0, 1 - m_2 = 0$. *If* $e_1 > 1, e_2 > 1$ *and* $k_1 k_2 > 1$, *then system* (2.6) *has a unique positive equilibrium* P^+, *which is globally asymptotically stable as shown in Figure 2a. Otherwise, all positive solutions of* (2.6) *converge to* O.
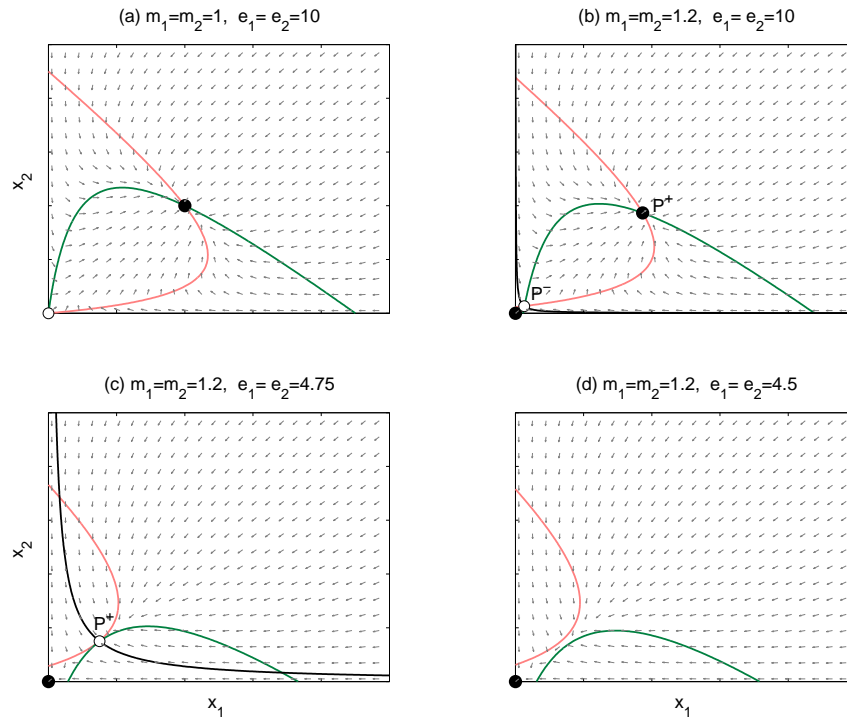
FIGURE 2. Population dynamics of (2.6). Red and green curves
are isoclines L_1 and L_2, and black lines are separatrices of saddle
points. Grey arrows denote the direction and strength of the vector
fields on the portrait, while filled and open circles represent the
stable and unstable equilibria, respectively. (a) Let $m_1 = m_2 =
1, e_1 = e_2 = 10$, $c_1 = c_2 = 0.001, d_1 = d_2 = 0.8$. Then system (2.6)
has a unique positive equilibrium, which is globally asymptotically
stable. (b-c) Fix $m_1 = m_2 = 1.2$, $c_1 = c_2 = 0.001, d_1 = d_2 = 0.8$
and let e_1, e_2 vary. When $e_1 = e_2 = 10$ in (b), there are two positive
equilibria P^- and P^+. P^- is unstable while P^+ is asymptotically
stable. When $e_1 = e_2 = 4.75$ in (c), P^- and P^+ coincide and
form a saddle-node point P^+. Separatrices of the saddle points
subdivide the first quadrant into two regions, which are basins of
attraction of O and P^+ respectively. When $e_1 = e_2 = 4.5$ in (d),
all solutions converge to O.

Proof. Since $1 - m_1 = 1 - m_2 = 0$, we obtain $e_1^{(1)} = e_2^{(1)} = 1$ and $O \in L_1 \cap
L_2$. A direct computation shows that $1/k_1$ and k_2 are slopes of L_1 and L_2 at O,
respectively. From $e_i > 1$, we have $k_i > 0$ and $L_i \cap \operatorname{int} R_+^2 \neq \emptyset, i = 1, 2$. If $1/k_1 < k_2$,
it follows from the convexity of L_1 and L_2 that they have a unique intersection point
P^+ in the first quadrant. By Lemma 2.2, P^+ is globally asymptotically stable. In
other situations, L_1 and L_2 have no intersection point in the first quadrant. Thus,
system (2.6) has no positive equilibrium, which implies that all positive solutions
of (2.6) converge to O by Lemma 2.2.   □

In the following result, we focus on the case of $1 - m_1 \leq 0, 1 - m_2 < 0$, while a similar one can be given for the case of $1 - m_1 < 0, 1 - m_2 \leq 0$.

Theorem 3.2. *Assume $1 - m_1 \leq 0, 1 - m_2 < 0$.*

(i) *Let $e_i > e_i^{(1)}, i = 1, 2$. There exist $e_1^{(2)}$ and $e_2^{(2)}$ such that when $e_1 > e_1^{(2)}$ or $e_2 > e_2^{(2)}$, there are two positive equilibria P^- and P^+ of (2.6) as shown in Figure 2b. P^- is a saddle point while P^+ is asymptotically stable. When $e_1 = e_1^{(2)}$ or $e_2 = e_2^{(2)}$, P^- and P^+ coincide and form a saddle-node point. Separatrices of the saddle point subdivide the first quadrant into two regions, one is the basin of attraction of O while the other is that of P^+, as shown in Figure 2b-c. In other situations, all positive solutions of (2.6) converge to O as shown in Figure 2d.*

(ii) *If $e_1 \leq e_1^{(1)}$ or $e_2 \leq e_2^{(1)}$, then equilibrium O is globally asymptotically stable.*

Proof. (i) When $e_i > e_i^{(1)}$, we obtain $L_i \cap \text{int} R_+^2 \neq \emptyset, i = 1, 2$. It follows from the convexity of L_2 and $\lim_{e_2 \to +\infty} x_2(x_1, e_2) = 1 - x_1$ in (2.12) that there is $e_2^{(2)} > 0$ such that when $e_2 > e_2^{(2)}$, L_1 and L_2 have two intersection points P^- and P^+; when $e_2 = e_2^{(2)}$, P^- and P^+ coincide and the isoclines are tangent. Thus, P^- and P^+ are positive equilibria of (2.6) if $e_1 > e_1^{(1)}, e_2 > e_2^{(1)}$ and $e_2 > e_2^{(2)}$.

The local stability of P^+ can be shown as follows. Let $r_i x_i F_i$ denote the right-hand sides of (2.6). Let k_1^+ (resp. k_2^+) denote the slope of L_1 (resp. L_2) at P^+. From the expression of F_i, we have

$$\frac{1}{k_1^+} = -\frac{\partial F_1}{\partial x_2} \Big/ \frac{\partial F_1}{\partial x_1}\Big|_{P^+}, \quad k_2^+ = -\frac{\partial F_2}{\partial x_1}\Big/ \frac{\partial F_2}{\partial x_2}\Big|_{P^+}$$

where

$$\frac{\partial F_1}{\partial x_1}\Big|_{P^+} = -x_1[1 + \frac{e_1 x_2}{1 + c_1 x_2} + d_1]|_{P^+} < 0,$$

$$\frac{\partial F_2}{\partial x_2}\Big|_{P^+} = -x_2[1 + \frac{e_2 x_1}{1 + c_2 x_1} + d_2]|_{P^+} < 0.$$

The Jacobian matrix of (2.6) at P^+ is

$$J(P^+) = \begin{pmatrix} r_1 x_1 \frac{\partial F_1}{\partial x_1} & r_1 x_1 \frac{\partial F_1}{\partial x_2} \\ r_2 x_2 \frac{\partial F_2}{\partial x_1} & r_2 x_2 \frac{\partial F_2}{\partial x_2} \end{pmatrix}_{P^+}. \tag{3.1}$$

Thus,

$$\text{tr}\, J(P^+) = (r_1 x_1 \frac{\partial F_1}{\partial x_1} + r_2 x_2 \frac{\partial F_2}{\partial x_2})|_{P^+} < 0.$$

Moreover, we have

$$\det J(P^+) = r_1 r_2 x_1 x_2 \Big[\frac{\partial F_1}{\partial x_1} \frac{\partial F_2}{\partial x_2} - \frac{\partial F_1}{\partial x_2} \frac{\partial F_2}{\partial x_1}\Big] = r_1 r_2 x_1 x_2 \frac{\partial F_1}{\partial x_1} \frac{\partial F_2}{\partial x_2}\Big|_{P^+}(1 - \frac{k_2^+}{k_1^+}).$$

Assume $k_1^+ < 0$ as shown in Figure 2b. Then P^+ is above the vertex of L_1. Notice that L_1 and the positive x_2-axis form a convex area Ω_1. At the point P^+, L_2 intersects with L_1 from the inside of Ω_1 to its outside. Thus, if $k_2^+ < 0$, then we have $k_1^+ < k_2^+$ as shown in Figure 2b, which implies that $\det J(P^+) > 0$. If $k_2^+ > 0$, we can see that $\det J(P^+) > 0$.

Assume $k_1^+ > 0$. Then P^+ is below the vertex of L_1. When $k_2^+ > 0$, we have $k_1^+ > k_2^+$, which implies that $\det J(P^+) > 0$. When $k_2^+ \leq 0$, we can see that

$\det J(P^+) > 0$. It follows from convexity of L_1 that $k_1^+ \neq 0$. Thus we have $\det J(P^+) > 0$, which implies that P^+ is asymptotically stable.

Similarly, let k_1^- (resp. k_2^-) denote the slope of L_1 (resp. L_2) at P^-. Then we have $k_1^- < k_2^-$ and $\det J(P^-) < 0$, which implies that P^- is a saddle point. By Lemma 2.2, the omega limit set of any interior point is an equilibrium since system (2.6) is analytic and has no graphic here. Therefore, the stable manifold of P^- subdivide the first quadrant into two regions, one is the basin of attraction of O while the other is that of P^+.

When $e_2 = e_2^{(2)}$, P^- and P^+ coincide and form a saddle-node point [15]. Thus, separatrices of the saddle point subdivide the first quadrant into two regions, one is the basin of attraction of O while the other is that of P^+. A similar discussion can be given for L_1 and $e_1^{(2)}$.

(ii) If $e_1 \leq e_1^{(1)}$ or $e_2 \leq e_2^{(1)}$, there is no positive equilibrium of (2.6), which implies that all solutions of (2.6) converge to O. $\square$

Theorems 3.1-3.2 demonstrate essential features of obligate mutualisms. *First,* mutualisms between species can lead to survival of obligate species. Recall that the mutualistic effect consists of two factors, e.g., $e_1 = \mu_1 \nu_2$, where ν_2 denotes the quantity of resources that an individual of species 2 produces for species 1, and μ_1 is the efficiency of species 1 in converting the resources into fitness. In this section, we focus on the role of resources such as food, while we focus on the role of efficiency in section 6. In the situation considered by Theorem 3.2, neither species can survive in the absence of the other. Theorem 3.2(i) exhibits that they can coexist if (a) mutualistic effects between them are above a threshold ($e_i > e_i^{(1)}$), (b) one of the effects is sufficiently strong (e.g., $e_2 > e_2^{(2)}$), and (c) population densities of the species are large. The reason is that under these conditions, each species can produce abundant food for the other, which results in persistence of both species. Ecologically, this result can provide an explanation for the reason why obligate bacteria can coexist by consuming products of the other. When one of the above conditions is not satisfies, at least one of the species cannot obtain sufficient food from the other, which eventually leads to extinction of both species. Since neither species can survive alone, it is the mutualism that leads to their persistence. A similar discussion can be given for Theorem 3.1.

Second, intermediate mutualism is beneficial in certain parameter ranges. In the situation considered by Theorems 3.1-3.2, we have $1 - m_i \leq 0, i = 1, 2$. $L_1 \cap \text{int } R_+^2 \neq \emptyset$ if $e_1 > e_1^{(1)}$. It follows from the convexity of L_1 that its vertex $\bar{P}(\bar{x}_1, \bar{x}_2)$ is in the first quadrant. For a fix $e_1 (> e_1^{(1)})$, it follows from the monotonicity of L_2 that there is $\bar{e}_2 > 0$ such that when $e_2 = \bar{e}_2$, we have $P^+ = \bar{P}$ and $x_1^+ = \bar{x}_1$. Thus, when $e_2 = \bar{e}_2$, species 1 approaches a maximal density $\bar{x}_1$, as shown in Figure 2b. An over-mutualism ($e_2 > \bar{e}_2$) or under-mutualism ($e_2 < \bar{e}_2$) means that $x_1^+ < \bar{x}_1$, which is not the best for species 1. The reason is as follows: (I) When $e_2 > \bar{e}_2$, the over-mutualism leads to the increase of species 2 who will occupy more sites and will decrease the density of species 1; (II) When $e_2 < \bar{e}_2$, the under-mutualism leads to the decrease of species 2. Thus species 2 cannot produce abundant food for species 1 to approach its maximum. Therefore, *only* the intermediate mutualistic effect $e_2 = \bar{e}_2$ is the best for species 1. A similar discussion can be given for species 2.

Third, extremely strong mutualism will lead to extinction of both species. Indeed, Theorem 3.2(i) exhibits that there is a stable positive equilibrium $P^+(x_1^+, x_2^+)$ if mutualistic effects (e_i) are large. From (2.12), we obtain $\lim_{e_2 \to +\infty} x_2(x_1, e_2) = 1 - x_1$. Since $P_2 \in L_2$, it follows from the convexity of L_1 and L_2 that when $e_2 \to +\infty$, P^+ tends to the x_2-axis with $x_1^+ \to 0$. That is, $\lim_{e_2 \to +\infty} x_1^+ = 0$. Similarly, we have $\lim_{e_1 \to +\infty} x_2^+ = 0$. Therefore, we conclude the following result.

Lemma 3.3. *If $P^+(x_1^+, x_2^+)$ is a positive equilibrium of* (2.6), *then*

$$\lim_{e_2 \to +\infty} x_1^+ = 0, \qquad \lim_{e_1 \to +\infty} x_2^+ = 0.$$

When the mutualistic effect of species 1 on 2 is extremely strong ($e_2 \to +\infty$), Lemma 3.3 shows that species 1 goes to extinction, which implies the extinction of species 2 who cannot survive alone. The reason is that the extremely strong mutualism leads to an explosive growth of species 2 who will occupy most of the sites and drive species 1 into extinction. Thus, both species will go to extinction since neither species can survive alone. Therefore, extremely strong mutualism will lead to extinction of both species.

Finally, extremely weak mutualism will result in extinction of both species. Indeed, when the mutualism is extremely weak (e.g., $e_2 \to 0$), Theorems 3.1-3.2 demonstrate that both species go to extinction. This is because one of the species will get little food from the other and will go to extinction, which implies extinction of both species since neither one can survive alone. Thus, extremely weak mutualism will result in extinction of both species.

4. Obligate-facultative mutualisms

In this section, we consider the situation where one species can persist in the absence of the other but the other cannot survive alone. We focus on the case of $1 - m_1 > 0, 1 - m_2 \leq 0$, while a similar discussion can be given for $1 - m_1 \leq 0, 1 - m_2 > 0$.

When $m_1 \neq 1, m_2 \neq 1$, we denote

$$
\begin{aligned}
e_1^{(3)} &= (c_1 + \frac{1 + d_2}{1 - m_2})(\frac{m_1 + d_2 m_1}{d_2 + m_2} - 1), \\
e_2^{(3)} &= (c_2 + \frac{1 + d_1}{1 - m_1})(\frac{m_2 + d_1 m_2}{d_1 + m_1} - 1).
\end{aligned}
\tag{4.1}
$$

It follows from (2.8) and (2.11) that if $e_1 > e_1^{(3)}$, P_2 is at the right of L_1; if $e_2 > e_2^{(3)}$, P_1 is below L_2.

Theorem 4.1. *Assume $1 - m_1 > 0, 1 - m_2 = 0$. If $e_2 > e_2^{(3)}$, system* (2.6) *has a unique positive equilibrium P^+, which is globally asymptotically stable. Otherwise, all positive solutions of* (2.6) *converge to P_1.*

Proof. From $m_2 = 1$, we have $O \in L_2$. If $e_2 > e_2^{(3)}$, then P_1 is below L_2 and is a saddle point. It follows from the convexity of L_1 and L_2 that they have a unique intersection point P^+ in the first quadrant. Thus system (2.6) has a unique positive equilibrium P^+. By Lemma 2.2, P^+ is globally asymptotically stable. If $e_2 \leq e_2^{(3)}$, system (2.6) has no positive equilibrium, which implies that all positive solutions of (2.6) converge to P_1. $\square$

Assume $1 - m_1 > 0, 1 - m_2 < 0$. When $e_2 > e_2^{(3)}$, equilibrium P_1 is below L_2 and is a saddle point. By a proof similar to that of Theorem 4.1, system (2.6) has a unique positive equilibrium P^+, which is globally asymptotically stable.

Suppose $e_2 < e_2^{(3)}$. Then P_1 is above L_2. When $e_1 \le e_1^{(3)}$, P_2 is at the left of L_1 and system (2.6) has no positive equilibrium. Thus P_1 is globally asymptotically stable. Let $e_1 > e_1^{(3)}$. It follows from the convexity of L_2 and $\lim_{e_2 \to +\infty} x_2(x_1, e_2) = 1 - x_1$ in (2.12) that there is $e_2^{(4)} > 0$ such that when $e_2 > e_2^{(4)}$, there is at least one intersection point of L_1 and L_2 in the first quadrant. Thus, when $e_2 > \max\{e_2^{(2)}, e_2^{(4)}\}$, L_1 and L_2 have two positive intersection points P^- and P^+. By Lemma 2.2, phase-portrait analysis shows that equilibrium P^- is a saddle point and P^+ is asymptotically stable. When $e_2 = e_2^{(2)} > e_2^{(4)}$, P^- and P^+ coincide and form a saddle-node point. In other situations, there is no positive equilibrium of (2.6).

Suppose $e_2 = e_2^{(3)}$. Then $P_1 \in l_2$. When $e_1 > e_1^{(2)}$, there is a unique positive equilibrium P^+, which is globally asymptotically stable. Otherwise, there is no positive equilibrium and all positive solutions of (2.6) converge to P_1. Therefore, we conclude the following result.

Theorem 4.2. *Assume $1 - m_1 > 0$, $1 - m_2 < 0$.*

(i) *If $e_2 > e_2^{(3)}$, system (2.6) has a unique positive equilibrium P^+, which is globally asymptotically stable as shown in Figure 3a.*

(ii) *If $e_2 < e_2^{(3)}$ and $e_1 \le e_1^{(3)}$, then all positive solutions of (2.6) converge to P_1.*

(iii) *Let $e_2 < e_2^{(3)}$ and $e_1 > e_1^{(3)}$.*

(a) *If $e_2 > \max\{e_2^{(2)}, e_2^{(4)}\}$, system (2.6) has two positive equilibria P^- and P^+. P^- is a saddle point and P^+ is asymptotically stable. If $e_2 = e_2^{(2)} > e_2^{(4)}$, P^- and P^+ coincide and form a saddle-node point. The separatrices of the saddle point subdivide the first quadrant into two regions, one is the basin of attraction of P_1 while the other is that of P^+, as shown in Figure 3b.*

(b) *In other situations, system (2.6) has no positive equilibrium and P_1 is globally asymptotically stableas shown in Figure 3b.*

(iv) *Let $e_2 = e_2^{(3)}$. If $e_1 > e_1^{(2)}$, system (2.6) has a unique positive equilibrium P^+, which is globally asymptotically stable. Otherwise, all positive solutions of (2.6) converge to P_1.*

Theorems 4.1-4.2 demonstrate essential features of obligate-facultative mutualisms. *First,* an obligate species can survive by cooperating with a facultative one. In the situation considered by Theorem 4.2, species 1 can persist in the absence of species 2, while species 2 cannot survive alone. If the mutualistic effect of species 1 on 2 is strong ($e_2 > e_2^{(3)}$), Theorem 4.2(i) exhibits that species 2 can survive. The reason is that in this case, species 1 can provide abundant food for species 2, which leads to its survival. Moreover, even when the mutualistic effect of species 1 on 2 is intermediate ($e_2^{(4)} < e_2 < e_2^{(3)}$), Theorem 4.2(iia) demonstrates that species 2 can survive if the effect of species 2 on 1 is strong ($e_1 > \max\{e_1^{(2)}, e_1^{(3)}\}$) and their population densities are large (Here, $e_1 > e_1^{(2)}$ is equivalent to $e_2 > e_2^{(2)}$ in guaranteeing that L_1 and L_2 can intersect in the first quadrant). The reason is that in this case, species 2 can provide abundant food for species 1, which leads to the increase of species 1. Thus, the amount of food produced by species 1 for
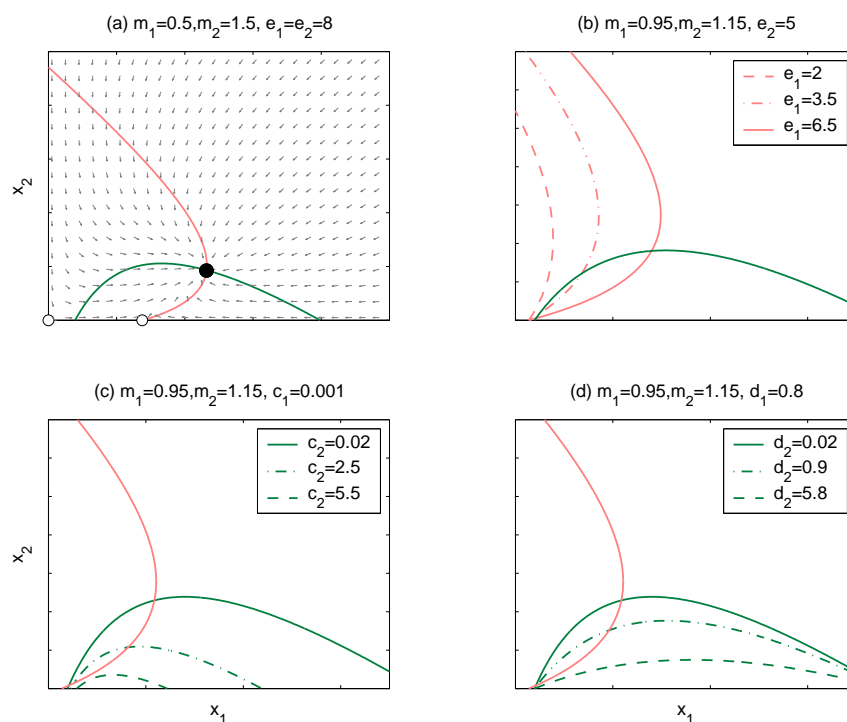
FIGURE 3. (a) Population dynamics of (2.6). Let $m_1 = 0.5, m_2 = 1.5$, $c_i = 0.001, d_i = 0.8, e_i = 8, i = 1, 2$. Then system (2.6) has a unique positive equilibrium, which is globally asymptotically stable. (b) Fix $m_1 = 0.95, m_2 = 1.15, e_2 = 5$, $c_1 = c_2 = 0.001, d_1 = d_2 = 0.8$ and Let e_1 vary. When e_1 increases from 2, 3.5 to 6.5, isocline L_1 increases monotonically while species 2 could persist at $e_1 \geq 3.5$. (c) Fix $m_1 = 0.95, m_2 = 1.15, e_1 = 4.5, e_2 = 5$, $c_1 = 0.001, d_1 = 0.8, d_2 = 0.02$ and let c_2 vary. When c_2 decreases from 5.5, 2.5 to 0.02, isocline L_2 increases monotonically while species 2 could persist at $c_2 = 2.5, 0.02$. (d) Fix $m_1 = 0.95, m_2 = 1.15, e_1 = 4.5, e_2 = 5$, $c_1 = c_2 = 0.001, d_1 = 0.8$ and let d_2 vary. When d_2 decreases from 5.8, 0.9 to 0.02, isocline L_2 increases monotonically while species 2 could persist at $d_2 = 0.9, 0.02$.

2 is enhanced, which leads to the survival of species 2 in return. Hence, Theorem 4.2(iia) exhibits a strategy for obligate species when cooperating with facultative ones: if the mutualistic effect from facultative species is intermediate, the obligate species can survive by strengthening its mutualistic effect on the facultative species (e.g., producing more food or providing better service for the obligate species) and enhancing its population density. A similar discussion can be given for Theorem 4.1.

Second, intermediate mutualism is beneficial in certain parameter ranges. By (2.12), there exists $\check{e}_1$ such that when $e_1 > \check{e}_1$, the vertex $\bar{P}(\bar{x}_1, \bar{x}_2)$ of L_1 is in

the first quadrant, as shown in Figure 3a. Similar to the discussion for obligate mutualisms, there is $\bar{e}_2 > 0$ such that when $e_2 = \bar{e}_2$, species 1 approaches a maximal density $\bar{x}_1$, as shown in Figure 3a. An over-mutualism $(e_2 > \bar{e}_2)$ or under-mutualism $(e_2 < \bar{e}_2)$ means that $x_1^+ < \bar{x}_1$, which is not the best for species 1. Therefore, *only* the intermediate mutualistic effect $e_2 = \bar{e}_2$ is the best for species 1. A similar discussion can be given for species 2.

Third, extremely strong mutualism will result in extinction of one/both species. (a) If the mutualistic effect of species 1 on 2 is extremely strong, Lemma 3.3 exhibits that species 1 goes to extinction, which implies extinction of species 2 who cannot survive alone. Thus, extremely strong mutualism from facultative species to obligate species will result in extinction of both species. (b) If the mutualistic effect of species 2 on 1 is extremely strong, Lemma 3.3 exhibits that species 2 goes to extinction, while species 1 approaches its carrying capacity. Thus, extremely strong mutualism from obligate species to facultative species will result in extinction of the obligate species itself.

Finally, extremely weak mutualism can result in extinction of obligate species. (a) If the mutualistic effect of species 1 on 2 is extremely weak, Theorems 4.1-4.2 show that species 2 goes to extinction because it depends upon the strong mutualism of species 1 for survival. (b) If the mutualistic effect of species 2 on 1 is extremely weak, species 2 goes to extinction when the mutualism from species 1 is not strong. An interesting phenomenon is: when the mutualism from species 1 on 2 is intermediate, Theorem 4.2(iia) shows that species 2 can survive if its mutualism on species 1 is strong. However, if its mutualism on species 1 is weak, species 2 goes to extinction. What a pity!
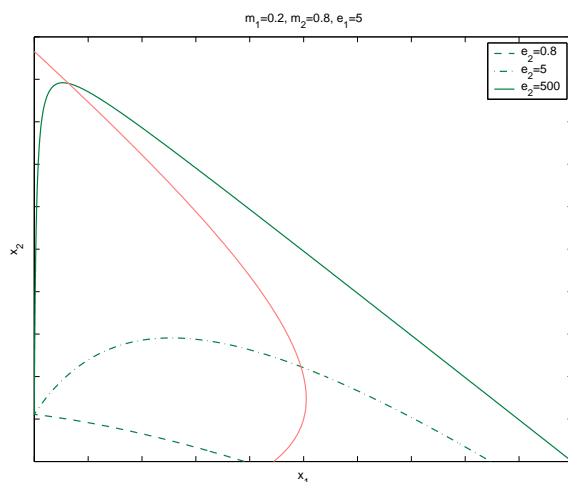
5. FACULTATIVE MUTUALISMS

FIGURE 4. Fix $m_1 = 0.2, m_2 = 0.8, e_1 = 5$, $c_1 = c_2 = 0.001, d_1 = d_2 = 0.8$ and let e_2 vary. When $e_2 = 0.8$, species 2 goes to extinction. When $e_2 = 5$, the two species coexist and form a win-win situation. When $e_2 = 500$(i.e. $e_2 \to +\infty$), species 1 goes to extinction.

In this section, we consider the situation of $1 - m_1 > 0, 1 - m_2 > 0$, where either species can survive in the absence of the other.

Theorem 5.1. *Assume* $1 - m_1 > 0$, $1 - m_2 > 0$.

(i) *If* $e_1 > e_1^{(3)}$ *and* $e_2 > e_2^{(3)}$, *system* (2.6) *has a unique positive equilibrium* P^+, *which is globally asymptotically stable as shown in Figure 4.*

(ii) *If* $e_1 \leq e_1^{(3)}$, *then* P_2 *is globally asymptotically stable. If* $e_2 \leq e_2^{(3)}$, *then* P_1 *is globally asymptotically stable as shown in Figure 4.*

Proof. (i) Since $e_1 > e_1^{(3)}$, P_2 is at the left of L_1 and is a saddle point. Since $e_2 > e_2^{(3)}$, P_1 is below L_2 and is a saddle point. Thus, L_1 and L_2 have intersection points in the first quadrant. Moreover, since L_1 and L_2 have asymptotes $x_2 = -\frac{1+d_1}{e_1+c_1+c_1d_1}$, $x_1 = -\frac{1+d_2}{e_2+c_2+c_2d_2}$ respectively, they have an intersection point in the third quadrant. Thus, L_1 and L_2 have a unique intersection point in the first quadrant by Lemma 2.1. Thus system (2.6) has a unique positive equilibrium P^+. By Lemma 2.2, P^+ is globally asymptotically stable.

(ii) Assume $e_2 \leq e_2^{(3)}$. Then P_1 is above L_2 and is asymptotically stable. Thus L_1 and L_2 have an intersection point in the fourth quadrant. Since they have an intersection point in the third quadrant as shown in (i), L_1 and L_2 have no intersection point in the first quadrant by Lemma 2.1. Thus system (2.6) has no positive equilibrium. By Lemma 2.2, P_1 is globally asymptotically stable. A similar discussion can be given for the case $e_1 \leq e_1^{(3)}$. $\qquad\qquad\square$

Theorem 5.1 demonstrates essential features of facultative mutualisms. *First,* mutualisms can lead to interaction outcomes $(+\ +)$, where each species can approach a density larger than its carrying capacity in the absence of the other. Indeed, when $(1 - m_1)/(1 + d_1) + (1 - m_2)/(1 + d_2) < 1$, it follows from the monotonicity of L_i with e_i that there is a region R_{12} such that when $(e_1, e_2) \in R_{12}$, P^+ is at the right of P_1 and above P_2, which implies that either species approaches a density larger than its carrying capacity in the absence of the other. Thus the interaction outcomes are $(+\ +)$.

Second, intermediate mutualism is beneficial in certain parameter ranges. By (2.12), there exists $\check{e}_1$ such that when $e_1 > \check{e}_1$, the vertex $\bar{P}(\bar{x}_1, \bar{x}_2)$ of L_1 is in the first quadrant. Similar to the discussion for obligate mutualisms, there is $\bar{e}_2 > 0$ such that when $e_2 = \bar{e}_2$, species 1 approaches a maximal density $\bar{x}_1$, as shown in Figure 4. An over-mutualism ($e_2 > \bar{e}_2$) or under-mutualism ($e_2 < \bar{e}_2$) means that $x_1^+ < \bar{x}_1$, which is not the best for species 1. Therefore, *only* the intermediate mutualistic effect $e_2 = \bar{e}_2$ is the best for species 1. A similar discussion can be given for species 2.

Third, extremely strong mutualism will result in extinction of species. If the mutualistic effect of species 1 on 2 is extremely strong ($e_2 \to +\infty$), Lemma 3.3 exhibits that species 1 goes to extinction while species 2 persists. A similar discussion can be given for $e_1 \to +\infty$.

Finally, extremely weak mutualism can result in extinction of species. If the mutualistic effect of species 1 on 2 is extremely weak, Theorem 5.1(ii) exhibits that species 2 goes to extinction while species 1 persists. The reason is that species 2 obtains little food from species 1, which leads to its failure in spatial competition with species 1. A similar discussion can be given for species 1.

6. Discussion

In this article, we extend a lattice gas model of mutualisms in [9] by considering saturated response and self-competition. Global dynamics of the extended model demonstrate some basic properties of mutualisms.

First, mutualisms (i.e. e_i) can lead to survival of mutualists. As discussed in Section 2, the mutualistic effect e_i consists of two factors: one is the quantity of resources provided by collaborators, while the other is the efficiency of the species in converting the resources into fitness. While we focus on resources (food) in Sections 3-5, we consider the efficiency in this section. In the situation considered by Theorem 4.2, species 1 can persist in the absence of species 2 while species 2 cannot survive alone. Theorem 4.2 demonstrate that species 2 can survive if its efficiency in converting the food (provided by species 1) into fitness is high. Even when the efficiency is intermediate, species 2 can survive if it has a large population density and the efficiency of species 1 is high. In numerical simulations of Figure 3b, we fix other parameters and let e_1 vary. Here, the mutualistic effect of species 1 on 2 is intermediate. When e_1 increases from 2 to 6.5, isocline L_1 increases monotonically and species 2 with large initial density can survive if $e_1 \geq 3.5$, which confirms that species 2 with large population density can survive if the efficiency of species 1 is high. A similar discussion can be given for Theorems 4.1, 7.1, 7.2, 8.1.

Second, intermediate mutualisms are favorable under certain parameter conditions, while extremely weak/strong mutualisms will lead to extinction of species. For example, when the mutualistic effect of species 2 on 1 is strong such that $\bar{x}_2 > 0$, there exists an interval of e_2 (intermediate mutualisms), in which species 1 can approach a density larger than its carrying capacity in the absence of species 2. On the other hand, as discussed in section 6, extremely weak mutualisms lead to little benefit to mutualists, while extremely strong mutualisms results in dramatic growth of one species, which implies extinction of the other. Therefore, extremely weak/strong mutualisms will lead to extinction of species. A similar discussion can be given for Theorems 7.1,7.2,8.1.

Third, parameters c_i and d_i play an important role in survival of species. By (2.6), e_i/c_i represents the saturation level while $1/c_i$ is the half-saturation density. Thus, the decrease of c_i promotes persistence of species i by enlarging the functional response $e_i x_j/(1 + c_i x_j)$ in (2.6). Similarly, d_i represents the degree of intraspecific competition in species i. The decrease of d_i promotes the growth of species i by enlarging the function $x_i = x_i(x_j, d_i)$ in (2.7). In Figure 3c, we fix other parameters but let c_2 vary. When c_2 decreases from 5.5 to 0.02, isocline L_2 increases monotonically while species 2 could persist at $c_2 = 0.02$. In Figure 3d, we fix $m_1 = 0.95$, $m_2 = 1.15$, $e_1 = 4.5$, $e_2 = 5$, $c_1 = c_2 = 0.001$, $d_1 = 0.8$ and let d_2 vary. When d_2 decreases from 5.8 to 0.02, isocline L_2 increases monotonically while species 2 could persist at $d_2 = 0.02$. Therefore, the decrease of c_i and/or d_i promotes persistence of the species.

Finally, population densities are crucial to survival of species. When neither species can survive in the absence of the other and the mutualistic effects are strong, Theorem 3.2 exhibits that the species can persist only if their initial densities are large. Otherwise, both species go to extinction. Therefore, Theorem 3.2 predicts the Allee effect in obligate mutualisms of two species. Similar discussions can be given for cases considered by Theorems 3.1,4.1-4.2.

Iwata et al [9] displayed seven typical types of dynamics of a lattice gas model in their Figure 4 and section 5.2. However, they did not obviously exhibit the type of coexistence in Theorems 4.2(i) as shown in Figure 3a. Indeed, if $c_i = d_i = 0$, $i = 1, 2$, then system (2.6) becomes the model in [9]. Let $c_i = d_i = 0$, $i = 1, 2$, $m_1 = 0.5$, $m_2 = 1.5$, $e_1 = e_2 = 8$. Numerical simulations could show that species 2 could survive by the mutualism of species 1. Thus Theorem 4.2(i) extends the result by Iwata et al [9].

Although there is no real data to verify dynamics of the model, the model demonstrates mechanisms which seems to be consistent with ecological situations. For example, as shown in Theorems 4.1-4.2 and Figure 3, different mutualistic effects (or exclusive competitions) can lead to different components of syntrophic colonies, which is crucial to the development of colony architectures. Thus, this model may be useful in the study of cooperative association like bacterial species. Although the model is simple, its global dynamics demonstrate some essential features of mutualisms, which may be helpful for understanding complexity of mutualisms in real situations.

7. Appendix: The case of $r_1 > 0, r_2 = 0$

In this case, species 1 can reproduce alone but species 2 cannot, while a similar discussion can be given for the case $r_1 = 0, r_2 > 0$, as shown by Iwata et al [9]. Denote

$$m_1 := \frac{m_1}{r_1}, \quad e_1 := \frac{e_1}{r_1}, \quad d_1 := \frac{d_1}{r_1}$$

then model (2.4) can be rewritten as

$$\frac{dx_1}{dt} = r_1 x_1 \big[-m_1 + (1 + \frac{e_1 x_2}{1 + c_1 x_2})(1 - x_1 - x_2) - d_1 x_1 \big],$$
$$\frac{dx_2}{dt} = x_2 \big[-m_2 + \frac{e_2 x_1}{1 + c_2 x_1}(1 - x_1 - x_2) - d_2 x_2 \big]. \tag{7.1}$$

The isoclines L_2 of (7.1) can be rewritten as

$$(\bar{\alpha}_1 - x_1 - x_2)(d_2 + e_2 x_1) = \bar{\gamma}_1$$

where

$$\bar{\alpha}_1 = \frac{e_2 + d_2 - m_2 c_2}{e_2}, \quad \bar{\gamma}_1 = m_1 + \frac{d_2(e_2 + d_2 - m_2 c_2)}{e_2}.$$

Thus, L_2 is a parabola with asymptotes

$$L_{21} : \bar{\alpha}_1 - x_1 - x_2 = 0, \quad L_{22} : x_1 = -\frac{d_2}{e_2}.$$

Denote

$$\bar{e}_1^{(1)} = e_1^{(1)}, \ \bar{e}_2^{(1)} = c_2 m_2 + 2m_2 + 2\sqrt{m_2(1 + c_2)}.$$

When $e_i > \bar{e}_i^{(1)}$, we have $L_i \cap \text{int } R_+^2 \neq \emptyset$, $i = 1, 2$.

The equilibria of (7.1) are as follows, while their local stability is determined by eigenvalues of Jacobian matrix of (7.1) at these equilibria.

(a) Equilibrium $O(0,0)$ always exists and has eigenvalues $r_1(1 - m_1), -m_2$.

(b) Equilibrium $P_1((1 - m_1)/(1 + d_1), 0)$ exists if $1 - m_1 > 0$. The eigenvalues of P_1 are $-r_1(1 - m_1), -\bar{D}_2$ with

$$\bar{D}_2 = m_2 - \frac{e_2(1 - m_1)(d_1 + m_1)}{(1 + d_1)[1 + d_1 + c_2(1 - m_1)]}.$$

(c) There are at most two positive equilibria P^- and P^+ of (7.1) by a proof similar to that in section 2. When they exist, P^- is a saddle point and P^+ is asymptotically stable.

Assume $1 - m_1 \leq 0$ and $e_i > \bar{e}_i^{(1)}, i = 1, 2$. Then $L_i \cap \operatorname{int} R_+^2 \neq \emptyset, i = 1, 2$. It follows from the convexity of L_2 that there is $\bar{e}_2^{(2)} > 0$ such that when $e_2 > \bar{e}_2^{(2)}$, L_1 and L_2 have two intersection points P^- and P^+; when $e_2 = \bar{e}_2^{(2)}$, P^- and P^+ coincide and the isoclines are tangent. Thus, P^- and P^+ are positive equilibria of (2.6) if $e_1 > \bar{e}_1^{(1)}, e_2 > \bar{e}_2^{(1)}$ and $e_2 \geq \bar{e}_2^{(2)}$. A similar discussion can be given for L_1 and $\bar{e}_1^{(2)}$. If $e_1 < \bar{e}_1^{(2)}$ or $e_2 < \bar{e}_2^{(2)}$, there is no positive equilibrium of (7.1), which implies that all solutions of (7.1) converge to O. Therefore, we conclude the following result.

Theorem 7.1. *Assume $1 - m_1 \leq 0$.*

(i) *Let $e_i > \bar{e}_i^{(1)}$, $i = 1, 2$. If $e_1 > \bar{e}_1^{(2)}$ or $e_2 > \bar{e}_2^{(2)}$, there are two positive equilibria P^- and P^+ of (7.1). P^- is a saddle point while P^+ is asymptotically stable. If $e_1 = \bar{e}_1^{(2)}$ or $e_2 = \bar{e}_2^{(2)}$, P^- and P^+ coincide and form a saddle-node point. Separatrices of the saddle point subdivide the first quadrant into two regions, one is the basin of attraction of O while the other is that of P^+. In other situations, all positive solutions of (7.1) converge to O.*

(ii) *If $e_1 \leq \bar{e}_1^{(1)}$ or $e_2 \leq \bar{e}_2^{(1)}$, then equilibrium O is globally asymptotically stable.*

Assume $1 - m_1 > 0$. Denote

$$\bar{e}_1^{(3)} = (c_1 - \frac{d_2}{m_2})(\frac{m_1 d_2}{m_2 + d_2} - 1), \quad \bar{e}_2^{(3)} = \frac{m_2(1 + d_1)[1 + d_1 + c_2(1 - m_1)]}{(1 - m_1)(d_1 + m_1)}.$$

When $e_2 > \bar{e}_2^{(3)}$, P_1 is below L_2 and $\bar{D}_2 < 0$; when $e_1 > \bar{e}_1^{(3)}$, $P_2(0, -m_2/d_2)$ is at the right of L_1. It follows from the convexity of L_2 that there is $\bar{e}_2^{(4)} > 0$ such that when $e_2 > \bar{e}_2^{(4)}$, there is at least one positive intersection point of L_1 and L_2. Thus, when $e_1 > \bar{e}_1^{(3)}$ and $e_2 > \max\{\bar{e}_2^{(2)}, \bar{e}_2^{(4)}\}$, L_1 and L_2 have two intersection points. Similar to the discussion in section 2, we conclude the following result.

Theorem 7.2. *Assume $1 - m_1 > 0$.*

(i) *If $e_2 > \bar{e}_2^{(3)}$, system (7.1) has a unique positive equilibrium P^+, which is globally asymptotically stable.*

(ii) *If $e_2 < \bar{e}_2^{(3)}$ and $e_1 \leq \bar{e}_1^{(3)}$, then all positive solutions of (7.1) converge to P_1.*

(iii) *Let $e_2 < \bar{e}_2^{(3)}$ and $e_1 > \bar{e}_1^{(3)}$.*

   (a) *If $e_2 > \max\{\bar{e}_2^{(2)}, \bar{e}_2^{(4)}\}$, system (7.1) has two positive equilibria P^- and P^+. P^- is a saddle point and P^+ is asymptotically stable. If $e_2 = \bar{e}_2^{(2)} > \bar{e}_2^{(4)}$, P^- and P^+ coincide and form a saddle-node point. The separatrices of the saddle point subdivide the first quadrant into two regions, one is the basin of attraction of P_1 while the other is that of P^+.*

   (b) *In other situations, system (7.1) has no positive equilibrium and P_1 is globally asymptotically stable.*

(iv) *Let $e_2 = \bar{e}_2^{(3)}$. If $e_1 > \bar{e}_1^{(2)}$, system (7.1) has a unique positive equilibrium P^+, which is globally asymptotically stable. Otherwise, all positive solutions of (7.1) converge to P_1.*

8. Appendix: The case of $r_1 = r_2 = 0$

In this case, neither species can reproduce alone, which is the same as reactions in a male-female system as shown by Iwata et al [9]. Let $r_1 = r_2 = 0$. Model (2.4) becomes

$$\frac{dx_1}{dt} = x_1[-m_1 + \frac{e_1 x_2}{1 + c_1 x_2}(1 - x_1 - x_2) - d_1 x_1]$$
$$\frac{dx_2}{dt} = x_2[-m_2 + \frac{e_2 x_1}{1 + c_2 x_1}(1 - x_1 - x_2) - d_2 x_2]. \tag{8.1}$$

The isoclines L_i of (8.1) can be rewritten as

$$L_1 : (\hat{\alpha}_1 - x_1 - x_2)(d_1 + e_1 x_2) = \hat{\gamma}_1,$$
$$L_2 : (\hat{\alpha}_2 - x_1 - x_2)(d_2 + e_2 x_1) = \hat{\gamma}_2$$

where

$$\hat{\alpha}_i = \frac{e_i + d_i - m_i c_i}{e_i}, \quad \hat{\gamma}_i = m_i + \frac{d_i(e_i + d_i - m_i c_i)}{e_i}, \; i = 1, 2.$$

Thus, L_i is a parabola with asymptotes

$$L_{i1} : \hat{\alpha}_i - x_1 - x_2 = 0, \quad L_{i2} : x_j = -\frac{d_i}{e_i}, \quad i \neq j, \; i, j = 1, 2.$$

Denote

$$\hat{e}_1^{(1)} = c_1 m_1 + 2m_1 + 2\sqrt{m_1(1 + c_1)}, \quad \hat{e}_2^{(1)} = c_2 m_2 + 2m_2 + 2\sqrt{m_2(1 + c_2)}.$$

When $e_i > \hat{e}_i^{(1)}$, we have $L_i \cap \operatorname{int} R_+^2 \neq \emptyset, i = 1, 2$.

The equilibria of (8.1) are as follows, while their local stability is determined by eigenvalues of Jacobian matrix of (8.1) at these equilibria.

(a) Equilibrium $O(0, 0)$ always exists and has eigenvalues $-m_1, -m_2$.

(b) There are at most two positive equilibria P^- and P^+ of (8.1) by a proof similar to that in section 2. When they exist, P^- is a saddle point and P^+ is asymptotically stable.

Assume $e_i > \hat{e}_i^{(1)}$, $i = 1, 2$. Then $L_i \cap \operatorname{int} R_+^2 \neq \emptyset$, $i = 1, 2$. It follows from the convexity of L_2 that there is $\hat{e}_2^{(2)} > 0$ such that when $e_2 > \hat{e}_2^{(2)}$, L_1 and L_2 have two intersection points P^- and P^+; when $e_2 = \hat{e}_2^{(2)}$, P^- and P^+ coincide and the isoclines are tangent. Thus, P^- and P^+ are positive equilibria of (8.1) if $e_1 > \hat{e}_1^{(1)}, e_2 > \hat{e}_2^{(1)}$ and $e_2 \geq \hat{e}_2^{(2)}$. A similar discussion can be given for L_1 and $\hat{e}_1^{(2)}$. If $e_1 < \hat{e}_1^{(2)}$ or $e_2 < \hat{e}_2^{(2)}$, there is no positive equilibrium of (8.1), which implies that all solutions of (8.1) converge to O.

Therefore, we conclude the following result.

Theorem 8.1. (i) *Let $e_i > \hat{e}_i^{(1)}, i = 1, 2$. If $e_1 > \hat{e}_1^{(2)}$ or $e_2 > \hat{e}_2^{(2)}$, there are two positive equilibria P^- and P^+ of (8.1). P^- is a saddle point while P^+ is asymptotically stable. If $e_1 = \hat{e}_1^{(2)}$ or $e_2 = \hat{e}_2^{(2)}$, P^- and P^+ coincide and form a saddle-node point. Separatrices of the saddle point subdivide the first quadrant into two regions, one is the basin of attraction of O while the other is that of P^+. In other situations, all positive solutions of (8.1) converge to O.*

(ii) *If $e_1 \leq \hat{e}_1^{(1)}$ or $e_2 \leq \hat{e}_2^{(1)}$, then equilibrium O is globally asymptotically stable.*

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