Dynamics of a lattice gas system of three species

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Abstract. This paper considers a mutualism system of three species in which each species provides resource for the next one in a one-directional loop, while there exists spatial competition among them. The system is characterized by a lattice gas model and the cases of obligate mutualisms, obligate-facultative mutualisms and facultative mutualisms are considered. Using dynamical systems theory, it is shown that (i) the mutualisms can lead to coexistence of species; (ii) A weak mutualism or an extremely strong mutualism will result in extinction of species, while even the superior facultative species will be driven into extinction by its over-strong mutualism on the next one; (iii) Initial population density plays a role in the coexistence of species. It is also shown that when there exists weak mutualism, an obligate species can survive by providing more benefit to the next one, and the inferior facultative species will not be driven into extinction if it can strengthen its mutualism on the next species. Moreover, Hopf bifurcation, saddle-node bifurcation and bifurcation of heteroclinic cycles are shown in the system. Projection method is extended to exhibit bistability in the three-dimensional model: when saddle-node bifurcation occurs, stable manifold of the saddle-node point divides $\text{int}R_+^3$ into two basins of attraction of two equilibria. Furthermore, Lyapunov method is applied to

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exhibit unstability of heteroclinic cycles. Numerical simulations confirm and extend our results.

Keywords. Cooperation; competition; persistence; Hopf bifurcation; saddle-node bifurcation; heteroclinic cycles

1 Introduction

Mutualism between species is often regarded as the interaction in which the increase of one species is beneficial to the growth of the other. However, in many situations, mutualism is density-dependant. For example, Mullerian mimics are mutualistic through facilitating the training of predators in recognizing unpalatable prey, while they are competitive since they share resources (Gilbert, 1983). Many bacterial species survive in a mutualistic association by consuming products of another one, while there is spatial competition between them since they live in the same body (Keller et al., 2006). In a light bulb powered by bacteria, several different species of microorganisms are contained in a jar, which form a closed ecosystem of synthetic biology (Zaiken et al., 2014). Each organism plays a role in the recycling of vital nutrients that each of the other microbes need to survive. Among the microorganisms, the bacteria of *E. coli* can produce light like jellyfish and the bulb could glow and recharge repeatedly. Although the microorganisms are mutualistic by recycling nutrients for others, there is spatial competition among them since they live in the same jar. Such mutualisms with negative feedbacks widely exist in natural environment (Zhang 2003, Begon et al. 2006, Agrawal et al. 2007, Holland and DeAngelis, 2010, Wang and Wu, 2011).

Iwata et al. (2011) established a lattice gas model to study a syntrophic association of species with spatial competition, in which the lattice consists of many sites. One empty site can be occupied by one individual of the species, and a site occupied by an individual becomes empty when the individual goes extinct (Harris, 1974; Konno, 1994). Any pair of sites on the lattice interact in a random and independent way. When an empty site is met by an individual of a species, it would be

Figure 1: Mutualisms with bidirectional interactions among three species. The red and solid lines represent positive effects, while the black and dashed lines represent negative effects. The red arrow from N_1 to N_2 denotes that species 1 provides benefit (e.g., food) for species 2, so does species 2 for species 3 and species 3 for species 1. On the other hand, the black arrow from N_i to N_j denotes the spatial competition between the species since they live on the same lattice.

occupied by the species if an offspring of the individual is placed on it. Thus, there exists spatial competition among different species because of limitation of sites on lattice. On the other hand, the species are mutualistic since each species provides benefit for the next one, which promotes reproduction of the species. Iwata et al. (2011) studied the lattice gas system of two species. Local stability analysis and numerical simulations demonstrate seven types of dynamics in the system. Wang and Wu (2015) exhibited the eighth type of dynamics by global stability analysis on an extended model. For more references, we refer to Tainaka (1989), Ruan and He (1998), Tainaka et al. (2014), Yokoi et al. (2014), Wang et al. (2015), etc. Since syntrophic associations usually consist of more than two species, extending the model of Iwata et al. (2011) to multiple species and demonstrating essential properties of the mutualisms is necessary.

In this paper, we consider a lattice gas model of three species $\mathcal{N}_1, \mathcal{N}_2$ and $\mathcal{N}_3$, whose population densities are represented by N_1, N_2 and N_3 respectively. Mutualisms between the species are cyclic as shown in Fig. 1: species 1 is beneficial to species 2, species 2 is beneficial to species 3, and species 3 is beneficial to species 1 in return. Thus, in our model, the three species are mutualistic in a one-directional

loop, while there exists competition among the species.

On the lattice, a site is labeled by $\mathcal{N}_1$ if it is occupied by an individual of species 1. When it is empty, it is labeled by O . If sites $\mathcal{N}_1$ and O interact, then the site O will become $\mathcal{N}_1$ in a birth rate B_1 . If a site is occupied by $\mathcal{N}_1$, then it will become O in a mortality rate m_1 . Thus the reactions in species 1 can be described by

where the birth rate of species 1 satisfies $B_1 = r_1 + a_1 N_3$ (Verhulst, 1838). For simplicity, we use Type I Holling functional response ($a_1 N_3$) to describe the mutualistic effect from species 3 to 1 (Hofbauer and Sigmund, 1998). Parameter r_1 represents the intrinsic growth rate of species 1 in the absence of species 3, and the term “ a_1 ” represents the mutualistic effect of an individual of species 3 on the growth of species 1. a_1 consists of two factors: $a_1 = e_1 s_3$, where s_3 represents the quantity of resource produced by an individual of species 3 and e_1 denotes the efficiency of species 1 in converting the resource into fitness. Since m_1 denotes the mortality rate of $\mathcal{N}_1$, we have $r_1 \geq 0, a_1 > 0, m_1 > 0$. In the following discussions, we focus on the resource (e.g., s_3) produced by another species, while a similar discussion can be given for the efficiency (e.g., e_1).

Similarly, the reactions in species $\mathcal{N}_2$ can be described by

where the birth rate of $\mathcal{N}_2$ satisfies $B_2 = r_2 + a_2 N_1$. Parameters r_2, a_2 have meanings similar to those for $\mathcal{N}_1$. Thus, we obtain $r_2 \geq 0, a_2 > 0, m_2 > 0$.

The reactions in species $\mathcal{N}_3$ can be described by

where the birth rate of $\mathcal{N}_3$ satisfies $B_3 = r_3 + a_3 N_2$. Parameters r_3, a_3 have meanings similar to those for $\mathcal{N}_1$. Thus, we have $r_3 \geq 0, a_3 > 0, m_3 > 0$.

Based on reactions in (1.1-1.3), we formed a mutualism model to characterize the lattice gas system and considered the cases of obligate mutualisms, obligate-facultative mutualisms and facultative mutualisms. In obligate mutualisms, neither species can survive alone and dynamics of the model demonstrate mechanisms by which the three species can coexist. In obligate-facultative mutualisms, at least one species cannot survive alone and dynamics of the model exhibit mechanisms by which the species can survive. In facultative mutualisms, each species can survive alone and dynamics of the model display mechanisms by which the mutualisms lead to coexistence/extinction of species.

The paper is organized as follows. The model is described in Section 2. Sections 3 and 4 exhibit stability of subsystems and equilibria. Sections 5, 6 and 7 consider obligate mutualisms, obligate-facultative mutualisms and facultative mutualisms, respectively. Discussion is in Section 8.

2 Model

First, we consider a lattice gas system of a single species $\mathcal{N}_1$. Let $N_3 = 0$ in reaction (1.1). When the number of sites on lattice is large, the “contact process” (Harris, 1974; Konno, 1994) in the system can be described by an ordinary differential equation, which is regarded as the mean-field theory of lattice model:

$$\frac{dN_1}{dt} = r_1 N_1 (1 - N_1) - m_1 N_1$$

where N_1 and $1 - N_1$ are the densities of species $\mathcal{N}_1$ and empty sites, respectively. The first and second terms in the right-hand side come from the birth and mortality processes. The equation can be rewritten as

$$\frac{dN_1}{dt} = R_1 N_1 \left(1 - \frac{N_1}{K_1}\right), \quad R_1 = r_1 - m_1, \quad K_1 = \frac{r_1 - m_1}{r_1}$$

which is a canonical logistic equation (Verhulst, 1838).

Second, we consider the lattice gas system of three species described by reactions (1.1)-(1.3). Similar to the lattice gas model of a single species, the three-species

system can be described by

$$\begin{aligned}\frac{dN_1}{dt} &= B_1 N_1 (1 - N_1 - N_2 - N_3) - m_1 N_1 \\ \frac{dN_2}{dt} &= B_2 N_2 (1 - N_1 - N_2 - N_3) - m_2 N_2 \\ \frac{dN_3}{dt} &= B_3 N_3 (1 - N_1 - N_2 - N_3) - m_3 N_3\end{aligned}\tag{2.1}$$

where $B_i = r_i + a_i N_{i-1}$, $i = 1, 2, 3$ and we count indices mod 3 in this work. The expression of $(1 - N_1 - N_2 - N_3)$ denotes the density of empty sites, which could be assumed to satisfy $1 - N_1 - N_2 - N_3 \geq 0$ as shown in the proof of Theorem 2.1. Thus, on the righthand side of each equation, the first term represents the birth process of the species, while the second one denotes the mortality process.

For simplicity, we take the replacement in (2.1)

$$\alpha_i = \frac{a_i}{m_i}, \quad \gamma_i = \frac{r_i}{m_i}, \quad i = 1, 2, 3$$

while we still use a_i and r_i to denote α_i and γ_i in the following discussions. Then system (2.1) becomes

$$\begin{aligned}\frac{dN_1}{dt} &= m_1 N_1 [-1 + (r_1 + a_1 N_3)(1 - N_1 - N_2 - N_3)] \\ \frac{dN_2}{dt} &= m_2 N_2 [-1 + (r_2 + a_2 N_1)(1 - N_1 - N_2 - N_3)] \\ \frac{dN_3}{dt} &= m_3 N_3 [-1 + (r_3 + a_3 N_2)(1 - N_1 - N_2 - N_3)].\end{aligned}\tag{2.2}$$

Since we are concerned with solutions of (2.2) with nonnegative initial values, we have $N_i(t) \geq 0$ as $t > 0, i = 1, 2, 3$. We also have the following results on the boundedness of solutions of system (2.2).

Theorem 2.1. *Solutions of system (2.2) are bounded.*

Proof. Assume $N_1 + N_2 + N_3 \geq 1$. Then from the righthand sides of (2.2), we have $dN_i/dt < 0, i = 1, 2, 3$. Thus, $\limsup_{t \rightarrow \infty} N_1(t) + N_2(t) + N_3(t) \leq 1$, which implies that solutions of system (2.2) are bounded. $\square$

Theorem 2.1 exhibits that orbits of (2.2) will finally satisfy $N_1(t) + N_2(t) + N_3(t) \leq 1$. Thus, in the following discussions, we focus on the region

$$\Omega = \{(N_1, N_2, N_3) \in R_+^3 : N_1 + N_2 + N_3 \leq 1\}.$$

3 Subsystems

In this section, we demonstrate dynamics of subsystems in (2.2). We focus on the subsystem consisting of species 1 and 2, while similar results are given for other subsystems in Corollary 3.3.

Let $N_3 = 0$. Then system (2.2) becomes the (N_1, N_2) -subsystem

$$\begin{aligned}\frac{dN_1}{dt} &= m_1 N_1 [-1 + r_1(1 - N_1 - N_2)] \\ \frac{dN_2}{dt} &= m_2 N_2 [-1 + (r_2 + a_2 N_1)(1 - N_1 - N_2)].\end{aligned}\tag{3.1}$$

It follows from Theorem 2.1 that solutions of (3.1) are bounded. The following result exhibits nonexistence of periodic solution of (3.1).

Theorem 3.1. *System (3.1) admits no periodic solution.*

Proof. Let P and Q be the righthand sides of (3.1), respectively. Let $D = 1/(N_1 N_2)$, which is defined in the interior of the first quadrant $\text{int}R_+^2$. Then we have

$$\frac{\partial(DP)}{\partial N_1} + \frac{\partial(DQ)}{\partial N_2} = -\frac{m_1 r_1}{N_2} - \frac{m_2(r_2 + a_2 N_1)}{N_1} < 0.$$

It follows from Bendixson-Dulac Theorem that (3.1) has no periodic solution. $\square$

The Jacobian matrix of (3.1) is

$$J = \begin{pmatrix} m_1[-1 + (1 - 2N_1 - N_2)r_1] & -m_1 r_1 N_1 \\ m_2 N_2[a_2(1 - 2N_1 - N_2) - r_2] & m_2[-1 + (r_2 + a_2 N_1)(1 - N_1 - 2N_2)] \end{pmatrix}.$$

Local stability of equilibria of (3.1) can be determined by eigenvalues of J , which is shown as follows.

(a) $E_0 = (0, 0)$. The trivial equilibrium E_0 always exists with eigenvalues

$$\mu_0^{(1)} = m_1(r_1 - 1), \quad \mu_0^{(2)} = m_2(r_2 - 1).$$

(b) $E_1 = (1 - \frac{1}{r_1}, 0)$. The semi-trivial equilibrium E_1 exists if $r_1 > 1$, in which it has eigenvalues

$$\mu_1^{(1)} = m_1(1 - r_1), \quad \mu_1^{(2)} = \frac{m_2}{r_1}[r_2 - r_1 + a_2(1 - \frac{1}{r_1})].$$

(c) $E_2 = (0, 1 - \frac{1}{r_2})$. The semi-trivial equilibrium E_2 exists if $r_2 > 1$, in which it has eigenvalues

$$\mu_2^{(1)} = m_1(1 - r_2), \quad \mu_2^{(2)} = \frac{m_2(r_2 - r_1)}{r_2}.$$

(d) $E_{12}(\bar{N}_1, \bar{N}_2)$. The positive equilibrium E_{12} exists if $\bar{N}_1 > 0$ and $\bar{N}_2 > 0$ where

$$\bar{N}_1 = \frac{r_1 - r_2}{a_2}, \quad \bar{N}_2 = 1 - \frac{1}{r_1} - \frac{r_1 - r_2}{a_2}.$$

The Jacobian matrix of (3.1) at E_{12} is

$$J_{12} = \begin{pmatrix} -m_1 r_1 \bar{N}_1 & -m_1 r_1 \bar{N}_1 \\ (\frac{a_2}{r_1} - r_1) m_2 \bar{N}_2 & -m_2 r_1 \bar{N}_2 \end{pmatrix}$$

which means that

$$\text{trace} J_{12} = -m_1 r_1 \bar{N}_1 - m_2 r_2 \bar{N}_2, \quad \det J_{12} = m_1 m_2 a_2 \bar{N}_1 \bar{N}_2.$$

Global dynamics of (3.1) are determined by relative positions of its isoclines.

Denote

$$l_1 : 1 - N_1 - N_2 = \frac{1}{r_1}$$

$$l_2 : (r_2 + a_2 N_1)(1 - N_1 - N_2) = 1.$$

Thus, l_1 is a straight line and l_2 is a hyperbola with asymptotes

$$1 - N_1 - N_2 = 0, \quad N_1 = -\frac{r_2}{a_2}.$$

The expression of l_2 can be written as

$$N_2(a_2, N_1) = 1 - N_1 - \frac{1}{r_2 + a_2 N_1}$$

then we have

$$\frac{\partial^2 N_2(a_2, N_1)}{\partial N_1^2} = \frac{-2a_2^2}{(r_2 + a_2 N_1)^3} < 0$$

which implies that the function $N_2 = N_2(a_2, N_1)$ is convex upward as shown in Fig. 2a.

Dynamics of (3.1) are shown in the following theorem.

Theorem 3.2. *Consider the (N_1, N_2) -subsystem (3.1).*

- (i) Assume $r_1 \leq 1$. If $r_2 > 1$, equilibrium E_2 of (3.1) is globally asymptotically stable. Otherwise, all solutions of (3.1) converge to E_0 .
- (ii) Assume $r_1 > 1, r_2 \leq 1$. If $\mu_1^{(2)} > 0$, equilibrium E_{12} is globally asymptotically stable. Otherwise, all solutions of (3.1) converge to E_1 , as shown in Fig. 2a.
- (iii) Assume $r_1 > 1, r_2 > 1$. If $r_1 \leq r_2$, all solutions of (3.1) converge to equilibrium E_2 , as shown in Fig. 2b. If $r_1 > r_2$ and $\mu_1^{(2)} > 0$, equilibrium E_{12} is globally asymptotically stable, as shown in Fig. 2c. If $r_1 > r_2$ and $\mu_1^{(2)} \leq 0$, all solutions of (3.1) converge to E_1 , as shown in Fig. 2d.

Proof. (i) Since $r_1 \leq 1$, we have $dN_1/dt < 0$ by the first equation of (3.1), which implies that $\lim_{t \rightarrow \infty} N_1(t) = 0$. Thus, if $r_2 > 1$, we have $\lim_{t \rightarrow \infty} N_2(t) = 1 - \frac{1}{r_2}$ by the second equation of (3.1). If $r_2 \leq 1$, we have $\lim_{t \rightarrow \infty} N_2(t) = 0$.

(ii) Since $r_2 \leq 1 < r_1$, E_2 is not in the first quadrant and we obtain

$$\mu_0^{(1)} > 0, \quad \mu_0^{(2)} \leq 0, \quad \mu_1^{(1)} < 0.$$

Thus E_0 is a saddle point. Indeed, assume $\mu_0^{(2)} = 0$. Let $V(N) = \log N_1$. Then

$$\frac{dV}{dt}|_{(3.1), E_0} = m_1(r_1 - 1) = \mu_0^{(1)} > 0$$

which implies that $N_1(t)$ increases exponentially in a small neighborhood of E_0 . Thus, E_0 cannot be the ω -limit point of any solution of (3.1) in $\text{int}R_+^2$ by the Lyapunov Theorem (Hofbauer and Sigmund, 1998). Since the positive N_2 -axis is a stable manifold of E_0 , E_0 is a saddle point.

If $\mu_1^{(2)} > 0$, then E_1 is a saddle point. It follows from Theorem 3.1 that all solutions of (3.1) converge to equilibria. Since equilibria E_0 and E_1 are unstable, E_{12} is globally asymptotically stable. If $\mu_1^{(2)} \leq 0$, then $\bar{N}_2 \leq 0$ and there is no positive equilibrium of (3.1). Since E_0 is unstable, E_1 is globally asymptotically stable by Theorem 3.1, as shown in Fig. 2a.

(iii) Since $r_1 > 1$ and $r_2 > 1$, we obtain

$$\mu_0^{(1)} > 0, \quad \mu_0^{(2)} > 0, \quad \mu_1^{(1)} < 0, \quad \mu_2^{(1)} < 0$$

which implies that E_0 is an unstable node.

If $r_1 \leq r_2$, then $\bar{N}_1 \leq 0$ and there is no positive equilibrium of (3.1). Since $\mu_1^{(1)} < 0, \mu_1^{(2)} > 0$, equilibrium E_2 is a saddle point. It follows from boundedness of solutions of (3.1) that E_2 is globally asymptotically stable, as shown in Fig. 2b.

Assume $r_1 > r_2$. If $\mu_1^{(2)} > 0$, then E_{12} is globally asymptotically stable by a proof similar to the case of $r_2 \leq 1 < r_1$, as shown in Fig. 2c. If $\mu_1^{(2)} \leq 0$, then $\bar{N}_2 \leq 0$ and there is no positive equilibrium of (3.1). E_1 is globally asymptotically stable by a proof similar to the case of $r_2 \leq 1 < r_1$, as shown in Fig. 2d. $\square$

We consider other subsystems as follows. Let $N_1 = 0$. Then system (2.2) becomes the (N_2, N_3) -subsystem

$$\begin{aligned}\frac{dN_2}{dt} &= m_2 N_2 [-1 + r_2 (1 - N_2 - N_3)] \\ \frac{dN_3}{dt} &= m_3 N_3 [-1 + (r_3 + a_3 N_2) (1 - N_2 - N_3)].\end{aligned}\tag{3.2}$$

Let $N_2 = 0$. Then system (2.2) becomes the (N_3, N_1) -subsystem

$$\begin{aligned}\frac{dN_3}{dt} &= m_3 N_3 [-1 + r_3 (1 - N_3 - N_1)] \\ \frac{dN_1}{dt} &= m_1 N_1 [-1 + (r_1 + a_1 N_2) (1 - N_3 - N_1)].\end{aligned}\tag{3.3}$$

Denote

$$\begin{aligned}\mu_j^{(j+1)} &= \frac{m_{j+1}}{r_j} [r_{j+1} - r_j + a_{j+1} (1 - \frac{1}{r_j})], \quad E_j = (1 - \frac{1}{r_j}, 0), \quad E_{j+1} = (0, 1 - \frac{1}{r_{j+1}}) \\ E_{j,j+1}(\bar{N}_j, \bar{N}_{j+1}) &\text{ with } \bar{N}_j = \frac{r_j - r_{j+1}}{a_{j+1}}, \quad \bar{N}_{j+1} = 1 - \frac{1}{r_j} - \frac{r_j - r_{j+1}}{a_{j+1}}, \quad j = 2, 3.\end{aligned}$$

Dynamics of (3.2) and (3.3) are given in the following corollary, which is obtained from Theorem 3.2.

Corollary 3.3. *Consider the subsystem (3.j), $j = 2, 3$.*

- (i) *Assume $r_j \leq 1$. If $r_{j+1} > 1$, equilibrium E_{j+1} of (3.j) is globally asymptotically stable. Otherwise, all solutions of (3.j) converge to E_0 .*
- (ii) *Assume $r_j > 1, r_{j+1} \leq 1$. If $\mu_j^{(j+1)} > 0$, equilibrium $E_{j,j+1}$ is globally asymptotically stable. Otherwise, all solutions of (3.j) converge to E_j .*

(iii) Assume $r_j > 1, r_{j+1} > 1$.

(iiia) If $r_j \leq r_{j+1}$, all solutions of (3.j) converge to equilibrium E_{j+1} .

(iiib) Suppose $r_j > r_{j+1}$. If $\mu_j^{(j+1)} > 0$, equilibrium $E_{j,j+1}$ is globally asymptotically stable. Otherwise, all solutions of (3.j) converge to E_j .

Remark 3.4. The subsystem (3.1) is different from the two-species system studied by Wang and Wu (2015). First, the model is different. While each species provides benefit for the other in their model, species 2 does not provide benefit for species 1 in system (3.1). Second, the result is different. For example, while obligate species can coexist in the system studied by Wang and Wu (2015), they will go extinct by Theorem 3.2(i) in system (3.1).

4 Equilibrium

In this section, we are concerned about equilibria of system (2.2). First, the Jacobian matrix of system (2.2) takes the form

$$A = \begin{pmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{pmatrix}$$

where

$$a_{11} = m_1[-1 + (r_1 + a_1 N_3)(1 - 2N_1 - N_2 - N_3)], \quad a_{12} = -m_1 N_1(r_1 + a_1 N_3)$$

$$a_{13} = m_1 N_1[-r_1 + a_1(1 - N_1 - N_2 - 2N_3)], \quad a_{21} = m_2 N_2[-r_2 + a_2(1 - 2N_1 - N_2 - N_3)]$$

$$a_{22} = m_2[-1 + (r_2 + a_2 N_1)(1 - N_1 - 2N_2 - N_3)], \quad a_{23} = -m_2 N_2(r_2 + a_2 N_1), \quad a_{31} = -N_3(r_3 + a_3 N_2)$$

$$a_{32} = m_3 N_3[-r_3 + a_3(1 - N_1 - 2N_2 - N_3)], \quad a_{33} = m_3[-1 + (r_3 + a_3 N_2)(1 - N_1 - N_2 - 2N_3)].$$

We now consider the equilibria and their eigenvalues of the corresponding Jacobian matrices. Let $\lambda_i^{(j)}$ denotes the the eigenvalue of equilibrium P_i in the N_j -axis direction.

(a) $O(0, 0, 0)$. The trivial equilibrium O has eigenvalues

$$\lambda_0^{(1)} = m_1(r_1 - 1), \quad \lambda_0^{(2)} = m_2(r_2 - 1), \quad \lambda_0^{(3)} = m_3(r_3 - 1).$$

(b) $P_1(1 - \frac{1}{r_1}, 0, 0)$. The semi-trivial equilibrium P_1 has eigenvalues

$$\lambda_1^{(1)} = m_1(1 - r_1), \quad \lambda_1^{(2)} = \frac{m_2}{r_1} \left[r_2 - r_1 + \frac{a_2(r_1 - 1)}{r_1} \right], \quad \lambda_1^{(3)} = m_3 \left(\frac{r_3}{r_1} - 1 \right).$$

Similarly, equilibrium $P_2(0, 1 - \frac{1}{r_2}, 0)$ has eigenvalues

$$\lambda_2^{(1)} = m_1 \left(\frac{r_1}{r_2} - 1 \right), \quad \lambda_2^{(2)} = m_2(1 - r_2), \quad \lambda_2^{(3)} = \frac{m_3}{r_2} \left[r_3 - r_2 + \frac{a_3(r_2 - 1)}{r_2} \right].$$

Equilibrium $P_3(0, 0, 1 - \frac{1}{r_3})$ has eigenvalues

$$\lambda_3^{(1)} = \frac{m_1}{r_3} \left[r_1 - r_3 + \frac{a_1(r_3 - 1)}{r_3} \right], \quad \lambda_3^{(2)} = m_2 \left(\frac{r_2}{r_3} - 1 \right), \quad \lambda_3^{(3)} = m_3(1 - r_3).$$

(c) $P_{12}(\bar{N}_1, \bar{N}_2, 0)$. When equilibrium P_{12} exists in the first quadrant, it is globally asymptotically stable on the (N_1, N_2) -plane by Theorem 3.2. Thus, we are concerned with its eigenvalue in the N_3 -axis direction

$$\lambda_{12}^{(3)} = \frac{m_3}{r_1} (r_3 - r_1 + a_1 \bar{N}_2) \quad \text{with} \quad \bar{N}_2 = 1 - \frac{1}{r_1} - \frac{r_1 - r_2}{a_2}. \quad (4.1)$$

Similarly, equilibrium $P_{23}(0, \hat{N}_2, \hat{N}_3)$ has an eigenvalue in the N_1 -axis direction

$$\lambda_{23}^{(1)} = \frac{m_1}{r_2} (r_1 - r_2 + a_2 \hat{N}_3) \quad \text{with} \quad \hat{N}_3 = 1 - \frac{1}{r_2} - \frac{r_2 - r_3}{a_3}. \quad (4.2)$$

Equilibrium $P_{31}(\tilde{N}_1, 0, \tilde{N}_3)$ has an eigenvalue in the N_2 -axis direction

$$\lambda_{31}^{(2)} = \frac{m_2}{r_3} (r_2 - r_3 + a_3 \tilde{N}_1) \quad \text{with} \quad \tilde{N}_1 = 1 - \frac{1}{r_3} - \frac{r_3 - r_1}{a_1}. \quad (4.3)$$

(d) $P^*(N_1, N_2, N_3)$. The positive equilibrium P^* can be obtained by the right-hand side of system (2.2). A direct computation shows that N_1 satisfies

$$a_2 M N_1^2 - D_2 N_1 + a_1 a_3 - r_2 C_2 = 0$$

where

$$M = a_1 a_2 + a_2 a_3 + a_3 a_1, \quad C_1 = a_2 a_3 + a_2 r_3 + a_3 r_2 - r_1(a_2 + a_3)$$

$$C_2 = a_3a_1 + a_3r_1 + a_1r_3 - r_2(a_3 + a_1), \quad C_3 = a_1a_2 + a_1r_2 + a_2r_1 - r_3(a_1 + a_2)$$

$$D_i = a_iC_i - r_iM, \quad i = 1, 2, 3.$$

Thus we have two roots of N_1

$$N_1^- = \frac{D_2 - \sqrt{\Delta_1}}{2a_2M}, \quad N_1^+ = \frac{D_2 + \sqrt{\Delta_1}}{2a_2M}$$

where

$$\Delta_i = D_{i+1}^2 - 4a_{i+1}M(a_ia_{i+2} - r_{i+1}C_{i+1}), \quad i = 1, 2, 3 \quad \text{and } i = i \bmod 3.$$

Similarly, we can obtain expressions of N_2 and N_3 . Thus there are at most two positive equilibria of (2.2)

$$\begin{aligned} P^- &= (N_1^-, N_2^-, N_3^-) = \left(\frac{D_2 - \sqrt{\Delta_1}}{2a_2M}, \frac{D_3 - \sqrt{\Delta_2}}{2a_3M}, \frac{D_1 - \sqrt{\Delta_3}}{2a_1M} \right) \\ P^+ &= (N_1^+, N_2^+, N_3^+) = \left(\frac{D_2 + \sqrt{\Delta_1}}{2a_2M}, \frac{D_3 + \sqrt{\Delta_2}}{2a_3M}, \frac{D_1 + \sqrt{\Delta_3}}{2a_1M} \right). \end{aligned} \quad (4.4)$$

The Jacobian matrix of (2.2) at a positive equilibrium $P^*(N_1^*, N_2^*, N_3^*)$ is

$$A|_{P^*} = \begin{pmatrix} \alpha_1 & \alpha_1 & \beta_1 \\ \beta_2 & \alpha_2 & \alpha_2 \\ \alpha_3 & \beta_3 & \alpha_3 \end{pmatrix}$$

where

$$\begin{aligned} \alpha_1 &= -N_1^*(r_1 + a_1N_3^*), \quad \alpha_2 = -N_2^*(r_2 + a_2N_1^*), \quad \alpha_3 = -N_3^*(r_3 + a_3N_2^*) \\ \beta_1 &= \frac{a_1 - (r_1 + a_1N_3^*)^2}{r_1 + a_1N_3^*}N_1^*, \quad \beta_2 = \frac{a_2 - (r_2 + a_2N_1^*)^2}{r_2 + a_2N_1^*}N_2^*, \quad \beta_3 = \frac{a_3 - (r_3 + a_3N_2^*)^2}{r_3 + a_3N_2^*}N_3^*. \end{aligned}$$

The characteristic equation of $A|_{P^*}$ is

$$\lambda^3 + b_1\lambda^2 + b_2\lambda + b_3 = 0$$

where

$$b_1 = -(\alpha_1 + \alpha_2 + \alpha_3) > 0, \quad b_2 = \alpha_1(\alpha_2 - \beta_2) + \alpha_2(\alpha_3 - \beta_3) + \alpha_3(\alpha_1 - \beta_1)$$

$$b_3 = \alpha_1\alpha_2\beta_3 + \alpha_1\alpha_3\beta_2 + \alpha_2\alpha_3\beta_1 - \beta_1\beta_2\beta_3 - 2\alpha_1\alpha_2\alpha_3.$$

Denote $\bar{\Delta}_1 = b_1, \bar{\Delta}_2 = b_1b_2 - b_3, \bar{\Delta}_3 = b_3\Delta_2$. Then $\bar{\Delta}_1 > 0$. From Hurwitz criterion, we conclude the following result.

Theorem 4.1. *Assume that P^* is a positive equilibrium of system (2.2). If*

$$b_3 > 0, \quad b_1 b_2 - b_3 > 0$$

then P^ is asymptotically stable.*

The result by Yu (2005) shows that when $\bar{\Delta}_2 = 0$, Hopf bifurcation occurs in system (2.2). Thus, we have the following result.

Theorem 4.2. *Assume that P^* is a positive equilibrium of system (2.2). If $b_1 b_2 = b_3$, then Hopf bifurcation occurs at P^* in system (2.2).*

Proposition 4.3. *Assume $m_i = m, r_i = r, i = 1, 2, 3$. The ω -limit set of solutions of system (2.2) consists of equilibria, while the α -limit set consists of equilibria and infinity.*

Proof. From (2.2) we have

$$\begin{aligned} \frac{d}{dt} \left(\frac{N_1}{N_3} \right) &= B(N) \frac{N_1}{N_3} \left(a_1 - a_3 \frac{N_2}{N_3} \right) \\ \frac{d}{dt} \left(\frac{N_2}{N_3} \right) &= B(N) \frac{N_2}{N_3} \left(a_2 \frac{N_1}{N_3} - a_3 \frac{N_2}{N_3} \right) \end{aligned} \quad (4.5)$$

with

$$B(N) = \frac{m(1 - N_1 - N_2 - N_3)}{N_3} > 0, \quad (N_1, N_2, N_3) \in \text{int}\Omega.$$

Denote

$$x_1 = \frac{N_1}{N_3}, \quad x_2 = \frac{N_2}{N_3}.$$

From equation (4.5), we have

$$\begin{aligned} \frac{dx_1}{dt} &= B(N) x_1 (a_1 - a_3 x_2) \\ \frac{dx_2}{dt} &= B(N) x_2 (a_2 x_1 - a_3 x_2). \end{aligned} \quad (4.6)$$

Under a strictly monotonic change in time scale, system (4.6) is topologically equivalent to the following Lotka-Volterra equations (Hofbauer and Sigmund, 1998)

$$\begin{aligned} \frac{dx_1}{d\tau} &= x_1 (a_1 - a_3 x_2) \\ \frac{dx_2}{d\tau} &= x_2 (a_2 x_1 - a_3 x_2). \end{aligned} \quad (4.7)$$

Let f and g be the righthand sides of (4.7). Denote $D(x_1, x_2) = 1/(x_1 x_2)$, which is defined in the interior of the first quadrant $\text{int}R_+^2$. Then we have

$$\frac{\partial(Df)}{\partial x_1} + \frac{\partial(Dg)}{\partial x_2} = -\frac{a_3}{x_1} < 0$$

which implies that there is no periodic solution of (4.7) by the Dulac's criterion (Hofbauer and Sigmund, 1998).

System (4.7) has two equilibria. $O(0, 0)$ is unstable, while $\bar{x}(\bar{x}_1, \bar{x}_2)$ is asymptotically stable with

$$\bar{x}_1 = \frac{a_1}{a_2}, \quad \bar{x}_2 = \frac{a_1}{a_3}.$$

Thus, $\bar{x}$ is globally asymptotically stable in system (4.7).

Let $M(t) = (M_1(t), M_2(t), M_3(t))$ be an orbit of (2.2) in the ω -limit set of (2.2). From the global stability of $\bar{x}$ in (4.7), we have

$$\frac{M_1(t)}{M_3(t)} = \frac{a_1}{a_2}, \quad \frac{M_2(t)}{M_3(t)} = \frac{a_1}{a_3}.$$

Thus we have $M_1(t) = a_1 M_3(t)/a_2$, $M_2(t) = a_1 M_3(t)/a_3$. It follows from the third equation of (2.2) that $M_3(t)$ satisfies

$$\frac{dM_3}{dt} = m M_3 \left\{ -1 + (r + a_1 M_3) \left[1 - \left(\frac{a_1}{a_2} + \frac{a_1}{a_3} + 1 \right) M_3 \right] \right\}. \quad (4.8)$$

Since the ω -limit set of (4.8) consists of equilibria, so does the ω -limit set of (2.2). Similarly, since the α -limit set of (4.8) consists of equilibria and infinity, so does the α -limit set of (2.2) in $\text{int}R_+^3$. $\square$

5 Obligate mutualisms

In this section, we consider obligate mutualisms (i.e., $r_i < 1, i = 1, 2, 3$), which means that neither species can survive alone. By Theorem 4.1, the three species can coexist at equilibrium P^+ if P^+ is positive and asymptotically stable. Because conditions in Theorem 4.1 are difficult to check, we consider a symmetric situation of (2.2) and demonstrate characteristics of obligate mutualisms by global dynamics of the system.

The symmetric situation is described by

$$m_i = m, \quad a_i = a, \quad r_i = r < 1, \quad i = 1, 2, 3. \quad (5.1)$$

Denote

$$\Delta_0 = a^2 - 6(2 - r)a + 9r^2, \quad a^\pm = 3(2 - r \pm 2\sqrt{1 - r}).$$

Thus, $\Delta_0 > 0$ if and only if $a > a^+$ or $a < a^-$.

Theorem 5.1. *Let (5.1) hold.*

(i) *Assume $a \geq a^+$. If $a > a^+$, there are two positive equilibria P^+ and P^- . P^+ is asymptotically stable while P^- is a saddle point. If $a = a^+$, equilibria P^+ and P^- coincide and form a saddle-node point. The global stable manifold S^2 of P^- divides $\text{int}R_+^3$ into two regions: one is the basin of attraction of P^+ , while the other is that of O , as shown in Fig. 3.*

(ii) *If $a < a^+$, all solutions of (2.2) converge to O .*

Proof. It follows from (2.2) and (5.1) that the positive equilibrium P^* has the form of (N, N, N) with

$$3aN^2 - (a - 3r)N + 1 - r = 0 \quad (5.2)$$

which has two roots

$$N^\pm = \frac{a - 3r \pm \sqrt{\Delta_0}}{6a}.$$

We can see that there are positive equilibria of (2.2) if and only if $a \geq a^+$. Indeed, (a) when $a \geq a^+$, we have $\Delta_0 \geq 0$ and $a - 3r \geq a^+ - 3r = 6[1 - r + \sqrt{1 - r}] > 0$. Thus, $N^+ + N^- = (a - 3r)/(3a) > 0$ and $N^+N^- = (1 - r)/(3a) > 0$, which implies that system (2.2) has two positive equilibria. (b) When $a^- < a < a^+$, we have $\Delta_0 < 0$, which implies that system (2.2) has no positive equilibrium. (c) When $a \leq a^-$, we have $\Delta_0 \geq 0$ and $a - 3r \leq a^- - 3r = 6[1 - r - \sqrt{1 - r}] < 0$. Thus, $N^+ + N^- = (a - 3r)/(3a) < 0$ and $N^+N^- = (1 - r)/(3a) > 0$, which implies that system (2.2) has no positive equilibria.

(i) Assume $a > a^+$. Then system (2.2) has two positive equilibria $P^\pm$. We show stability of $P(N, N, N)$ by applying Theorem 4.1. From the notation in Theorem

4.1, we have

$$\alpha_i = \alpha = -N(r + aN), \beta_i = \beta = -N[r + aN - a/(r + aN)]$$

$$b_1 = -3\alpha > 0, \quad b_2 = 3\alpha(\alpha - \beta), \quad b_3 = -(\alpha - \beta)^2(2\alpha + \beta).$$

Then we obtain

$$b_1 b_2 - b_3 = -(\alpha - \beta)[6\alpha^2 + (\alpha^2 + \alpha\beta + \beta^2)] > 6a\alpha^2/(r + aN) > 0$$

$$b_3|_{N^\pm} = -\frac{a^2}{18(r + aN^\pm)^3}[(a + 3r)^2 - 12a \pm (a + 3r)\sqrt{(a + 3r)^2 - 12a}].$$

Thus we have $b_3|_{N^+} > 0$ and $b_3|_{N^-} < 0$. It follows from Hurwitz criterion that all eigenvalues of P^+ have negative real parts, which implies that P^+ is asymptotically stable. Let λ_i be the eigenvalues of P^- , $i = 1, 2, 3$. Since $\lambda_1 + \lambda_2 + \lambda_3 = -b_1 < 0$ and $\lambda_1 \lambda_2 \lambda_3 = -b_3|_{N^-} > 0$, two eigenvalues of P^- have negative real parts and the third eigenvalue is positive. Thus, P^- has a two-dimensional stable manifold s^2 in a small neighborhood of P^- by the Stable Manifold Theorem (Perko, 2001). By Proposition 4.3, the α -limit set of orbits of (2.2) on s^2 consists of equilibria or infinity. Since equilibria O and P^+ are asymptotically stable, the α -limit set of orbits (except P^-) on s^2 is infinity. Thus, the local stable manifold s^2 can be expanded to a global stable manifold S^2 by

$$S^2 = \bigcup_{t \leq 0, N(0) \in s^2} N(t).$$

By Proposition 4.3, the ω -limit set of orbits of (2.2) consists of equilibria. Therefore, the global stable manifold S^2 divides the first quadrant into two regions: one is the basin of attraction of P^+ , while the other is that of O , as shown in Fig. 3.

Assume $a = a^+$. Then P^+ and P^- coincide and form a saddle-node point P^- , which is shown as follows. Let $\mathbf{f}(N, a)$ be the righthand side of (2.2). According to the Sotomayer's Theorem (Perko, 2011), a saddle-node bifurcation occurs at (P^-, a^+) if (a) the matrix $C = D\mathbf{f}(P^-, a^+)$ has two eigenvalues with negative real parts and has a simple eigenvalue $\lambda = 0$ with eigenvector v , while C^T has an eigenvector w corresponding to the eigenvalue $\lambda = 0$. (b) The following conditions are satisfied

$$w^T \mathbf{f}_a(P^-, a^+) \neq 0, \quad w^T [D^2 \mathbf{f}(P^-, a^+)(v, v)] \neq 0.$$

A direct computation shows that

$$C = \begin{pmatrix} c_0 & c_1 & c_2 \\ c_2 & c_0 & c_1 \\ c_1 & c_2 & c_0 \end{pmatrix}$$

with $c_0 = c_1 = -N(r + aN)$, $c_2 = -N[(r + aN) - a(1 - 3N)]$. The matrix C is circulant and has eigenvalues (Hofbauer and Sigmund, 1998)

$$\lambda_0 = 0, \quad \lambda_{1,2} = -\frac{aN(1 - 3N)}{2} \pm i\frac{\sqrt{3}a(1 - 3N)}{2}$$

while $v = (1, 1, 1)$ and $w = (1, 1, 1)$ are eigenvectors of C and C^T corresponding to the eigenvalue $\lambda = 0$.

Since $1 - 3N = (a^+ + 3r)/2a^+ > 0$, the real parts of $\lambda_{1,2}$ are negative. Direct computations show that

$$w^T \mathbf{f}_a(P^-, a^+) = 3mN^2(1 - 3N) > 0, \quad w^T [D^2 \mathbf{f}(P^-, a^+)(v, v)] = -3m(a - 3r) < 0$$

which implies that P^- is a saddle-node point as $a = a^+$. Moreover, we can see that there is a center manifold $L_0 : N_1 = N_2 = N_3$. On the straight line L_0 , solutions of (2.2) above P^- converge to P^+ , while those below P^- converge to O .

(ii) Assume $a < a^+$. Then system (2.2) has no positive equilibrium. By Proposition 4.3, the ω -limit set of orbits of (2.2) consists of equilibria. Since O is the unique nonnegative equilibrium and is asymptotically stable, all solutions of (2.2) converge to O . $\square$

Theorem 5.1 demonstrates basic properties of obligate mutualisms, in which each species cannot survive alone. *First*, mutualisms can lead to coexistence of the three species. As shown in Theorem 5.1(i), the three species with high initial densities can coexist at equilibrium P^+ if the mutualistic effect between them is large ($a \geq a^+$). Moreover, from (4.1) we have $\lim_{a \rightarrow \infty} N^+ = 1/3$, which implies that the three species would occupy almost all sites on lattice if each of the mutualistic effects is large. Thus, balanced strong mutualisms (i.e., a_1, a_2 and a_3 increase synchronously) are

beneficial to expansion of the system. The biological reason is that with the strong mutualisms, each species can provide sufficient food for the next one, which leads to survival/expansion of each species in return. Since neither species can survive alone, it is the mutualism that leads to coexistence of the species.

Second, a weak mutualism can result in extinction of all species. Indeed, when a mutualistic effect is small (e.g., $a_1 < 1 - r_1$), the comparison theorem (Cosner, 1996) shows that the first equation of (2.2) satisfies

$$\frac{dN_1}{dt} \leq m_1 N_1 [-1 + (r_1 + a_1)(1 - N_1 - N_2 - N_3)] < -m_1 N_1 (N_1 + N_2 + N_3) < 0$$

where $(N_1, N_2, N_3) \in \Omega$. Thus we have $\lim_{t \rightarrow \infty} N_1(t) = 0$. From Theorem 3.2 we obtain $\lim_{t \rightarrow \infty} N_i(t) = 0, i = 2, 3$. Thus one weak mutualism (e.g., a_1) can result in extinction of the three species although other mutualisms (e.g., a_2 and a_3) may be strong. The reason is that when the food produced by species 3 is not sufficient for survival of species 1, species 1 goes extinct, which results in extinction of species 2 and 3 that cannot survive alone.

Finally, initial population density plays a role in the survival of species. As shown in Theorem 5.1(i), the three species with strong mutualisms can coexist at equilibrium P^+ if their initial densities are high. The reason is that with the high densities, each species can produce a large amount of food for the next one, which leads to the survival of itself in return. However, when the densities are low, the amount of food for each species is not sufficient and all species go extinct.

Remark 5.2. In order to show global dynamics of (2.2), Theorem 5.1 considers a symmetric case of (5.1) and exhibits three properties of obligate mutualisms. When the condition in (5.1) is not satisfied, the properties are still valid for general cases of obligate mutualisms. We focus on the first property, while similar discussion can be given for others. Indeed, Theorem 4.1 implies that mutualisms can lead to species coexistence by showing local dynamics of (2.2): if the condition in Theorem 4.1 is satisfied, equilibrium P^* is locally asymptotically stable, which means that the three species coexist at P^* when their initial densities are near P^* .

6 Obligate-facultative mutualisms

There are two types of obligate-facultative mutualisms: one facultative species with two obligate species (F-O-O), and two facultative species with one obligate species (F-F-O).

6.1 F-O-O mutualisms

Without loss of generality, we assume $r_1 > 1 \geq \max\{r_2, r_3\}$, which implies that species 1 can survive alone but the others cannot.

By Theorem 3.2, equilibrium O is globally asymptotically stable on the (N_2, N_3) -plane, while P_1 is globally asymptotically stable on the (N_3, N_1) -plane. When $\lambda_1^{(2)} > 0$, equilibrium P_{12} exists and is globally asymptotically stable on the (N_1, N_2) -plane. Thus, if $\lambda_{12}^{(3)} > 0$, system (2.2) is uniformly persistent by the Acyclic Theorem (Butler and Waltman 1986, Butler et al. 1986, Freedman and Moson 1990, Freedman et al. 1994). If $\lambda_1^{(2)} \leq 0$, P_1 is globally asymptotically stable on the (N_1, N_1) -plane, and thus is asymptotically stable in R_+^3 ; if $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, P_{12} is asymptotically stable, which implies that system (2.2) is not persistent. Therefore, we conclude the following result.

Theorem 6.1. *Assume $r_1 > 1, r_2 \leq 1, r_3 \leq 1$.*

- (i) *If $\lambda_1^{(2)} > 0$ and $\lambda_{12}^{(3)} > 0$, system (2.2) is uniformly persistent.*
- (ii) *If $\lambda_1^{(2)} \leq 0$, or $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, system (2.2) is not persistent.*

Denote

$$\bar{a}_2 = \frac{r_1(r_1 - r_2)}{r_1 - 1}, \quad \bar{a}_3 = \frac{r_2(r_2 - r_3)}{r_2 - 1}, \quad \hat{a}_3 = \frac{r_1 - r_3}{\bar{N}_2}, \quad \hat{a}_1 = \frac{r_2 - r_1}{\hat{N}_3} \quad (6.1)$$

where $\bar{N}_2$ and $\hat{N}_3$ are defined in Section 4. Then the condition of $\lambda_1^{(2)} > 0$ can be written as $a_2 > \bar{a}_2$, while $\lambda_{12}^{(3)} > 0$ is $a_3 > \hat{a}_3$.

Theorem 6.1 demonstrates basic properties of F-O-O mutualisms. *First*, mutualisms can lead to persistence of the system. In the situation of Theorem 6.1(i),

species 2 and 3 cannot survive alone while species 1 can persist in the absence of others. System (2.2) is persistent if the mutualistic effects are large ($a_2 > \bar{a}_2$, $a_3 > \hat{a}_3$).

Second, a weak mutualism can result in extinction of one/two species. As shown in Theorem 6.1(ii), if the mutualistic effect of species 1 on 2 is small ($a_2 < \bar{a}_2$), species 2 and 3 with low initial densities go extinct since P_1 is asymptotically stable. When $a_2 > \bar{a}_2$ but $a_3 < \hat{a}_3$, species 3 with low initial density will go extinct since P_{12} is asymptotically stable.

Third, the obligate species can survive by strengthening its mutualism on the next one when there is weak mutualism. Indeed, while weak mutualism implies asymptotical stability of P_1 or P_{12} , the positive equilibrium P^+ can still be asymptotically stable under the conditions of Theorem 4.1. In numerical simulations of Fig. 4, we have $\bar{a}_2 = 2.2$. If $a_2 = 2.5$, then $\hat{a}_3 = 27.5$. Fig. 4a shows that the system persists when $a_2 (= 2.5 > \bar{a}_2)$ and $a_3 (= 30 > \hat{a}_3)$ are large. However, when $a_2 (= 2)$ is small, species 2 and 3 go extinct as shown in Fig. 4b. On the other hand, when $a_2 (= 2)$ is small but $a_1 (= 28)$ is large, species 2 and 3 can survive as shown in Fig. 4c. Moreover, when $a_3 (= 20)$ is small but $a_1 (= 30)$ is large, species 3 can still survive as shown in Fig. 4d. Similar simulation can show that when both of a_2 and a_3 are small but a_1 is large, species 3 can survive. Similar discussion can be given for the survival of species 2 by enhancing a_3 when a_1 is small.

Finally, initial density plays a role in coexistence of species. In the situation of Fig. 4c, since $a_2 < \bar{a}_2$, both P_1 and P^+ are asymptotically stable. Thus, initial densities in the basin of attraction of P^+ imply coexistence of species, while those in the basin of attraction of P_1 imply extinction of species 2 and 3. A similar discussion can be given for the situation of Fig. 4d, where both P_{12} and P^+ are asymptotically stable.

6.2 F-F-O mutualisms

Without loss of generality, we consider two situations: $r_3 \leq 1 < r_1 \leq r_2$ and $r_3 \leq 1 < r_2 < r_1$, which implies that species 1 and 2 can survive alone but species 3

cannot. When $r_2 < r_1$, species 1 and 2 are called the superior and inferior facultative species, respectively.

(I) The situation of $r_3 \leq 1 < r_1 \leq r_2$

By Theorem 3.2, equilibrium P_1 is globally asymptotically stable on the (N_3, N_1) -plane, while P_2 is globally asymptotically stable on the (N_1, N_2) -plane. If $\lambda_2^{(3)} > 0$, then P_{23} exists. Thus, when $\lambda_{23}^{(1)} > 0$, the Acyclic Theorem implies that system (2.2) is uniformly persistent. If $\lambda_2^{(3)} \leq 0$, then P_2 is globally asymptotically stable on the (N_2, N_3) -plane and thus is asymptotically stable in R_+^3 ; if $\lambda_2^{(3)} > 0$ but $\lambda_{23}^{(1)} < 0$, then P_{23} is asymptotically stable, which imply that system (2.2) is not persistent. Therefore, we conclude the following result.

Theorem 6.2. *Assume $r_3 \leq 1 < r_1 \leq r_2$.*

- (i) *If $\lambda_2^{(3)} > 0$ and $\lambda_{23}^{(1)} > 0$, system (2.2) is uniformly persistent.*
- (ii) *If $\lambda_2^{(3)} \leq 0$, or $\lambda_2^{(3)} > 0$ but $\lambda_{23}^{(1)} < 0$, system (2.2) is not persistent.*

(II) The situation of $r_3 \leq 1 < r_2 < r_1$

By Theorem 3.2, P_1 is globally asymptotically stable on the (N_3, N_1) -plane. If $\lambda_1^{(2)} > 0$, then P_{12} exists. If $\lambda_2^{(3)} > 0$, then P_{23} exists and we have $\lambda_{23}^{(1)} > 0$ by $r_2 < r_1$. If $\lambda_2^{(3)} \leq 0$, then P_2 is globally asymptotically stable on the (N_2, N_3) -plane.

Assume $\lambda_2^{(3)} = 0$. Then no positive solution of (2.2) converges to P_2 . Indeed, let $V(N) = \ln N_1$. Then

$$\frac{dV}{dt}|_{(2.2), P_2} = m_1 \left(\frac{r_1}{r_2} - 1 \right) = \mu_2^{(1)} > 0$$

which implies that $N_1(t)$ increases exponentially in a small neighborhood of P_2 . Thus, P_2 cannot be the ω -limit point of any solution of (2.2) in $\text{int} R_+^3$ by the Lyapunov Theorem (Hofbauer and Sigmund, 1998). Since $\mu_2^{(1)} > 0$, P_2 is a saddle point.

When $\lambda_1^{(2)} > 0$, $\lambda_{12}^{(3)} > 0$ and $\lambda_2^{(3)} > 0$, or when $\lambda_1^{(2)} > 0$, $\lambda_{12}^{(3)} > 0$ and $\lambda_2^{(3)} \leq 0$, the Acyclic Theorem implies that system (2.2) is uniformly persistent.

If $\lambda_1^{(2)} \leq 0$, P_1 is globally asymptotically stable on the (N_1, N_2) -plane and thus is asymptotically stable in R_+^3 ; if $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, P_{12} is asymptotically stable, which imply that system (2.2) is not persistent. Therefore, we conclude the following result.

Theorem 6.3. *Assume $r_3 \leq 1 < r_2 < r_1$.*

- (i) *If $\lambda_1^{(2)} > 0$ and $\lambda_{12}^{(3)} > 0$, system (2.2) is uniformly persistent.*
- (ii) *If $\lambda_1^{(2)} \leq 0$, or $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, system (2.2) is not persistent.*

Theorems 6.2-6.3 demonstrate basic properties of F-F-O mutualisms. Recall that by (6.1), $\lambda_2^{(3)} > 0$ can be written as $a_3 > \bar{a}_3$, while $\lambda_{23}^{(1)} > 0$ is $a_1 > \hat{a}_1$.

First, mutualisms can lead to persistence of the system. In the situation of Theorem 6.2(i), species 1 cannot survive in the (N_1, N_2) -subsystem. However, in the three-species system, species 1 can persist if the mutualistic effects are large ($a_3 > \bar{a}_3$, $a_1 > \hat{a}_1$). A similar discussion can be given for survival of the obligate species 3. In the situation of Theorem 6.3, species 3 cannot survive alone while species 2 cannot survive in the (N_1, N_2) -subsystem if $a_2 \leq \bar{a}_2$. Theorem 6.3(i) shows that when the mutualisms are strong ($a_2 > \bar{a}_2$, $a_3 > \hat{a}_3$), species 2 and 3 can survive.

Second, a weak mutualism can result in extinction of species. In the situation of Theorem 6.2(ii), when $a_3 \leq \bar{a}_3$, species 3 with small density goes extinct, which implies extinction of species 1 that cannot coexist with species 2. Even when $a_3 > \bar{a}_3$, species 1 with small density still goes extinct if $a_1 < \hat{a}_1$. In the situation of Theorem 6.3(ii), when $a_2 \leq \bar{a}_2$, species 2 with small density will go extinct, which implies extinction of species 3 that cannot survive alone. Even when $a_2 > \bar{a}_2$, species 3 with small density still goes extinct if $a_3 < \hat{a}_3$.

Third, the obligate species and the inferior facultative species can survive by strengthening its mutualism on the next one when there exists weak mutualism. In numerical simulations of Fig. 5, we have $\bar{a}_3 = 2.2$. If $a_3 = 2.5$, then $\hat{a}_1 = 27.5$. Here, species 1 is the inferior facultative species and species 3 is obligate. We focus on species 1, while a similar discussion can be given for species 3. Fig. 5a shows that species 1 persists when the mutualisms $a_3 (= 2.5 > \bar{a}_3)$ and $a_1 (= 30 > \hat{a}_1)$

are strong. Fig. 5b displays that species 1 goes extinct when there exists weak mutualism ($a_1 = 0.01$) with $a_2 = 3, a_3 = 2.5$. Fig. 5c exhibits that species 1 can survive when there exists weak mutualism ($a_1 = 20$) with $a_2 = 28, a_3 = 2.5$. That is, species 1 can persist by enhancing its mutualism on species 2 ($a_2 = 28$). Fig. 5d shows that species 1 can still survive when there exists weak mutualism ($a_3 = 2$) with $a_2 = 30, a_1 = 30$. That is, species 1 can persist by enhancing its mutualism on species 2 ($a_2 = 30$).

In numerical simulations of Fig. 6, we have $\bar{a}_2 = 0.6$. If $a_2 = 1$, then $\hat{a}_3 = 4.5$. Here, species 2 is the inferior facultative species and species 3 is obligate. We focus on species 3, while a similar discussion can be given for species 2. Fig. 6a shows that species 3 persists when the mutualisms $a_2 (= 1 > \bar{a}_2)$ and $a_3 (= 5 > \hat{a}_3)$ are strong. Fig. 6b displays that species 2 and 3 go extinct when there exists weak mutualism ($a_2 = 0.1$) with $a_1 = 1, a_3 = 5$. Fig. 6c exhibits that species 3 can survive when there exists weak mutualism ($a_2 = 0.59$) with $a_1 = 4, a_3 = 5$. That is, species 3 can persist by enhancing its mutualism on species 1 ($a_1 = 4$). Fig. 6d shows that species 3 can still survive when there exists weak mutualism ($a_3 = 4.4$) with $a_1 = 5, a_2 = 1$. That is, species 1 can persist by enhancing its mutualism on species 1 ($a_1 = 5$).

Finally, initial density plays a role in coexistence of species. In the situation of Fig. 5c, since $a_1 < \hat{a}_1$, both P_{23} and P^+ are asymptotically stable. Thus, initial densities in the basin of attraction of P^+ imply coexistence of species, while those in the basin of attraction of P_{23} imply extinction of species 1. A similar discussion can be given for the situation of Figs. 5d, 6c-d, where there are bistable equilibria.

7 Facultative mutualisms

In this section, we consider facultative mutualisms (i.e., $r_i > 1, i = 1, 2, 3$), which means that each species can survive alone. Without loss of generality, we assume $r_1 \geq \max\{r_2, r_3\}$. Thus, there are three situations: $r_1 > \max\{r_2, r_3\}$, $r_1 = r_2 > r_3$ and $r_1 = r_2 = r_3$.

Suppose $r_1 > r_2 > r_3$. Since $r_1 > r_3$, equilibrium P_1 is globally asymptotically stable on the (N_3, N_1) -plane by Theorem 3.2. Since $r_1 > r_2$, equilibrium P_{12} exists

if $\lambda_1^{(2)} > 0$. Since $r_2 > r_3$, equilibrium P_{23} exists if $\lambda_2^{(3)} > 0$. From $r_1 > r_2$, we have $\lambda_{23}^{(1)} > 0$. Thus, (a) when $\lambda_1^{(2)} > 0$, $\lambda_{12}^{(3)} > 0$ and $\lambda_2^{(3)} > 0$, the Acyclic Theorem implies that system (2.2) is uniformly persistent. Similarly, (b) when $\lambda_1^{(2)} > 0$, $\lambda_{12}^{(3)} > 0$ and $\lambda_2^{(3)} < 0$, system (2.2) is also uniformly persistent. (c) Assume $\lambda_1^{(2)} > 0$, $\lambda_{12}^{(3)} > 0$ and $\lambda_2^{(3)} = 0$. Since $\lambda_2^{(3)} = 0$, equilibrium P_{23} does not exist and P_2 is globally asymptotically stable on the (N_2, N_3) -plane by Theorem 3.2. The orbit of (2.2) in $\text{int}R_+^3$ will not converge to P_2 by a proof similar to that for Theorem 6.3. Hence, system (2.2) is uniformly persistent. On the other hand, if $\lambda_1^{(2)} \leq 0$, then P_1 is asymptotically stable; if $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, then P_{12} is asymptotically stable, which imply that system (2.2) is not persistent.

Suppose $r_1 > r_3 \geq r_2$. Since $r_1 > r_3$, equilibrium P_1 is globally asymptotically stable on the (N_3, N_1) -plane. Since $r_3 \geq r_2$, equilibrium P_3 is globally asymptotically stable on the (N_2, N_3) -plane. Since $r_1 > r_2$, equilibrium P_{12} exists if $\lambda_1^{(2)} > 0$. Thus, when $\lambda_1^{(2)} > 0$ and $\lambda_{12}^{(3)} > 0$, the Acyclic Theorem implies that system (2.2) is uniformly persistent. If $\lambda_1^{(2)} \leq 0$, then P_1 is asymptotically stable; if $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, then P_{12} is asymptotically stable, which imply that system (2.2) is not persistent. Therefore, we conclude the following result.

Theorem 7.1. *Assume $r_1 > \max\{r_2, r_3\} > 1$.*

- (i) *If $\lambda_1^{(2)} > 0$ and $\lambda_{12}^{(3)} > 0$, system (2.2) is uniformly persistent.*
- (ii) *If $\lambda_1^{(2)} \leq 0$, or $\lambda_1^{(2)} > 0$ but $\lambda_{12}^{(3)} < 0$, system (2.2) is not persistent.*

Suppose $r_1 = r_2 > r_3$. Since $r_1 > r_3$, equilibrium P_1 is globally asymptotically stable on the (N_3, N_1) -plane. Since $r_1 = r_2$, equilibrium P_2 is globally asymptotically stable on the (N_1, N_2) -plane. Thus, when $\lambda_2^{(3)} > 0$, P_{23} exists. From (4.2) and $r_1 = r_2$, we have $\lambda_{23}^{(1)} > 0$, which implies that system (2.2) is uniformly persistent. When $\lambda_2^{(3)} \leq 0$, P_{23} is asymptotically stable and system (2.2) is not persistent. Therefore, we conclude the following result.

Theorem 7.2. *Assume $r_1 = r_2 > r_3 > 1$. If $\lambda_2^{(3)} > 0$, system (2.2) is uniformly persistent. Otherwise, (2.2) is not persistent.*

Theorem 7.3. Assume $r_i = r > 1, i = 1, 2, 3$. Then there is a heteroclinic cycle Γ on the boundary, which connects P_1, P_2 and P_3 . Γ is unstable and system (2.2) is uniformly persistent. If $m_i = m, i = 1, 2, 3$, then all solutions of (2.2) in $\text{int } R_+^3$ converge to the positive equilibrium P^+ .

Proof. Since $r_i = r > 1$, it follows from Theorem 3.2 and Corollary 3.3 that equilibrium P_i is globally asymptotically stable on the (N_{i-1}, N_i) -plane, $i = 1, 2, 3$. Thus, there is a heteroclinic cycle Γ on the boundary of R_+^3 , which is in the form of $P_1 \rightarrow P_2 \rightarrow P_3 \rightarrow P_1$.

The heteroclinic cycle Γ is unstable. Indeed, let

$$c_1 = 1, \quad c_2 = \frac{m_1 a_1}{m_2 a_2}, \quad c_3 = \frac{m_1 a_1}{m_3 a_3}$$

then $c_1 m_1 a_1 = c_2 m_2 a_2 = c_3 m_3 a_3 = a$. Denote

$$V = \sum_{i=1}^3 c_i \ln N_i = \ln(N_1^{c_1} N_2^{c_2} N_3^{c_3})$$

then

$$\frac{dV}{dt}|_{(2.2), P_1} = -C + (rC + aN)(1 - N)|_{P_1} = \frac{a(r-1)}{r^2} = \epsilon_0 > 0$$

where $C = \sum_{i=1}^3 c_i m_i, N = \sum_{i=1}^3 N_i$. Thus, there exists $\delta_1 > 0$ such that when $P \in O(P_1, \delta_1) \cap \text{int } R_+^3$, we have

$$\frac{dV}{dt}|_{(2.2), P} > \frac{\epsilon_0}{2} > 0.$$

Similarly, there exists $\delta_i > 0$ such that when $P \in O(P_i, \delta_i) \cap \text{int } R_+^3$, we have

$$\frac{dV}{dt}|_{(2.2), P} > \frac{\epsilon_0}{2} > 0, \quad i = 2, 3.$$

It follows from the continuity of solutions of (2.2) on initial values, there exists $0 < \delta < \max_{1 \leq i \leq 3} \{\delta_i\}$ such that when $P \in O(\Gamma, \delta) \cap \text{int } R_+^3$, we have

$$\frac{dV}{dt}|_{(2.2), P} > \frac{\epsilon_0}{4} > 0$$

which implies that $N_1(t)^{c_1} N_2(t)^{c_2} N_3(t)^{c_3}$ increases exponentially in the neighborhood $O(\Gamma, \delta) \cap \text{int } R_+^3$. Thus, the heteroclinic cycle Γ is repellant.

Since O is unstable, system (2.2) is uniformly persistent.

Assume $m_i = m, i = 1, 2, 3$. It follows from Proposition 4.3 that all solutions of (2.2) converge to equilibria. Since P_1 is globally asymptotically stable on the (N_3, N_1) -plane with $\lambda_1^{(2)} > 0$, solutions of (2.2) in $\text{int}R_+^3$ will not converge to P_1 by a proof similar to that for Theorem 6.3. Similarly, solutions of (2.2) in $\text{int}R_+^3$ will not converge to P_2 and P_3 .

From the righthand side of (2.2), the positive equilibrium $P^*(N_1, N_2, N_3)$ satisfies

$$N_2 = \frac{a_2}{a_3}N_1, \quad N_3 = \frac{a_2}{a_1}N_1.$$

Thus, N_1 satisfies

$$a_2bN_1^2 - (a_2 - rb)N_1 + 1 - r = 0$$

which has a unique positive root since $1 - r < 0$. Thus there is a unique positive equilibrium P^+ of (2.2).

Since O is hyperbolic and unstable, all solutions of (2.2) in $\text{int} R_+^3$ converge to P^+ . $\square$

Theorems 7.1-7.3 demonstrate basic properties of facultative mutualisms. We focus on Theorem 7.1, while similar discussion can be given for Theorems 7.2-7.3. Recall that by (6.1), $\lambda_1^{(2)} > 0$ can be written as $a_2 > \bar{a}_2$, and $\lambda_{12}^{(3)} > 0$ is $a_3 > \hat{a}_3$.

First, mutualisms can lead to persistence of the system. In the situation of Theorem 7.1, species 3 cannot survive in the (N_3, N_1) -subsystem. However, in the three-species system, species 3 can persist if the mutualistic effects are large ($a_2 > \bar{a}_2$, $a_3 > \hat{a}_3$).

Second, a weak mutualism can result in extinction of species. In Theorem 7.1(ii), when $a_2 < \bar{a}_2$, species 2 with small density goes extinct, which implies extinction of species 3 that cannot coexist with species 1. Even when $a_2 > \bar{a}_2$, species 3 with small density still goes extinct if $a_3 < \hat{a}_3$.

Third, the inferior facultative species can survive by strengthening its mutualism on the next one when there exists weak mutualism. In numerical simulations of Fig. 7, we have $\bar{a}_2 = 0.7$. If $a_2 = 1$, then $\hat{a}_3 = 3.5$. Here, species 2 and 3 are the inferior species. We focus on species 3, while a similar discussion can be given for species

2. Fig. 7a shows that species 3 persists when the mutualisms $a_2(= 1 > \bar{a}_2)$ and $a_3(= 4 > \hat{a}_3)$ are strong. Fig. 7b displays that species 3 goes extinct when there exists weak mutualism ($a_2 = 0.1$) with $a_1 = 1, a_3 = 4$. Fig. 7c exhibits that species 3 can survive when there exists weak mutualism ($a_2 = 0.69$) with $a_1 = 5, a_3 = 4$. That is, species 3 can persist by enhancing its mutualism on species 1 ($a_1 = 5$). Fig. 7d shows that species 3 can still survive when there exists weak mutualism ($a_3 = 3.49$) with $a_1 = 8, a_2 = 1$. That is, species 3 can persist by enhancing its mutualism on species 1 ($a_1 = 8$).

Finally, initial density plays a role in coexistence of species. In the situation of Fig. 7c, since $a_2 < \bar{a}_2$, both P_1 and P^+ are asymptotically stable. Thus, initial densities in the basin of attraction of P^+ imply coexistence of species, while those in the basin of attraction of P_1 imply extinction of species 2 and 3. A similar discussion can be given for the situation of Fig. 7d, where both P_{12} and P^+ are asymptotically stable.

Remark 7.4. The bifurcation of heteroclinic cycles can occur in facultative mutualisms. Indeed, fix $r_1 = r_2 > 1$ and let $r_3 > 1$ vary. When $r_3 < r_1 = r_2$, there is no a heteroclinic cycle and Theorem 7.2 shows that P_2 is asymptotically stable, while system (2.2) is not persistent. When $r_3 = r_1 = r_2$, a heteroclinic cycle emerges and Theorem 7.3 exhibits that system (2.2) is uniformly persistent. When $r_3 > r_1 = r_2$, the heteroclinic cycle disappears and Theorem 7.1 shows that P_3 is asymptotically stable, while system (2.2) is not persistent. Thus, when r_3 increases, the bifurcation of heteroclinic cycles occurs and dynamics of the system fluctuate between persistence and non-persistence.

8 Discussion

In this paper, we considered mutualisms in a three-species system where each species provides benefit to the next one in a one-directional loop, but there exists spatial competition among them. Dynamics of the model demonstrate mechanisms by which the mutualisms lead to coexistence/extinction of the species.

Periodic oscillations can occur in the system by Hopf bifurcation as shown in

Theorem 4.2. In numerical simulations of Fig. 8a-b, the length of time-axis is 40 and the time step is 0.01. We fix $r_1 = 0.9, r_2 = 0.8, r_3 = 0.7, m_i = 1$ and initial values $N_i(0) = 0.3, a_i = a, i = 1, 2, 3$. Since $r_i < 1$ for $i = 1, 2, 3$, each species cannot survive alone. Fig. 8a displays that the species coexist at an equilibrium when the mutualisms are intermediate ($a = 6.5$). Moreover, when the mutualisms are strong ($a = 50$), Hopf bifurcation occurs and the species coexist in periodic oscillations as shown in Fig. 8b. Further simulations show that when a_i increases, the amplitude of the periodic oscillations decreases while the frequency increases. The biological meaning is: the stronger the mutualism, the more stable the species coexistence. Periodic oscillations also occur in other mutualism systems with bidirectional interactions. For example, Bachelot et al. (2015) built a multiprey species/predator model combined with a bidirectional resource exchange system. Numerical simulations exhibit that periodic oscillations appear in the model consisting of plant, natural enemy of the plant, and mycorrhizal fungi. Moreover, when the benefits of the mycorrhizal symbiosis are greater than the costs, there is a mismatch between plant and mycorrhizal fungal dynamics; when the benefits are less than the costs, plant and mycorrhizal fungal dynamics are synchronous.

Both weak mutualism and extremely strong mutualism will result in extinction of species. Since we have discussed weak mutualism in Sections 5-7, we focus on extremely strong mutualism. Indeed, from (4.4) we have $\lim_{a_3 \rightarrow \infty} N_2^+ = 0$, which implies extinction of species 2 as its mutualism on species 3 is extremely strong. Thus, even the superior facultative species will be driven into extinction by its over-strong mutualism on the next one. The biological reason is that there exists spatial competition between the species. In numerical simulations of Figs. 8c-d, the length of time-axis is 40 and the time step is 0.01. We fix $r_1 = 0.9, r_2 = 0.8, r_3 = 0.7, a_1 = a_2 = 6.5, m_i = 1, N_i(0) = 0.3, i = 1, 2, 3$, and let a_3 vary. Fig. 8c shows that all species go extinct when a mutualism is weak ($a_3 = 1$). Fig. 8d displays that when a_3 increases from 50, 100 to 500, the density of species 2 (N_2^+) decreases monotonically and tends toward 0. Thus species 2 goes extinct, which implies extinction of species 3 and 1 that cannot survive alone. Since the species can coexist in intermediate

mutualisms as shown in Fig. 8a, it is the extremely strong/weak mutualism that leads to the extinction.

Results in this work may be helpful for understanding mutualisms in a one-directional loop in real situations. For example, in the light bulb powered by bacteria, Theorem 5.1 shows that if the mutualisms between the bacteria are symmetric and intermediate, the closed ecosystem would persist at a steady state as shown in Fig. 8a, which implies that the bulb can produce stable light. Moreover, Theorem 4.2 and the simulation in Fig. 8b exhibits that if the mutualisms become strong, there may exist periodic solutions, which implies that light produced in bulb may be in oscillations. While this work focuses on three-species systems, considering n-species systems may be important and interesting. We'll pursue this in a future work.

Acknowledgements: We grateful to the three anonymous reviewers for their careful reading, helpful comments and suggestions that really helped me to improve the presentation of the paper. This work was supported by NSFC (11571382) of “Bi-directional mutualisms based on pollen-transportation”, NSF of Guangdong (S2012010010320), and Student Research Creation Program of Sun Yat-sen University.

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Figure 2: Dynamics of the (N_1, N_2) -subsystem (3.1). Fix $r_1 = 2, m_1 = m_2 = 1$ and let r_2, a_2 vary. (a) When $r_2 \leq 1$ and $a_2 (= 2)$ is small, species 2 goes extinct. (b) When $r_2 \geq r_1 > 1$, species 1 goes extinct. (c) When $1 < r_2 < r_1$ and $a_2 (= 4)$ is large, the two species coexist at equilibrium E_{12} . (d) When $1 < r_2 < r_1$ and $a_2 (= 1)$ is small, species 2 goes extinct.

Figure 3: Dynamics of obligate mutualisms. Let $r_i = 0.9, m_i = 1, a_i = 7$. There are two positive equilibria P^+ and P^- . P^+ is asymptotically stable while P^- is a saddle point. The global stable manifold S^2 of P^- divides $\text{int}R_+^3$ into two regions: one is the basin of attraction of P^+ , while the other is that of O .

Figure 4: Solutions in F-O-O mutualisms. The red, blue and black curves represent solutions of $N_1(t)$, $N_2(t)$ and $N_3(t)$, respectively. Fix $r_1 = 1.1, r_2 = 0.9, r_3 = 0.8, m_i = 1$ and initial values $N_i(0) = 0.3, i = 1, 2, 3$. (a) When the mutualistic effects $a_2(= 2.5)$ and $a_3(= 30)$ are large, the three species persist. (b) When $a_2(= 2.0)$ and $a_1(= 3)$ are small, species 2 and 3 go extinct while species 1 persists. (c) When $a_2(= 2.0)$ is small but $a_1(= 28)$ is large, the three species coexist at equilibrium P^+ . (d) When $a_2(= 2.5)$ is large but $a_3(= 20)$ is small, species 3 can survive if $a_1(= 30)$ is large.

Figure 5: Solutions in F-F-O mutualisms. The red, blue and black curves represent solutions of $N_1(t)$, $N_2(t)$ and $N_3(t)$, respectively. Fix $r_1 = r_2 = 1.1, r_3 = 0.9, m_i = 1$ and initial values $N_i(0) = 0.3, i = 1, 2, 3$. (a) When the mutualistic effects $a_1(= 30)$ and $a_3(= 2.5)$ are large, system (2.2) is persistent. (b) When $a_1(= 0.01)$ is small with $a_3(= 2.5)$, species 2 and 3 persist while species 1 goes extinct. (c) When $a_1(= 20)$ is small but $a_2(= 28)$ is large, the three species coexist at equilibrium P^+ . (d) When $a_3(= 2)$ is small but $a_2(= 30)$ is large, species 3 can survive if $a_1(= 30)$ is large.

Figure 6: Solutions in F-F-O mutualisms. The red, blue and black curves represent solutions of $N_1(t)$, $N_2(t)$ and $N_3(t)$, respectively. Fix $r_1 = 1.2, r_2 = 1.1, r_3 = 0.9, m_i = 1$ and initial values $N_i(0) = 0.3, i = 1, 2, 3$. (a) When the mutualistic effects $a_2(= 1)$ and $a_3(= 5)$ are large, system (2.2) is persistent. (b) When $a_2(= 0.1)$ is small and $a_1(= 1)$ is small, species 2 and 3 go extinct while species 1 persists. (c) When $a_2(= 0.59)$ is small but $a_1(= 4)$ is large, the three species coexist at equilibrium P^+ . (d) When $a_2(= 1)$ is large and $a_3(= 4.4)$ is small, species 3 can survive if $a_1(= 5)$ is large.

Figure 7: Solutions in facultative mutualisms. The red, blue and black curves represent solutions of $N_1(t)$, $N_2(t)$ and $N_3(t)$, respectively. Fix $r_1 = 1.4, r_2 = 1.2, r_3 = 1.1, m_i = 1$ and initial values $N_i(0) = 0.3, i = 1, 2, 3$. (a) When the mutualistic effects $a_2(= 1)$ and $a_3(= 4)$ are large, system (2.2) is persistent. (b) When $a_2(= 0.1)$ is small and $a_1(= 1)$ is small, species 2 and 3 go extinct while species 1 persists. (c) When $a_2(= 0.69)$ is small but $a_1(= 5)$ is large, the three species coexist at equilibrium P^+ . (d) When $a_2(= 1)$ is large and $a_3(= 3.49)$ is small, species 3 can survive if $a_1(= 8)$ is large.

Figure 8: Hopf bifurcation and extreme mutualism in obligate mutualisms. The red, blue and black curves represent solutions of $N_1(t)$, $N_2(t)$ and $N_3(t)$, respectively. Fix $r_1 = 0.9, r_2 = 0.8, r_3 = 0.7, m_i = 1$ and initial values $N_i(0) = 0.3, i = 1, 2, 3$. (a) When $a_i (= 6.5)$ are intermediate, the species coexist at an equilibrium. (b) When $a_i (= 50)$ are strong, the species coexist in periodic oscillations. (c) When the mutualistic effects $a_1 = a_2 (= 6.5)$ are large but $a_3 (= 1)$ is extremely small, all species go extinct. (d) Fix $a_1 = a_2 = 6.5$ and let a_3 vary. When a_3 increases from 50, 100 to 500, the density of species 2 (N_2^+) decreases monotonically and tends to 0.