



A mutualism-competition model characterizing competitors with mutualism at low density

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ABSTRACT

A macroscopic model of two species is considered, in which mutualism is the dominant interaction when the species are at low density and competition is the dominant interaction when they are at high density. Our aim is to show that species using the same or similar resources can coexist without niche differentiation and that mutualism at low population density can lead to high production. The specific model is a novel combination of the Lotka–Volterra cooperative (mutualism) model and Lotka–Volterra competitive model. By comparing the dynamics of the specific system with those of the Lotka–Volterra competitive model, we demonstrate the mechanism by which the mutualism at low density promotes competitive coexistence by creating regions of mutualism that maintain coexistence. We also show situations in which high production occurs by (i) displaying regions of net mutualism in which the species with higher competitive ability (the superior) approaches a density larger than its carrying capacity when in isolation from the inferior species, and (ii) displaying regions of net mutualism in which both of the species approach densities larger than their carrying capacities, respectively. By comparing the dynamics of the specific system with those of the Lotka–Volterra mutualism model, we show that competition at high density promotes stability of the system.

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1. Introduction

The Lotka–Volterra competitive model and cooperative (mutualism) model characterize competitive and cooperative interactions between species, respectively. While both models have been powerful in both explaining and predicting ecological phenomena for years, the interaction types between species remain constant in these models; i.e. the feedback from the other species is either positive or negative, with no variation. These inflexible kinds of models need to be improved to describe the situation in which interaction types between species are density-dependent, e.g. mutualism happens when the species are at low density while competition happens at high density. Indeed, many examples of such varying interactions have been found in natural environments.

There are both mutualistic and competitive interactions in many animal communities. This is certainly true within species, for example, in predators that forage in groups. As shown by Rita and Ranta [1], moderate groups of carnivores communicate information of the whereabouts of profitable food patches with each other. They also share food patches encountered by one of them through using public information. Hence, the mutualism between them improves their hunting efficiency. However, when the sizes of the groups are large, the total food in the environment cannot support the need of all groups. Then their competition for the limited food occurs. On the other hand, when one group is moderate and the other is large, the information and/or food patches encountered by the moderate group will be shared by the large one.

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Then the large group consumes most of the public benefit of the two groups. While the moderate group also shares the information and/or food patches encountered by the large one, the interaction between them is host-parasite as a whole. But this phenomenon can also occur between different species. Wading birds of one species will land to forage for prey at sites where birds of another species are already foraging [2]. This use of information from individuals of other species is mutualistic at low densities, but becomes competitive when the foraging site becomes overcrowded.

The mutualism and competition interaction also exists in plant communities. In low-marsh habitats that are periodically flooded by tides, plant growth is limited by anoxic soil [3]. However, *Spartina alterniflora*, a low-marsh plant, provides oxygen to below-ground tissue through its aerenchyma tissue, and then aerates the anoxic soil. Thus the plant improves the soil conditions and is beneficial to its neighboring plants when it is at low density. However, when the plant is at high density, it competes with its neighbors for light and CO₂. The net balance of its beneficial and detrimental effects on other plants is negative. Similarly, leguminous plants provide nitrogen to their neighboring plants, while they compete with them for resources such as water and minerals when they are at high density [4]. The mutualism at low density is regarded as both the reason of coexistence of multiple species and the reason of high production of some species. More examples can be seen in [2,5–10,20–24] etc.

Hernandez and Barradas [11] established four models to describe the interaction between mutualism and competition. Stability analysis shows that the introduction of mutualism at low density increases the number of stable equilibria, and that species in strong competition can coexist if there is mutualism at low density. Meanwhile, Zhang [12] analyzed the existence of mutualism and competition interaction from a viewpoint of traditional philosophy, and presented a macroscopic model to characterize the interaction. The analysis by Zhang [12] showed that the mutualism at low density promotes the competitive coexistence. The results by both Hernandez and Barradas [11] and Zhang [12] imply that ecologically identical species can coexist if there is mutualism between them. This result is different from that described by Gause's competition and the exclusion rule [13]. Gause's rule shows that two ecologically identical species cannot coexist, based on dynamics of the Lotka–Volterra competitive model. This rule has been brought into doubt in several studies [14–16], and strongly brought into doubt by the work of Hernandez and Barradas [11] and Zhang [12]. While the results of Hernandez and Barradas [11] and Zhang [12] are very effective in demonstrating the promotion of competitive coexistence in a qualitative way, a quantitative description of this promotion is needed. Furthermore, situations in which high production can occur through mutualism need to be shown.

In this paper, the global dynamics of a two-species system is described. The system is the same as the Lotka–Volterra mutualism model when the species are at low density and the same as the Lotka–Volterra competition model when the species are at high density. By comparing the dynamics of the specific system presented here with those of the Lotka–Volterra competition model, we display the mechanism by which mutualism promotes the competitive coexistence in a quantitative way. We also demonstrate situations in which the high production of the species occurs. Then by comparing the dynamics of the specific system with those of the Lotka–Volterra mutualism model, we show that competition at high density promotes stability of the system.

2. Models and analysis

In this section, we establish a general mutualism-competition model and present a specific mutualism-competition system of two species. Then we analyze the dynamics of the specific system and display their applications.

As defined by Hernandez and Barradas [11, p. 574], the mutualism-competition interaction among multiple species means that mutualism happens when the species are at low population density while competition happens when they are at high population density. Hence, the general mutualism-competition model of n ($n \geq 2$) species can be established as follows.

$$\frac{dN_i}{dt} = N_i f_i(N_1, N_2, \dots, N_n), \quad (2.1)$$

where N_i denotes the population density of the i -th species and $f_i(N_1, N_2, \dots, N_n)$ represents its per capita growth rate. The function $f_i(N_1, N_2, \dots, N_n)$ has continuously partial derivatives $\partial f_i / \partial N_j$, $i, j = 1, 2, \dots, n$, that is, $f_i \in C^1$. The mutualism-competition interaction is set by requiring that for each i , $1 \leq i \leq n$, there is $b_i > 0$ such that

$$\partial f_j / \partial N_i > 0 \quad \text{as } 0 < N_i < b_i, \quad \partial f_j / \partial N_i < 0 \quad \text{as } N_i > b_i,$$

where $j \neq i$, $i, j = 1, 2, \dots, n$. The ecological meaning is that the i -th species has a positive effect on other species as it is at low density ($0 < N_i < b_i$), while it has negative effect on them as it is at high density ($N_i > b_i$).

2.1. A specific system

In order to show how the mutualism at low density promotes the competitive coexistence, we consider the following specific system:

$$\begin{aligned} dN_1/dt &= r_1 N_1 [c_1 + a_1 b_2 - N_1 - a_1 |N_2 - b_2|^*], \\ dN_2/dt &= r_2 N_2 [c_2 + a_2 b_1 - N_2 - a_2 |N_1 - b_1|^*], \end{aligned} \quad (2.2)$$

where N_i denotes the population density of the i -th species and all parameters in the system are positive, $i = 1, 2$.

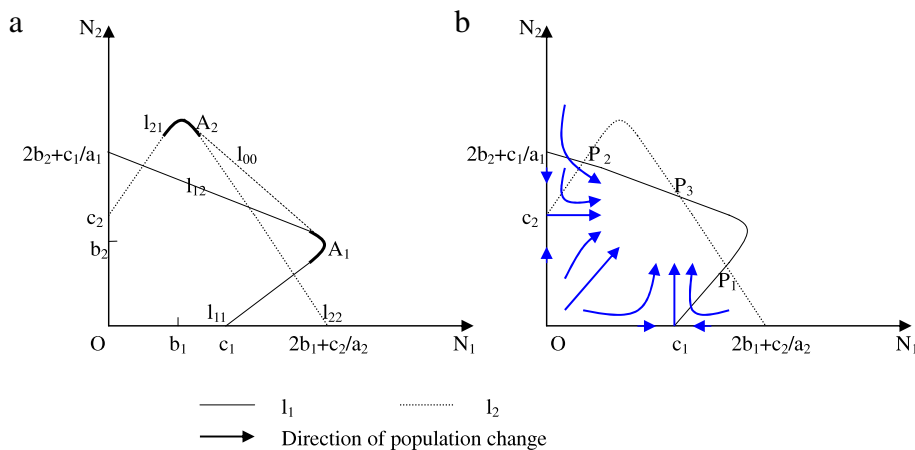


Fig. 1. In (a), the smoothed parts of the isoclines l_1 and l_2 at their vertices are shown. In (b), the species in (2.2) coexist if $c_1 < 2b_1 + c_2/a_2$ and $c_2 < 2b_2 + c_1/a_1$.

We focus on explaining the first equation in (2.2) while a similar description can be given for the second one. Let $N_2 = 0$ in the first equation, we have $dN_1/dt = r_1 N_1 (c_1 - N_1)$, then the parameter c_1 represents the carrying capacity of species 1 when in isolation from species 2, and the parameter $r_1 c_1$ denotes its intrinsic growth rate. Let $L_1(N_1, N_2) = c_1 + a_1 b_2 - N_1 - a_1 |N_2 - b_2|^*$. Here, the function $|N_2 - b_2|^*$ is defined as the absolute function $|N_2 - b_2|$ while the function $N_1 = |N_2 - b_2|$ is smoothed in a very small neighborhood of its vertex $(0, b_2)$. Hence, the isocline $l_1 : L_1(N_1, N_2) = 0$ is smooth as shown in Fig. 1(a) (l_{11} and l_{12}). Then the function $f_1(N_1, N_2) = r_1 N_1 L_1(N_1, N_2) \in C^1$ and satisfies

$$\begin{aligned} \partial f_1 / \partial N_2 &= a_1 r_1 N_1 > 0 \quad \text{as } N_2 < b_2, \\ \partial f_1 / \partial N_2 &= -a_1 r_1 N_1 < 0 \quad \text{as } N_2 > b_2. \end{aligned}$$

That is, species 2 has a positive effect on species 1 when it is at low density ($N_2 < b_2$), while it has negative effect on species 1 when it is at high density ($N_2 > b_2$). Hence, the parameter b_2 denotes the critical density of species 2 near which the effect of species 2 on species 1 would transition from positive to negative effects. Therefore, the interval of low density, $0 < N_2 < b_2$, represents the region of net mutualism of species 2 to species 1. In the example about carnivores as mentioned in Section 1 of this paper, the parameter b_2 represents the critical density of the second group by (i) when its density is less than b_2 , the second group has a positive effect on the first one by providing foraging information and then increasing the hunting efficiency, and (ii) when its density is larger than b_2 , the second group has negative effect on the first one since the net balance of providing information and competing for the resources is negative.

While we consider the situation that the two species in the system use the same or similar resources, we suppose $b_2 \leq c_2$. In fact, if $b_2 > c_2$, then the interval $c_2 < N_2 < b_2$ is in the mutualism region of species 2. However, species 2 with $c_2 < N_2 < b_2$ cannot be beneficial to species 1 since too many individuals of species 2 ($N_2 > c_2$) will compete with species 1 for the resources. This contradicts the definition of the mutualism region $0 < N_2 < b_2$. By the symmetry of N_1 and N_2 , we also suppose $b_1 \leq c_1$. It follows from the Lotka-Volterra models that the parameter a_1 represents both the mutualism (at low density) and competition (at high density) degrees of species 2 to species 1. Similarly, the parameter a_2 represents both the mutualism (at low density) and competition (at high density) degrees of species 1 to species 2. The low density of species 1, $0 < N_1 < b_1$, represents the region of net mutualism species 1 to species 2, and the isocline $l_2 : L_2(N_1, N_2) = c_2 + a_2 b_1 - N_2 - a_2 |N_1 - b_1|^* = 0$ is smooth as shown in Fig. 1(a) (l_{21} and l_{22}).

The system (2.2) is a combination of the Lotka-Volterra competitive model and cooperative model. Indeed, when the species are at low density, i.e. $N_1 < b_1$ and $N_2 < b_2$, the system (2.2) becomes the Lotka-Volterra cooperative model

$$\begin{aligned} dN_1/dt &= r_1 N_1 (c_1 - N_1 + a_1 N_2), \\ dN_2/dt &= r_2 N_2 (c_2 - N_2 + a_2 N_1). \end{aligned} \quad (2.3)$$

However, when the species are at high density, i.e. $N_1 > b_1$ and $N_2 > b_2$, the system (2.2) becomes the Lotka-Volterra competitive model

$$\begin{aligned} dN_1/dt &= r_1 N_1 (c_1 + 2a_1 b_2 - N_1 - a_1 N_2), \\ dN_2/dt &= r_2 N_2 (c_2 + 2a_2 b_1 - N_2 - a_2 N_1). \end{aligned} \quad (2.4)$$

2.2. Equilibria

The equilibria of (2.2) on axes are $O(0, 0)$, $O_1(c_1, 0)$ and $O_2(0, c_2)$. The Jacobian matrices of (2.2) at the equilibria are

$$J(O) = \begin{pmatrix} r_1 c_1 & 0 \\ 0 & r_2 c_2 \end{pmatrix},$$

$$J(O_1) = \begin{pmatrix} -r_1 c_1 & r_1 c_1 a_1 \\ 0 & r_2(c_2 + 2a_2 b_1 - a_2 c_1) \end{pmatrix},$$

$$J(O_2) = \begin{pmatrix} r_1(c_1 + 2a_1 b_2 - a_1 c_2) & 0 \\ r_2 c_2 a_2 & -r_2 c_2 \end{pmatrix}.$$

Since $\text{tr}(J(O)) = r_1 c_1 + r_2 c_2 > 0$ and $\det(J(O)) = r_1 c_1 r_2 c_2 > 0$, O is an unstable node. If

$$c_1 + 2a_1 b_2 - a_1 c_2 > 0, \quad c_2 + 2a_2 b_1 - a_2 c_1 > 0, \quad (2.5)$$

then $\det(J(O_i)) < 0$, $i = 1, 2$. That is, O_1 and O_2 are saddles as shown in Fig. 1(b). It follows from the phase portrait analysis that the following result is proven.

Proposition 1. *If conditions in (2.5) are satisfied, the species in system (2.2) coexist.*

Since our aim is to show the promotion of competitive coexistence by the introduction of b_1 and b_2 , we suppose the conditions in (2.5) are always satisfied in this paper.

The following theorem shows that there is no periodic oscillation in (2.2).

Theorem 1. *System (2.2) admits no periodic orbit.*

Proof. Let

$$B(N_1, N_2) = \frac{1}{N_1 N_2},$$

then we have

$$\frac{\partial(Bf_1)}{\partial N_1} + \frac{\partial(Bf_2)}{\partial N_2} = -\frac{r_1}{N_2} - \frac{r_2}{N_1} < 0.$$

It follows from the Bendixson–Dulac theorem [17] that (2.2) admits no periodic orbit. \square

2.3. Dynamics

In the following analysis, we suppose the conditions in (2.5) are satisfied, that is, the two species in (2.2) coexist. In order to show the equilibria of (2.2), we divide the isocline l_1 of species 1 into l_{11} and l_{12} as follows.

$$l_{11} : c_1 - N_1 + a_1 N_2 = 0, \quad 0 < N_2 < b_2,$$

$$l_{12} : c_1 + 2a_1 b_2 - N_1 - a_1 N_2 = 0, \quad N_2 > b_2,$$

where l_1 is smoothed in a small neighborhood of its vertex $A_1(c_1 + a_1 b_2, b_2)$ as shown in Fig. 1(a). Similarly, we divide the isocline l_2 into l_{21} and l_{22} as follows.

$$l_{21} : c_2 - N_2 + a_2 N_1 = 0, \quad 0 < N_1 < b_1,$$

$$l_{22} : c_2 + 2a_2 b_1 - N_2 - a_2 N_1 = 0, \quad N_1 > b_1,$$

where l_2 is smoothed in a small neighborhood of its vertex $A_2(b_1, c_2 + a_2 b_1)$ as shown in Fig. 1(a).

While the line segments l_{11} and l_{21} are defined in intervals $(c_1, c_1 + a_1 b_2)$ and $(0, b_1)$ respectively, they do not intersect since $b_1 \leq c_1$. Then there are at most three isolated positive equilibria of (2.2). As shown in Fig. 1(b), let $P_1(p_{11}, p_{12})$ denote the intersection of l_{11} and l_{22} ; let $P_2(p_{21}, p_{22})$ denote the intersection of l_{12} and l_{21} ; let $P_3(p_{31}, p_{32})$ denote the intersection of l_{12} and l_{22} . Then we have

$$p_{11} = \frac{c_1 + 2a_1 a_2 b_1 + a_1 c_2}{1 + a_1 a_2}, \quad p_{12} = \frac{c_2 + 2a_2 b_1 - a_2 c_1}{1 + a_1 a_2},$$

$$p_{21} = \frac{c_1 + 2a_1 b_2 - a_1 c_2}{1 + a_1 a_2}, \quad p_{22} = \frac{c_2 + 2a_1 a_2 b_2 + a_2 c_1}{1 + a_1 a_2},$$

$$p_{31} = \frac{a_1 c_2 + 2a_1 a_2 b_1 - c_1 - 2a_1 b_2}{a_1 a_2 - 1}, \quad p_{32} = \frac{a_2 c_1 + 2a_1 a_2 b_2 - c_2 - 2a_2 b_1}{a_1 a_2 - 1}.$$

Let k_1 (respectively, k_2) denote the slope of the line l_{12} (respectively, l_{22}). Let k denote the slope of the line $A_1 A_2$, which is represented by l_{00} in Fig. 1(a). Then we have

$$k_1 = -\frac{1}{a_1} < 0, \quad k_2 = -a_2 < 0, \quad k = -\frac{c_2 + a_2 b_1 - b_2}{c_1 + a_1 b_2 - b_1}.$$

It follows from $b_1 \leq c_1$ and $b_2 \leq c_2$ that $k < 0$.

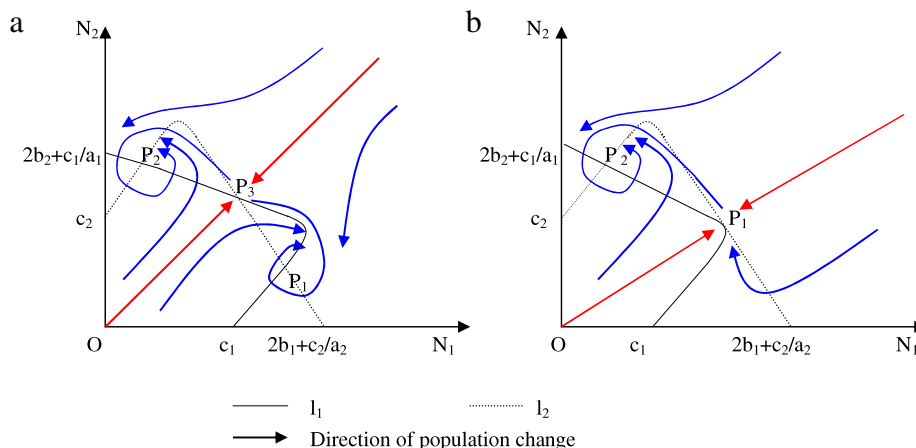


Fig. 2. In (a), we have $|k_1| < |k| < |k_2|$. There are three positive equilibria P_1 , P_2 and P_3 in (2.2). Orbits below the separatrix (the red line) of P_3 converge to P_1 while those above the separatrix tend to P_2 . In (b), we have $|k_1| < |k| = |k_2|$. There are two positive equilibria P_1 and P_2 in (2.2). Orbits below the separatrix (the red line) of P_1 converge to P_1 while those above the separatrix tend to P_2 . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Dynamics of (2.2) are displayed in five cases, while we discuss the situation of $|k_1| \leq |k_2|$ in cases 1–4 and that of $|k_1| > |k_2|$ in case 5.

Case 1. $|k_1| < |k| < |k_2|$.

In this case, there are three positive equilibria P_1 , P_2 and P_3 as shown in Fig. 2(a). The Jacobian matrix of (2.2) at P_1 is

$$J(P_1) = \begin{pmatrix} -r_1 p_{11} & a_1 r_1 p_{11} \\ -a_2 r_2 p_{12} & -r_2 p_{12} \end{pmatrix},$$

then $\text{tr}(J(P_1)) = -r_1 p_{11} - r_2 p_{12} < 0$ and $\det(J(P_1)) = r_1 r_2 p_{11} p_{12} (1 + a_1 a_2) > 0$. That is, P_1 is asymptotically stable. Similarly, P_2 is asymptotically stable.

The Jacobian matrix of (2.2) at P_3 is

$$J(P_3) = \begin{pmatrix} -r_1 p_{31} & -a_1 r_1 p_{31} \\ -a_2 r_2 p_{32} & -r_2 p_{32} \end{pmatrix},$$

then $\det(J(P_3)) = r_1 r_2 p_{31} p_{32} (1 - a_1 a_2)$. By $|k_1| < |k_2|$, we have $1 - a_1 a_2 < 0$ and then $\det(J(P_3)) < 0$. That is, P_3 is a saddle. It follows from Theorem 1 that in $\text{int } R_+^2$, all orbits but P_3 and the separatrices of P_3 converge to equilibria P_1 and P_2 , as shown in Fig. 2(a).

Case 2. $|k_1| < |k| = |k_2|$.

In this case, there are two positive equilibria P_1 and P_2 as shown in Fig. 2(b). Here, equilibria P_1 and P_3 in Fig. 2(a) coincide. Similar to the discussions in case 1, P_2 is asymptotically stable. Since $\text{tr}(J(P_1)) = -r_1 p_{11} - r_2 p_{12} < 0$ and $\det(J(P_1)) = 0$, it follows from the saddle–node rule [18] that P_1 is a saddle–node equilibrium. By Theorem 1, we can draw the dynamics of (2.2) as shown in Fig. 2(b). Similar discussions can be given for the case $|k_1| = |k| < |k_2|$ in which there are two positive equilibria P_1 and P_2 while P_1 is asymptotically stable and P_2 is a saddle–node equilibrium.

Case 3. $|k_1| \leq |k_2| < |k|$.

In this case, there is a unique positive equilibrium P_2 . Similar to the discussions in case 1, P_2 is asymptotically stable. By Theorem 1, P_2 is globally stable as shown in Fig. 3(a). Similar discussions can be given for the case $|k| < |k_1| \leq |k_2|$ in which P_1 is globally stable.

Case 4. $|k_1| = |k_2| = |k|$.

In this case, the isoclines l_{12} and l_{22} coincide and points on the line segment $A_1 A_2$ are positive equilibria. By Theorem 1, all orbits of (2.2) in $\text{int } R_+^2$ converge to the set of equilibria as shown in Fig. 3(b).

Case 5. $|k_2| < |k_1|$.

When $|k_2| < |k_1| < |k|$, discussions similar to those in case 3 can be given and P_2 is globally stable as shown in Fig. 3(a). When $|k| < |k_2| < |k_1|$, discussions similar to those in case 3 can be given and P_1 is globally stable. When $|k_2| \leq |k| < |k_1|$ or $|k_2| < |k| \leq |k_1|$, there is a unique positive equilibrium P_3 of (2.2) and P_3 is globally stable, as shown in Fig. 4.

2.4. Mechanism of coexistence and reality of mutualism

In this section, we show features of the system (2.2) by comparing dynamics of (2.2) with those of the Lotka–Volterra models.

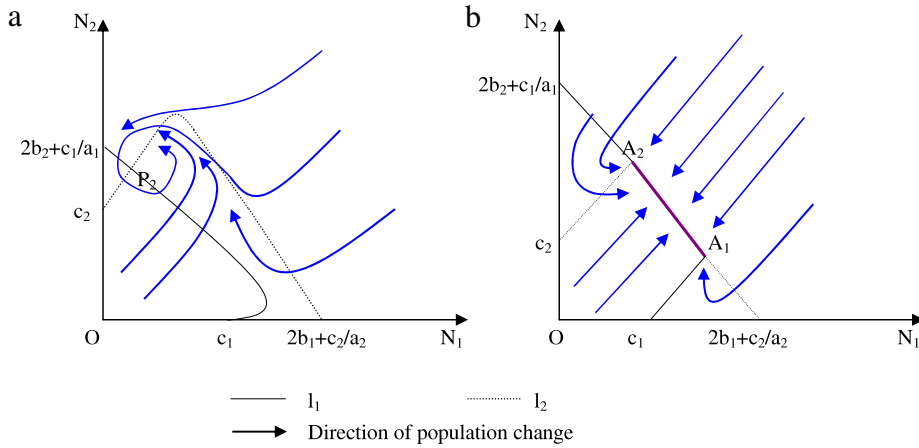


Fig. 3. In (a), we have $|k_1| \leq |k_2| < |k|$. There is a unique positive equilibrium P_2 in (2.2). All orbits of (2.2) converge to P_2 . In (b), we have $|k_1| = |k| = |k_2|$. Points on the line segment A_1A_2 are positive equilibria of (2.2) and all orbits of (2.2) converge to the equilibrium set.

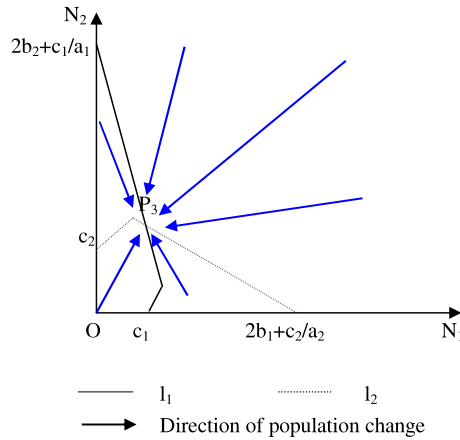


Fig. 4. Here, we have $|k_2| \leq |k| < |k_1|$, there is a unique equilibrium P_3 of (2.2) and P_3 is globally stable.

We show that the mutualism at low density in (2.2) promotes coexistence by comparing the system (2.2) with the Lotka–Volterra competitive model (2.4). Indeed, when species 2 is at a low density ($N_2 < b_2$), it follows from the first equation of (2.4) that the effect of species 2 on species 1 is negative ($-a_1N_2 < 0$) while it follows from the first equation of (2.2) that the effect of species 2 on species 1 is positive ($+a_1N_2 > 0$), which comes from the mutualism of species 2 at low density. Hence, the persistence of species 1 is promoted when species 2 is at low density. On the other hand, when species 2 is at high density ($N_2 > b_2$), the negative effect of species 2 on species 1 in (2.4) is ‘ $-a_1N_2$ ’ while that in (2.2) is ‘ $-a_1(N_2 - b_2)$ ’. Since $-a_1(N_2 - b_2) > -a_1N_2$, the negative effect is cut down by the mutualism in (2.2). Hence, the mutualism in (2.2) promotes the persistence of species 1. Similarly, the mutualism in (2.2) also promotes the persistence of species 2. Therefore, the mutualism in (2.2) promotes the coexistence of the species. The mechanism by which the promotion happens can be quantitatively shown as follows. Let

$$c_2 \geq c_1/a_1 \quad \text{and/or} \quad c_1 \geq c_2/a_2, \quad (2.6)$$

the species in (2.4) cannot coexist. However, it follows from Proposition 1 that they will coexist if there is mutualism at low density and the mutualism regions satisfy:

$$b_1 > \frac{1}{2} \left(c_2 - \frac{c_1}{a_1} \right), \quad b_2 > \frac{1}{2} \left(c_1 - \frac{c_2}{a_2} \right). \quad (2.7)$$

Therefore, the mutualism in the mutualism-competition system (2.2) will lead to the coexistence while the species cannot coexist in the pure competition model (2.4).

We show the mutualism at low density in (2.2) can be beneficial to both competitors as follows. Without loss of generality, it follows from (2.6) that two situations need to be considered: (i) $a_1 \geq c_1/c_2$, $a_2 < c_2/c_1$, and (ii) $a_1 \geq c_1/c_2$, $a_2 \geq c_2/c_1$.

(i) Let $a_1 \geq c_1/c_2$, $a_2 < c_2/c_1$. That is, species 2 is the superior species (i.e. the species with high competitive ability) while species 1 is the inferior one (i.e. the species with low competitive ability). When there is no mutualism at low density,

it follows from (2.4) that species 1 goes extinct while species 2 approaches its carrying capacity when in isolation from species 1. The following result (Proposition 2) shows mutualism regions in which the inferior species will persist while the superior species approaches a density larger than its carrying capacity.

We denote

$$H_{11}(b_2) = \frac{2a_1}{1+a_1a_2}b_2 + \frac{c_1-a_1c_2}{1+a_1a_2},$$

$$H_{12}(b_2) = a_1b_2 + \frac{1}{2}(c_1 - a_1c_2),$$

$$H_{21}(b_1) = \frac{2a_2}{1+a_1a_2}b_1 + \frac{c_2-a_2c_1}{1+a_1a_2},$$

$$H_{22}(b_1) = a_2b_1 + \frac{1}{2}(c_2 - a_2c_1).$$

Proposition 2. Let $a_1 \geq c_1/c_2$, $a_2 < c_2/c_1$ and $b_i \leq c_i$, $i = 1, 2$. Let (2.5) hold. Then for all positive initial densities, species 1 persists and species 2 approaches a density larger than its carrying capacity if and only if $b_1 > H_{12}(b_2)$ and $b_2 < H_{21}(b_1)$.

Proof. It follows from Proposition 1 that species 1 persists when conditions in (2.5) are satisfied. By the analysis in Section 2.3, species 2 approaches a density larger than its carrying capacity for all positive initial densities if and only if P_2 is globally stable, or P_3 is globally stable with $p_{32} > c_2$. P_2 is globally stable if and only if $|k_1| < |k|$ and $|k_2| < |k|$. By $|k_1| < |k|$, we have

$$\frac{1}{a_1} < \frac{c_2 + a_2b_1 - b_2}{c_1 + a_1b_2 - b_1},$$

that is,

$$b_1 > \frac{2a_1}{1+a_1a_2}b_2 + \frac{c_1-a_1c_2}{1+a_1a_2},$$

which corresponds to $b_1 > H_{11}(b_2)$. By $|k_2| < |k|$, we have

$$a_2 < \frac{c_2 + a_2b_1 - b_2}{c_1 + a_1b_2 - b_1},$$

that is,

$$b_2 < \frac{2a_2}{1+a_1a_2}b_1 + \frac{c_2-a_2c_1}{1+a_1a_2},$$

which corresponds to $b_2 < H_{21}(b_1)$. Hence, P_2 is globally stable if and only if $b_1 > H_{11}(b_2)$ and $b_2 < H_{21}(b_1)$.

By the analysis in Section 2.3, P_3 is globally stable with $p_{32} > c_2$ if and only if $|k_2| < |k| \leq |k_1|$ and $p_{32} - c_2 > 0$. By $|k_2| < |k_1|$, we have $a_1a_2 < 1$. By $|k| \leq |k_1|$, we have $b_1 \leq H_{11}(b_2)$. By $|k_2| < |k|$, we have $b_2 < H_{21}(b_1)$. By $p_{32} - c_2 > 0$, we have

$$p_{32} - c_2 = \frac{2a_2}{1-a_1a_2} \left[b_1 - \left(a_1b_2 + \frac{1}{2}(c_1 - a_1c_2) \right) \right] > 0,$$

which corresponds to $b_1 > H_{12}(b_2)$. Hence, P_3 is globally stable with $p_{32} > c_2$ if and only if $H_{12}(b_2) < b_1 \leq H_{11}(b_2)$ and $b_2 < H_{21}(b_1)$. By combining conditions $b_1 > H_{11}(b_2)$, $b_2 < H_{21}(b_1)$ with condition $H_{12}(b_2) < b_1 \leq H_{11}(b_2)$, $b_2 < H_{21}(b_1)$, we have $b_1 > H_{12}(b_2)$ and $b_2 < H_{21}(b_1)$. \square

Proposition 2 shows that for any positive initial density, the superior species (species 2) benefits from the mutualism if its mutualism region is moderate and that of the inferior species (species 1) is large, which corresponds to the analysis in cases 3 and 5 of Section 2.3. When both of the mutualism regions are large, the superior species can also benefit from the mutualism by approaching a density larger than its carrying capacity. Indeed, in cases 1 and 2, we have $|k_1| < |k| \leq |k_2|$, i.e. $b_1 > H_{11}(b_2)$ and $b_2 \geq H_{21}(b_1)$. Since P_2 is asymptotically stable with $p_{22} > c_2$, species 2 approaches a high density if its initial density is so large that the initial density point $(N_1(0), N_2(0))$ is above the separatrixes of P_3 (the red line), as shown in Fig. 2(a) and Fig. 2(b). In case 4, we have $|k_1| = |k| = |k_2|$, i.e. $b_1 = H_{11}(b_2)$ and $b_2 = H_{21}(b_1)$. Since P_2 (i.e. A_2) is stable with $p_{22} > c_2$, species 2 approaches a high density if its initial density is relatively large, as shown in Fig. 3(b).

The following proposition shows the mutualism area in which both of the species approach densities larger than their carrying capacities respectively, which corresponds to the analysis in case 5 of Section 2.3.

Proposition 3. Let $a_1 \geq c_1/c_2$, $a_2 < c_2/c_1$ and $b_i \leq c_i$, $i = 1, 2$. Let (2.5) hold. P_3 is globally stable with $p_{31} > c_1$ and $p_{32} > c_2$ if and only if $H_{12}(b_2) < b_1 \leq H_{11}(b_2)$ and $H_{22}(b_1) < b_2 < H_{21}(b_1)$.

Proof. Similar to the proof in Proposition 2, $p_{31} > c_1$ corresponds to $b_2 > H_{22}(b_1)$. By Proposition 2, P_3 is globally stable with $p_{32} > c_2$ if and only if $H_{12}(b_2) < b_1 \leq H_{11}(b_2)$ and $b_2 < H_{21}(b_1)$. Then Proposition 3 is proven. \square

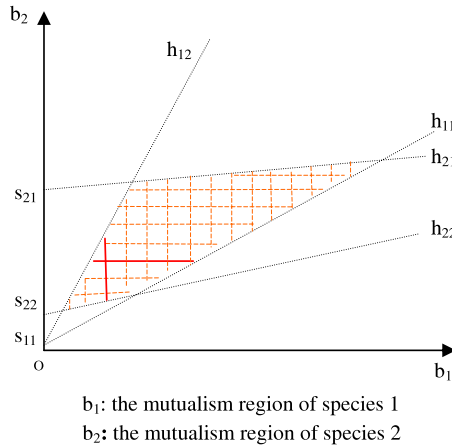


Fig. 5. Here, the optimal mutualism region is surrounded by four lines h_{11} , h_{12} , h_{21} and h_{22} , in which both species approach densities larger than their carrying capacities when in isolation from the other one. The overstriking vertical segment corresponds to $b_1 = 3/4$ and $17/8 < b_2 < 3$, which is bounded by h_{12} and h_{22} . The overstriking horizontal segment corresponds to $b_2 = 5/2$ and $5/8 < b_1 \leq 10/9$, which is bounded by h_{11} and h_{12} .

The mutualism area in Proposition 3 is as follows. We denote the lines on the parameter b_1b_2 plane by

$$\begin{aligned} h_{11} : b_1 &= H_{11}(b_2), & h_{12} : b_1 &= H_{12}(b_2), \\ h_{21} : b_2 &= H_{21}(b_1), & h_{22} : b_2 &= H_{22}(b_1) \end{aligned}$$

and denote the intersections of the lines with b_2 -axis by:

$$\begin{aligned} s_{11} &= s_{12} = \frac{1}{2} \left(c_2 - \frac{c_1}{a_1} \right), \\ s_{21} &= \frac{c_2 - a_2c_1}{1 + a_1a_2}, & s_{22} &= \frac{1}{2} (c_2 - a_2c_1). \end{aligned}$$

Then the mutualism area in Proposition 3 is surrounded by the four lines as shown in Fig. 5.

A numerical example is given as follows. Fix

$$a_1 = \frac{1}{4}, \quad a_2 = \frac{1}{2}, \quad c_1 = 1, \quad c_2 = 4.$$

First, let $b_1 = 3/4$. A straightforward computation shows that the parameter b_2 should satisfy

$$\frac{17}{8} < b_2 < 3.$$

The interval of b_2 is bounded by the lines h_{12} and h_{22} as shown by the overstriking vertical segment in Fig. 5. Then for every parameter point (b_1, b_2) on the segment, the unique equilibrium $P_3(p_{31}, p_{32})$ of (2.2) is globally stable and

$$p_{31} = \frac{8b_2 - 3}{14} > 1 = c_1, \quad p_{32} = \frac{34 - 2b_2}{7} > 4 = c_2,$$

which means both species approach high densities.

Secondly, let $b_2 = 5/2$. Similar computations show that the parameter b_1 should satisfy

$$5/8 < b_1 \leq 10/9,$$

the interval of b_1 is bounded by the lines h_{11} and h_{12} as shown by the overstriking horizontal segment in Fig. 5, and

$$p_{31} = \frac{10 - 2b_1}{7} \geq \frac{74}{63} > 1 = c_1, \quad p_{32} = \frac{8b_1 + 23}{7} > 4 = c_2.$$

The mutualism area in Proposition 2 is larger than that in Proposition 3. Indeed, it follows from $b_1 > H_{12}(b_2)$ and $b_2 < H_{21}(b_1)$ that the mutualism area in Proposition 2 is below both the lines h_{12} and h_{21} in Fig. 5.

(ii) Let $a_1 \geq c_1/c_2$, $a_2 \geq c_2/c_1$, i.e. the competitive degrees of both species are large and the competition between the species is fierce. In the pure competition model (2.4), the species with high initial density will approach its carrying capacity while the other one is excluded. According to the analysis in Section 2.3, we display that the species with high initial density will benefit from the mutualism in (2.2) as follows.

Since $a_1 \geq c_1/c_2$, $a_2 \geq c_2/c_1$, we have $1/a_1 \leq a_2$, i.e., $|k_1| \leq |k_2|$. First, when $|k_1| < |k| \leq |k_2|$, we have $b_1 > H_{11}(b_2)$ and $b_2 > H_{21}(b_1)$. That is, both mutualism regions are large. As discussed in cases 1 and 2, almost all orbits of (2.2) converge

to equilibria P_1 and P_2 as shown in Fig. 2. Since $p_{11} > c_1$ and $p_{22} > c_2$, the species with high initial density benefits from the mutualism in (2.2) by approaching a density larger than its carrying capacity when in isolation from the other one. Similar discussions can be given for $|k_1| = |k| < |k_2|$. *Second*, when $|k_1| < |k|$ and $|k_2| < |k|$, we have $b_1 > H_{11}(b_2)$ and $b_2 < H_{21}(b_1)$. That is, only the mutualism region of species 1 is large. As discussed in case 3, all orbits of (2.2) converge to equilibrium P_2 with $p_{22} > c_2$ as shown in Fig. 3(a). Then species 2 will approach a high density based on the large mutualism region of species 1. Similar discussions can be given for $|k_1| > |k|$ and $|k_2| > |k|$. *Third*, when $|k_1| = |k|$ and $|k_2| = |k|$, we have $b_1 = H_{11}(b_2)$ and $b_2 = H_{21}(b_1)$. That is, both mutualism regions are moderate. As discussed in case 4, points on line segment A_1A_2 are equilibria of (2.2) and all orbits of (2.2) converge to the set of equilibria as shown in Fig. 3(b). Then the species with high initial density will approach a density larger than its carrying capacity when in isolation from the other one.

We show that the competition in (2.2) promotes stability of the system by comparing the system (2.2) with the Lotka–Volterra cooperative model (2.3). When the mutualism degrees in (2.2) and (2.3) are not well-balanced, i.e., $a_1a_2 \geq 1$, the population densities of both species in (2.3) tend to infinity. This will not happen in (2.2). In fact, it follows from the first equation of (2.2) that

$$\begin{aligned} dN_1/dt &= r_1N_1[c_1 + a_1b_2 - N_1 - a_1|N_2 - b_2|^*] \\ &< r_1N_1(c_1 + a_1b_2 - N_1). \end{aligned}$$

Since all solutions in the logistic model $dN_1/dt = r_1N_1(c_1 + a_1b_2 - N_1)$ are bounded, the population density $N_1(t)$ in (2.2) is bounded. Similar discussions can be given for $N_2(t)$. That is, the tendency to infinity in (2.3) is prohibited in (2.2). By Theorem 1, orbits of (2.2) will converge to equilibria. Hence, the competition at high density promotes the stability of the system.

3. Discussion

In this paper, we demonstrated the dynamics of a specific mutualism-competition system of two species. By comparing the dynamics with those of the Lotka–Volterra models, we elucidated the mechanism by which the mutualism promotes competitive coexistence. We also displayed mutualism regions in which the superior approached a density larger than its carrying capacity when in isolation from the inferior. Furthermore, we showed the domain of mutualism in which both species approach densities larger than their carrying capacities, respectively.

As mentioned by May [19], ‘mutualism between species tends to have a destabilizing effect on the community dynamics’ based on dynamics of the Lotka–Volterra mutualism model. According to the analysis in the present paper, the destabilizing effect of mutualism will not occur in the mutualism-competition system. The reason is that in the mutualism-competition system, competition occurs at high density, which prohibits the species’ tendency to infinity. Detailed discussions concerning this phenomenon were given by Holland and DeAngelis [10]. On the other hand, the mutualism at low density brings a positive effect on the system by promoting coexistence and making the species approach high densities, which makes the system complex and robust. The results in this paper also have potential applications: (i) species that compete so intensely that they cannot coexist in the pure competition system, but can coexist if they are mutualistic at low densities; (ii) when in coexistence, the species with strong competitive ability and/or high initial density would benefit from the mutualism by approaching a density larger than its carrying capacity, and (iii) when mutualism occurs in certain domains, a win–win situation emerges in which both species approach densities larger than their carrying capacities, respectively. For example, if the groups of carnivores mentioned by Rita and Ranta [1] had been in strong competition without mutualism, one of the groups would have gone extinct, while the other one would have approached its carrying capacity according to the Lotka–Volterra competition model. When the competition between them is still strong at high density but there is mutualism at low density, they will coexist if the regions of mutualism are sufficiently large (i.e. the conditions in (2.5) are satisfied). If the mutualistic domains satisfy the conditions in Proposition 2, the superior species will approach a density larger than its carrying capacity, while the inferior persists. Furthermore, if the mutualism regions satisfy the conditions in Proposition 3, both of the species will approach densities larger than their carrying capacities, respectively.

In the specific mutualism-competition system studied in this paper, both of the degree of mutualism and degree of competition are represented by the same parameter (a_i). When they are represented by different parameters, results similar to those of this paper can be obtained in the same way. Furthermore, varying these degrees will have the same effects as those produced by the mutualism regions. Despite the simplicity in our model’s assumptions, this work provides an insightful explanation of the mechanisms involved in the mutualism-competition systems, and may be helpful to understand the mutualism-competition interactions in nature.

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